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OF THE
JOHNS HOPKINS UNIVERSITY

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WILLIAM K. BROOKS, EDITOR

THE CUBOMEDUSÆ

A DISSERTATION PRESENTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY, IN THE JOHNS HOPKINS UNIVERSITY, 1897

BY

FRANKLIN STORY CONANT

A MEMORIAL VOLUME

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With the kind regards of
Franklin Story Conant.

FRANKLIN STORY CONANT

SEPTEMBER 21, 1870—SEPTEMBER 13, 1897

A BIOGRAPHICAL SKETCH

This Treatise is printed after the author's death, as a Memorial by his friends, fellow-students and instructors, with the aid of the Johns Hopkins University. It consists of his Dissertation, reprinted from the copy which was accepted by this University at his examination for the degree of Doctor of Philosophy in June, 1897.

As he had made many notes on the embryology of the Cubomedusæ, and had hoped to complete and publish them together with an account of physiological experiments with these medusæ, he had described the Dissertation on the title-page as Part I, Systematic and Anatomical, and he went to Jamaica immediately after his examination to continue his studies and to procure new material, and he there lost his life.

Franklin Story Conant was born in Boston on September 21, 1870, and he died in Boston on September 13, 1897, a few days after his arrival from Jamaica, where he had contracted yellow fever through self-sacrificing devotion to others.

He was educated in the public schools of New England; at the University of South Carolina; at Williams College, where he received the degree of Bachelor of Arts in 1893; and in the Johns Hopkins University, where he received the degree of Doctor of Philosophy in 1897, and where he was appointed a Fellow in 1896 and Adam T. Bruce Fellow in 1897.

Most of his instructors have told us that they quickly discovered that Conant was a young man of unusual intelligence and energy and uprightness, and as his education progressed he secured the esteem and the affectionate interest of all who had him in charge, so that they continued to watch his career with increasing pride and satisfaction.

He entered the Johns Hopkins University in the spring of 1894, and at once joined the party of students in zoology who were working, under my direction, in the marine laboratory of the University at Beaufort, North Carolina; and from that time until his death he devoted himself continually, without interruption, to his chosen subject—spending his winters in the laboratory in Baltimore, and devoting his summers to out-of-door studies at Beaufort and at Wood's Holl, and in Jamaica.

It is as a student and not as an investigator that we must remember Conant, for most of his time was given to reading and study on subjects of general educational value; although he had begun, before his death, to make original contributions to science and to demonstrate his ability to think and work on independent lines.

His study of the Chaetognaths was undertaken only for the purpose of verifying the account of their anatomy and development in the text books, but it soon showed the presence at Beaufort of several undescribed species. Without interrupting his more general studies, he employed his odd moments for three years in their systematic analysis, and at last published two papers, "Description of Two New Chaetognaths," and "Notes on the Chaetognaths," which show notable power of close and accurate observation and of exact description; and, while short, are valuable contributions to our knowledge of this widely distributed but difficult group.

As he appreciated the value to one who has devoted himself to zoology of thorough acquaintance with physiological problems and the means for solving them, he wished, after he had completed his general course in physiology, to attempt original research in this field; and, at the suggestion of Professor Howell, he, in company with H. L. Clark, his fellow student, undertook and successfully completed an investigation of which Professor Howell gives the following account:

> In connection with Mr. H. L. Clark, Mr. Conant undertook to investigate the character of the nervous control of the heart beat in decapod crustaceans. They selected the common edible crab, Callinectes hastatus, and made a series of most careful experiments and dissections which resulted in proving the existence of one inhibitory nerve and two accelerator nerves passing to the heart on each side from the thoracic ganglion. They not only demonstrated the physiological reaction of these nerves, but traced out successfully their anatomical course from the ganglion to the pericardial plexus. It seemed hardly probable from an a priori standpoint that in an animal like the crab there should be any necessity for an elaborate nervous mechanism to regulate the beat of the heart, but their experiments placed the matter beyond any doubt, and have since served to call attention to this animal as a promising organism for the study of some of the fundamental problems in the physiology of the heart. As compared with previous work upon the same subject it may be said that their experiments are the most definite and successful that have yet been made.

His chief completed work, the Dissertation on The Cubomedusæ, is here printed; and through it the reader who did not know Conant must decide whether he was well fitted, by training and by natural endowments, for advancing knowledge. I myself felt confident that the career on which he had entered would be full of usefulness and honor. I was delighted when he was appointed to the Adam T. Bruce Fellowship, for I had discovered that he was rapidly becoming an inspiring influence among his fellow students in the laboratory, and I had hoped that we might have him among us for many years, and that we might enjoy and profit by the riper fruits of his more mature labors.

Immediately after his examination for the degree of Doctor of Philosophy in June, 1897, he set out for Jamaica to continue his studies at the laboratory which this University had established for the summer at Port Antonio, and he there worked for nearly three months on the development, and on the physiology of the sense-organs, of the Cubomedusæ.

His notes and specimens are so complete that I hope it will be possible to complete in Baltimore, at an early day, the work which he had expected to carry on this year.

After the sudden and alarming death of the director of the expedition, Dr. J. E. Humphrey, Conant took the burden of responsibility upon himself, and while he fully appreciated his own great danger, he devoted himself calmly and methodically to the service of others who, in their afflictions, needed his help, and he fell in the path of duty, where he had always walked, leaving behind him a clear and simple account of all the business of the laboratory and of his scientific work, and of his own affairs, complete to the day before his death.

Immediately after the opening of the University in October his friends and companions and instructors assembled to express the sorrow with which they had heard the sad news of his death, and to record their love and esteem for the generous, warm-hearted friend who in all the relations of life had proved himself so worthy of their affectionate remembrance. At this meeting those who had worked at his side in our laboratories recalled his steadfast earnestness in the pursuit of knowledge, and the encouragement they had found in his bright example; while those who had been his instructors spoke of him as one who had bettered their instruction and enriched all that he undertook by sound and valuable observations and reflections. While all united in mourning the untimely loss of one who had shown such rich promise of a life full of usefulness and honor and distinction, it was pointed out with pride that his end was worthy of one who had devoted it to the fearless pursuit of truth, and to generous self-sacrifice and noble devotion to others; and it was resolved, "That we prize the lesson of the noble life and death of Franklin Story Conant."

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INTRODUCTION.

Jelly-fish offer to the lover of natural history an inexhaustible store of beauty and attractiveness. One who has studied them finds within him a ready echo to Haeckel's statement that when first he visited the seacoast and was introduced to the enchanted world of marine life, none of the forms that he then saw alive for the first time exercised so powerful an attraction upon him as the Medusæ. The writer counts it a rare stroke of fortune that he was led to the study of a portion of the group by the discovery of two new species of Cubomedusæ in Kingston Harbor, Jamaica, W. I., while he was with the Johns Hopkins Marine Laboratory in June of 1896.

The Cubomedusæ are of more than passing interest among jelly-fish, both because of their comparative rarity and because of the high degree of development attained by their nervous system. One fact alone suffices to attract at once the attention of the student of comparative morphology —that here among the lowly-organized Cœlenterates we find an animal with eyes composed of a cellular lens contained in a pigmented retinal cup, in its essentials analogous to the vertebrate structure. Perhaps this and other facts about the Cubomedusæ would be more generally known, had they not been to a certain extent hidden away in Claus's paper on Charybdea marsupialis ('78), which, while a record of careful and accurate work, is in many respects written and illustrated so obscurely that it is very doubtful whether one could arrive at a clear understanding of its meaning who was not pretty well acquainted with Charybdea beforehand.

Before Claus's paper was received at this laboratory, H. V. Wilson went over essentially the same ground upon a species of Chiropsalmus taken at Beaufort, N. C. When the article on Charybdea marsupialis appeared, however, the results were so similar that Wilson did not complete for publication the careful notes and drawings he had made.

Haeckel's treatment of the Cubomedusæ in his "System" ('79) in the Challenger Report ('81) is much more lucid than Claus's; but the extended scope of his work and the imperfect preservation of his material prevented a detailed investigation, and for a more complete and readily intelligible account of the structure of the Cubomedusæ a larger number of figures is desirable.

In the foregoing facts lies whatever excuse is necessary for repeating in the present paper much that has already seen print in one form or another.

PART I: SYSTEMATIC.

It seems advisable first of all to establish the systematic position of the two newly found species, Charybdea Xaymacana and Tripedalia cystophora. Haeckel's classification, as given in his "System der Medusen," is an excellent one and will be followed in this case. One of the new species, however, will not classify under either of Haeckel's two families, so that for it a new family has been formed and named the Tripedalidæ. In showing the systematic position of the two new forms, an outline of Haeckel's classification will be given, so far as it concerns our species, together with the additions that have been made necessary.

CUBOMEDUSÆ (Haeckel, 1877).

Characteristics: Acraspeda with four perradial sensory clubs which contain an auditory club with endodermal otolith sac and one or several eyes. Four interradial tentacles or groups of tentacles. Stomach with four wide perradial rectangular pockets, which are separated by four long and narrow interradial septa, or cathammal plates. Gonads in four pairs, leaf-shaped, attached along one edge to the four interradial septa. They belong to the subumbrella, and are developed from the endoderm of the stomach pockets, so that they project freely into the spaces of the pockets.

Family I: CHARYBDEA (Gegenbaur, 1856).

Cubomedusæ with four simple interradial tentacles; without marginal lobes in the velarium, but with eight marginal pockets; without pocket arms in the four stomach pockets.

Genus: *Charybdea.*

Charybdeidæ with four simple interradial tentacles with pedalia; with velarium suspended, with velar canals and four perradial frenula. Stomach flat and low, without broad suspensoria. Four horizontal groups of gastric filaments, simple or double, tuft or brush-shaped, limited to the interradial corners of the stomach.

Species: *Charybdea Xaymacana* (Fig. 1).

Bell a four-sided pyramid with the corners more rounded than angular, yet not so rounded as to make the umbrella bell-shaped. The sides of the pyramid parallel in the lower two-thirds of the bell, in the upper third curving inward to form the truncation; near the top a slight horizontal constriction. Stomach flat and shallow. Proboscis with four oral lobes, hanging down in bell cavity a distance of between one-third and one-half the height of bell; very sensitive and contractile, so that it can be inverted into the stomach. The four phacelli epaulette-shaped, springing from a single stalk. Distance of the sensory clubs from the bell margin one-seventh or one-eighth the height of bell. Velarium in breadth about one-seventh the diameter of the bell at its margin. Four velar canals in each quadrant; each canal forked at the ends, at times with more than two branches. Pedalia flat, scalpel-shaped, between one-third and one-half as long as the height of bell. The four tentacles, when extended, at least eight times longer than the bell. Sexes separate. Height of bell, 18–23 mm.; breadth, about 15 mm. (individuals with mature reproductive elements); without pigment. Found at Port Henderson, Kingston Harbor, Jamaica.

As may be seen from the above, C. Xaymacana differs only a little from the C. marsupialis of the Mediterranean. Claus mentions in the latter a more or less well defined asymmetry of the bell, which he connects with a supposed occasional attachment by the proboscis to algæ. In C. Xaymacana I never noticed but that the bell was perfectly symmetrical. C. Xaymacana is about two-thirds the size given by Claus for his examples of C. marsupialis, which were not then sexually mature. It has 16 velar canals instead of 24 (32), as given by Haeckel, or 24 as figured by Claus. Difference in size and in number of velar canals are essentially the characteristics upon which Haeckel founded his Challenger species, C. Murrayana.

Family II: CHIRODROPIDÆ (Haeckel, 1877).

Cubomedusæ with four interradial groups of tentacles; with sixteen marginal pockets in the marginal lobes of the velarium, and with eight pocket arms, belonging to the exumbrella, in the four stomach pockets.

This family is represented in American waters by a species of Chiropsalmus, identified by H. V. Wilson as C. quadrumanus, found at Beaufort, North Carolina.

Family III: Tripedalidæ (1897).

Cubomedusæ with four interradial groups of tentacles, each group having three tentacles carried by three distinct pedalia; without marginal lobes in the velarium; with sixteen marginal pockets; without pocket arms in the stomach pockets.

Genus: *Tripedalia.*

For the present the characteristics of family and genus must necessarily be for the most part the same. The genus is distinguished by having twelve tentacles in four interradial groups of three each; velarium suspended by four perradial frenula; canals in the velarium; stomach projecting somewhat convexly into the bell cavity, with relatively well-developed suspensoria; four horizontal groups of gastric filaments, each group brush-shaped, limited to the interradial corners of the stomach.

Species: *Tripedalia cystophora* (Fig. 17).

Shape of bell almost exactly that of a cube with rounded edges; the roof but little arched. The horizontal constriction commonly seen near the top of the bell in the Cubomedusæ not present. Proboscis with four oral lobes; hanging down in the bell cavity generally more than half the depth of the cavity and at times even to the bell margin. In the gelatine of the proboscis an irregular number (15–21) of sensory organs resembling otocysts, from the presence of which comes the specific name. Phacelli brush-shaped, composed of from seven to thirteen filaments springing from a single stalk in each quadrant, or rarely from two separate stalks in one of the quadrants. Distance of the sensory clubs from the bell margin about one-fifth or one-fourth of the height of bell. Breadth of velarium about one-sixth the diameter of bell at margin; with six velar canals in each quadrant; the canals simple, unforked. Pedalia flattened, shaped like a slender knife blade, about half as long as the height of the bell. Tentacles at greatest extension observed two and a half times the length of pedalia. Sexes separate. Height of bell in largest specimens (reproductive elements mature) eight or nine mm. Breadth same as height or even greater. Color a light yellowish brown, due in large part to eggs or embryos in the stomach pockets. The reproductive organs especially prominent by reason of their similar color. Found in Kingston Harbor, Jamaica.

It will be seen from the above that Tripedalia possesses two of the characteristics of the Charybdeidæ and two of the Chirodropidæ. The family was named from the prominent feature of the arrangement of the tentacles, in groups of three with separate pedalia. The small size of T. cystophora is worthy of note in connection with the fact that of the twenty species of Cubomedusæ given by Haeckel in his "System" only two are smaller than 20 mm. in height, and those are the two representatives of Haeckel's genus Procharagma, the prototype form of the Cubomedusæ, without pedalia and without velarium. While Tripedalia has both pedalia and velarium, it may be perhaps that its small size, taken in connection with characteristics just about midway between the Charybdeidæ and the Chirodropidæ, indicate that it is not a recently acquired form of the Cubomedusæ.

PART II: GENERAL DESCRIPTION OF THE ANATOMY OF THE CUBOMEDUSÆ.

A: CHARYBDEA XAYMACANA.

a. *Environment and habit of life.*

1. The Cubomedusæ are generally believed to be inhabitants of deep water which come to the surface only occasionally. Both of the Jamaica species, however, were found at the surface of shallow water near the shore, and only under these circumstances. Whether these were their natural conditions, or whether the two forms were driven by some chance from the deep ocean into the Harbor and there found their surroundings secondarily congenial, so to speak, can be a matter of conjecture only. C. Xaymacana was taken regularly a few yards off-shore from a strip of sandy beach not ten minutes row from the laboratory at Port Henderson. It was seen only in the morning before the sea-breeze came in to roughen the water and to turn the region of its placid feeding-ground into a dangerous lee-shore. Some of the specimens taken contained in the stomach small fish so disproportionately large in comparison with the stomach that they lay coiled up, head overlapping tail. The name Charybdea, then, from the Greek χαρύβδις (a gulf, rapacious), seems to be no misnomer. It is worth mentioning that the digestive juices left the nervous system of the fish intact, so that from the stomach of a Charybdea could be obtained beautiful dissections, or rather macerations, of the brain, cord, and lateral nerves of a small fish.

In size C. Xaymacana agrees very well with the average of the genus. The four single tentacles characteristic of the genus are very contractile, varying from two or three to six or seven inches in length, and probably if measurements could be taken while the animal was swimming freely about, the length would be found to be greater still. Charybdea is a strong and active swimmer, and presents a very beautiful appearance in its movements through the water, the quick, vigorous pulsations contrasting sharply with the sluggish contractions seen in most Scyphomedusæ. With its tentacles streaming gracefully behind, an actively swimming Charybdea presents a fanciful resemblance to a comet or meteor. When an attempt is made to capture one, it will often escape by going down into deeper water—as indeed do other jelly-fish. Escape from observation is all the more easy by reason of the entire absence of pigment excepting for the small amount in the sensory clubs. The yellowish or brownish color usually stated as common in the Cubomedusæ is nowhere present in C. Xaymacana.

b. *External Anatomy.*

2. *Form of Bell.* C. Xaymacana shows the typical division of the external surface into four almost vertical perradial areas (Figs. 1–3, *p*), separated by four stoutly arched interradial ribs or bands (Figs. 1–3, *i*). These ribs thus play the part of corners to the Cubomedusan pyramid. They are formed by the thickenings of the jelly of the exumbrella, and serve to give the necessary strength to the four interradial corners, each of which bears one of the four tentacles at its base. Each rib is further divided into two longitudinal strips by a vertical furrow lying exactly in the interradius (Fig. 2, *ifr*). The surface of the exumbrella is thus marked by twelve longitudinal furrows, as seen in the same figure (2). Of these, four are the interradial furrows just mentioned; the other eight are the adradial (*afr*) furrows, which set off the four perradial surfaces of the pyramid from the four interradial ribs or bands of the corners, each of which is again subdivided, as mentioned above, by the shallower interradial furrows. Each interradial furrow ends above the base of the corresponding pedalium, at about the level of the sensory club; each adradial furrow diverges toward the perradius in the lower third of its course, and thus with its companion furrow narrows down the perradial surface of the pyramid in the lower part of the bell to an area of not much greater width than the niches in which the sensory clubs lie. The projecting interradial corners are of course correspondingly enlarged in the lower part of the bell, and in this way the contours of the surface are changed from those figured in the view of the bell from above (Fig. 2) to those of Fig. 3, which represents a view of the bell margin from below.

3. *Pedalia.* From the base of the interradial corner bands spring the four pedalia (Fig. 1, *pe*), gelatinous appendages of the margin having much the same shape as the blade of a scalpel. These in turn bear on their distal ends, as direct continuations, the long, contractile, simple tentacles. The relatively stiff pedalia have the same relation to the flexible tentacles that a driver's whip-stock has to the long lash. In the living animal the pedalia are found attached to the margin at an angle

of about 45° with the longitudinal axis of the bell. In the preserved specimens they are bent in toward the axis by the contraction of the strong muscles at their base, in which position they are figured by Claus for C. marsupialis ('78, Taf. I., Figs. 1 and 2).

The pedalia are in reality processes belonging to the *subumbrella*, as will be shown in the section treating of the vascular lamella. They are composed chiefly of gelatine covered with thin surface epithelium and carrying within the gelatine the basal portion of the tentacle canals. They have received various names at the hands of the writers. Gegenbaur called them "Randblätter." Claus gave them the name of "Schirmlappen," and incorrectly homologized them with the marginal lobes of other Acraspeda. Claus's error was corrected by Haeckel, who termed them "Pedalia" or "Gallertsockel," and homologized them with the pedalia of the Peromedusæ. Besides furnishing a base of support for the tentacles they may perhaps also serve as steering apparatus, a function for which their thin blade-like form would be admirably adapted.

Internal to the base of each pedalium, between it and the velarium, is found a funnel-shaped depression of the ectodermal surface. This is shown in Fig. 5 (*ft*) in longitudinal section, and in cross-section in Fig. 16. In the latter figure the epithelium of the outer wall of the funnel (*mt*) is shown much thickened, the result of a stout development of muscle fibres. These are the muscles that in the preserved specimens cause the inward contraction of the pedalia referred to above.

4. *Sensory Clubs* (marginal bodies, rhopalia). In spite of their position above the bell margin, the four sensory clubs, representing as they do transformations of the four perradial tentacles, are properly classed with the pedalia and interradial tentacles as appendages of the margin. They lie protected in somewhat heart-shaped excavations or niches in the perradial areas of the exumbrella. Each sensory niche is partially roofed over by a covering scale, a hood-like projection from the exumbrella. Below the covering scale the water has free access to the niche and to the sensory club within it. The sensory club consists of a hollow stock directly homologous with tentacle and canal, and a terminal, knob-like swelling, the sensory portion proper. The latter contains on its inner surface—the surface turned towards the bell cavity—two complicated unpaired eyes with lens, retina, and pigment, lying one above the other in the median line; and at the sides of these, two pairs of small, simple, pigmented, bilaterally symmetrical eye spots. At the end of the club, that is, on its lowermost point, lies a sac that contains a

concretion and is usually considered auditory. The canal of the stalk is directly continuous with the gastro-vascular system. In the swollen knob of the sensory club it forms an ampulla-like terminal expansion.

As was pointed out by Claus, the bottom of the sensory niche—by bottom is meant the vertical wall that separates the space of the niche from the bell cavity—is formed from the subumbrella only. This arrangement of parts, apparently impossible for a structure so far removed from the bell margin as the sensory niche, will be explained more fully under the special topic of the vascular lamellæ, or cathammal plates. It is sufficient at this point to refer to Fig. 44, which shows the shield-shaped area mapped out by a vascular lamella that connects the endoderm of the stomach pocket with the ectoderm of the bottom of the niche. By this the exumbrella is completely cut off from any part in the formation of the bottom of the niche. Cross and vertical sections through the niche (Figs. 39 and 37) help to a better understanding of these relations. Since the base of the stalk of the sensory niche lies within the ring of vascular lamella, the whole organ as well as the bottom of the niche belongs to the subumbrella, and so in spite of its position some distance upwards from the bell margin the sensory club is very properly called a "marginal body" (Randkörper).

The epithelium of the sensory niche consists entirely of the flattened ectodermal surface layer common to the whole exumbrella. No differentiation suggestive of nervous function in addition to that of the sensory clubs can be discovered, although it would be quite natural to expect to find something of the sort, as intimated by Claus ('78, p. 27).

It is worth while to mention again the fact that the eyes are directed inwardly toward the cavity of the bell. The larger and lower of the two median eyes looks into the bell cavity horizontally; the smaller upper eye is turned upward toward the region of the proboscis. This is in the normal pendant position of the sensory club. The stalk, however, is very flexible, and a range of other positions of the sense organs is possible, although nothing was observed to suggest that such positions were within the control of the animal. The eyes evidently have as their chief function to receive impressions of what is going on *inside* the bell, not outside. Perhaps the strongly biconvex, almost spherical lenses of the median eyes also point to a focus on near and small objects.

5. *The Bell Cavity and its Structures.* In general, the bell cavity repeats the external form of the bell, being almost cubical. In cross-section it appears very nearly square with the angles in the interradii as

seen in the series of drawings that figure sections of the whole jelly-fish at different levels (Figs. 6–16). Above, the bell cavity is roofed over by the stomach; below, it is open freely to the water, the opening being narrowed somewhat by the diaphragm-like velarium (Fig. 3, *v*); the four flat perradial sides are bounded by the walls of the four broad stomach pockets, to be described when we come to the internal anatomy.

(a) *The Proboscis.* From the stomach there hangs down into the bell cavity the proboscis or manubrium, which consists of a short funnel-shaped stalk bearing on its distal end the four mouth lobes or lips. The latter are somewhat broadly V-shaped processes lying in the perradii with the convexity directed outwards, and with the concavity on the inside forming the beginnings of four perradial furrows that are continued upwards to the stomach. The four furrows are shown in the stalk of the proboscis in Fig. 11, which represents a section taken a little above the level of the mouth lobes. The same cross-shaped section of the stalk shows the four perradial prominences or ridges overlying the furrows, which are the direct continuations of the four projecting mouth lobes.

(b) *The Suspensoria or Mesogonia.* The stomach (leaving out of consideration the proboscis) hangs down into the bell cavity as a slightly sagging saucer-shaped roof (Figs. 4 and 5). In the four perradii it is attached to the lateral walls of the subumbrella by four slenderly developed mesentery-like structures, the suspensoria or mesogonia. These are simple ridges of gelatine, covered of course with the epithelium of the bell cavity, which serve to keep the stomach in position much in the way that a shelf is supported by brackets (Fig. 4, *su*). The suspensorium accordingly has two parts, curved so as to lie at right angles with each other: a vertical portion lying along the wall of the subumbrella, and a horizontal which passes over from the vertical on to the basal wall of the stomach. In Fig. 10 the suspensorium in each quadrant is shown cut across just below the angle between the two parts, so that the two appear in the section as projections on the wall of the stomach and on the wall of the subumbrella.

(c) *The Interradial Funnels or Funnel Cavities.* It will be seen at once that the four suspensoria serve as partitions to divide the upper portion of the bell cavity, the part that lies between the stomach and the lateral walls of the subumbrella, into four compartments. These compartments extend upwards in the four interradii like inverted funnels, whence their name. In the series of cross-sections they can be traced upwards with constantly diminishing area from the level of the suspensoria, Fig. 10 (*if*), to Fig. 6, which is taken very near the top of the bell. Homologous structures exist in all the Scyphomedusæ, and in some of the Lucernaridæ they are continued up even into the stalk of the attached jelly-fish.

(d) *The Velarium.* Charybdea, like most of the Cubomedusæ, possesses a velum-like structure around the opening of the bell cavity (Fig. 3, *v*). The velarium is a thin muscular diaphragm, resembling the true velum in position and essential structures, but differing from the velum in its origin, and in the possession of diverticula from the gastrovascular system, the velar canals. Of these there are in C. Xaymacana very regularly sixteen, four in each quadrant. Their outline is seen in Fig. 3 to be forked with small irregular accessory processes. As for its origin, the velarium of the Cubomedusæ is commonly accounted to have arisen by fusion of marginal lobes, as in the case of the velarium of the Discomedusæ. Pending decisive ontological evidence, the slight notches in the four perradii seen in Fig. 3 may perhaps be taken as slight indications of a primitive unfused condition, but the question will be brought up again when the vascular lamellæ are discussed.

(e) *The Frenula.* Just as the stomach is attached to the walls of the subumbrella in the four perradii by the suspensoria, so in the lower part of the bell cavity the velarium is attached to the wall of the subumbrella in the perradii by four structures similar to the suspensoria, the frenula velarii. The frenula, like the suspensoria, resemble the brackets of a shelf, with the difference that in the case of the frenula the bracket is above the shelf, their purpose being evidently to keep the velarium stiff against the outflow of water produced by the pulsations of the bell. According to the greater need of strength in this case, we find the frenula stouter, more buttress-like than the suspensoria. The gelatinous ridge that gives them the necessary firmness is thickened so as to be triangular in section, as shown in Fig. 16 (*frn*).

(f) *Musculature.* As is general in medusæ, the muscular system, so far as known, is restricted to the subumbrella. It has a very simple arrangement, consisting of a continuous sheet of circular (*i. e.* horizontal) striated fibres, which is interrupted only in the four perradii by the radially directed muscle fibres of the suspensoria and the frenula. In each quadrant, between the muscle of the suspensorium above and that of the frenulum below, in an area just internal to the sensory niche, there lies a space free from muscle. This interruption of the muscle layer is shown in Fig. 39. Under the head of musculature belonging to the subumbrella must be included also the radial, or longitudinal muscles at the bases of the pedalia, which were mentioned before (Fig. 16, *mt*). The mouth lobes and proboscis also are highly contractile and muscular.

(g) *Nerve Ring.* It is in the possession of a clearly defined nerve ring that the Cubomedusæ differ from all other Scyphomedusæ whose nervous system has been carefully studied. The nerve ring shows very plainly on the surface of the subumbrella as a well-defined clear streak. Its course is zig-zag or festoon-like. In the interradii, at the basis of the tentacles, it lies not far from the bell margin. In the perradii it rises to the level of the sensory clubs. This very striking arrangement is understood at once when it is remembered that the sensory clubs represent the four perradial primary tentacles, and were originally situated on the margin. When all the rest of the margin grew down and away from the four sensory clubs, fusing below them to form the present intact edge of the bell, the four portions of the nerve ring that lay in the perradii were left at the level of the sensory clubs, and the originally straight nerve ring was thus bent into a bow in each quadrant. The finer structure of the nerve will be treated of in the special part to be devoted to the nervous system.

c. *Internal Anatomy.*

6. *Stomach.* The shape of the stomach is approximately that of a biconvex lens, as seen in Fig. 4, which represents a Charybdea cut in halves longitudinally in the perradius. The lumen of the proboscis (the buccal stomach according to Haeckel's terminology) communicates directly by a funnel-shaped enlargement with the stomach proper, or central stomach of Haeckel. The term basal stomach is carried over by Haeckel from the Stauromedusæ, where it has considerable significance, to the Cubomedusæ, and applied to the upper part of the central stomach. In the stalkless Cubomedusæ, however, it has no significance so far as actual structure goes, and our knowledge of the development of the Cubomedusæ is as yet too simple for us to say that the upper part of the main stomach represents what remains of the basal stomach of an earlier pedunculated stage.

The epithelium of the roof of the stomach is not specially differentiated and apparently has little or no part in digestion. The epithelium of the floor, on the other hand, is composed chiefly of very high and thickly crowded columnar cells which are usually described as coarsely granular, but under high powers appear to be filled with vacuoles surrounded by a network of cell substance. Thickly interspersed among these columnar cells are goblet cells filled with mucus. The floor is thrown into numerous wrinkles by ridges in the supporting gelatine resulting in increase of digestive surface. The four perradial grooves of the proboscis are continued in the perradii along the floor of the stomach as four fairly deep furrows, which lead directly to the gastric ostia and stomach pockets—structures to be described presently. These furrows are lined with crowded columnar cells, smaller and denser than the other cells of the digestive epithelium, containing no granules and but little beside the relatively large, compact, deeply staining nuclei. The furrows probably represent special ciliated courses.

7. *Phacelli.* Lying in the four interradial corners of the stomach are the four phacelli or tufts of gastral filaments to the number of thirty or thirty-five in each tuft. The filaments are attached to a single stalk, like the fringe of an epaulette or the hairs of a coarse brush. The stalk bearing the filaments is an outgrowth of the lower wall of the stomach just at the point where it fuses with the upper. The phacelli are therefore structures of the subumbrella, proof of which will be found under the special topic of the vascular lamellæ. The stalk, an indication of which appears in *sph.* Fig. 6 (the section being a little below the axis of the stalk, which lies horizontally), consists of a firm core of gelatine covered with the high columnar epithelium of the floor of the stomach. The filaments themselves are slender processes repeating the structure of the stalk and having a central axis of gelatine for support covered with glandular epithelium, which in the case of the filaments bears numerous nettle cells. These processes are extremely contractile, and in the living animal show a continuous, slow, squirming movement like a mass of worms. The section just referred to (Fig. 6) shows diagrammatically three of these filaments (*fph*) cut across in each quadrant.

8. *Peripheral Part of the Gastro-vascular System.* The proboscis and stomach proper comprise the central part of the gastro-vascular system. In direct communication with the central is a peripheral part composed of pouches or pockets lying in the vertical sides of the cube-shaped bell, just as the central stomach lies in its roof. The peripheral part may be subdivided for convenience of description into the stomach pockets, the marginal pockets, and the canals of the tentacles and sensory clubs.

(a) *Stomach Pockets.* These are four broad, thin pouches lying between the exumbrella and the subumbrella in the four perradii (*e. g.*

Fig. 9, *sp*) and separated from one another in the interradii merely by four thin vertical strips of vascular lamella (*ivl*) or fusion between the two endodermal surfaces of a primitively single undivided peripheral cavity. The structure is exactly that which we should have if in a Hydromedusa, for example Liriope (Trachomedusæ), the four radial canals broadened out and the intervening cathammal plates correspondingly narrowed, until the relations in size were just reversed, and instead of four narrow radial canals separated from one another by four broad cathammal plates, we had four broad radial canals or pouches separated by four narrow cathammal plates.

The stomach pockets communicate at their top with the central stomach by means of four moderately large openings, the gastric ostia. These are seen in a side view of the whole animal as triangular spaces (Fig. 1, *g. o.*) near the top of the broad perradial sides. In Figures 7 and 8 they are seen in cross-sections, in Fig. 4 in vertical section.

The communication between the stomach and each stomach pocket is guarded by a valve that can cut the one entirely off from the other. The valve is simply the flexible lower margin of the gastric ostium, a thin vertical fold of the floor of the stomach, semilunar in shape, just at the point where it is passing over into the stomach pocket. A longitudinal section, such as is shown in Fig. 4, gives the best idea of the form and position of the valve that can be obtained from any simple section. Internal to the valve is seen a depression of the stomach wall, almost worthy to be called a pocket. The valve itself lies as a wall across the end of this depression, obstructing a free course to the stomach pocket. It will be seen at once that any pressure of fluids in the stomach against this vertical wall, or valve, would serve only to press it against the inner surface of the exumbrella, and thus effectually close the entrance into the stomach pocket. Such a closure would both keep the juices of the stomach from entering the pockets and the embryos in the pockets from entering the stomach before the proper time.

The depression of the floor of the stomach just internal to the valve may possibly be a structure of some morphological significance. In one series of sections it was found that in two of the quadrants the depression was deeper than that represented in Fig. 4, and extended perceptibly into the outer or vertical portion of the suspensorium. Fig. 32 is a diagram giving a vertical reconstruction in the perradius of the cross-sections in which this deepened depression was noticed. Fig. 31 is a drawing (the outline by camera lucida) of one of the cross-sections, through the lowermost point of the depression. The figure gives the wall of the stomach lined with high columnar epithelium (*ens*), and the wall of the stomach pockets, with the suspensorium (*su*) connecting them. The section is taken just above the broad angle that lies between the two parts of the suspensorium, that is, in a plane parallel to the arrow *a–b* in Fig. 32, but a little lower down. At the points to which the reference letter *x* (Fig. 31) refers are seen the first indications of the division into two parts, *i. e.* of the apex of the angle. The next section or two lower down show the relation seen in Fig. 10 (*su*). There can be no doubt in this case that the depression or pocket lies in the outer vertical limb of the suspensorium. It is the position that gives it at least the appearance of some morphological significance. In two genera of Lucernaridæ named and described by Clark ('78), Halicyathus and Craterolophus, the mesogonia or suspensoria in all four perradii contain broad pockets. These mesogonial pockets in the Lucernaridæ have given rise to considerable misunderstanding owing to the fact that in some forms the reproductive organs bulge out from the stomach pockets in which they structurally lie, and come to take up a secondary position in the walls of the mesogonial pockets. The sections of Charybdea above referred to indicate that among the Cubomedusæ we may have the same structure reduced to its lowest terms, and may be a feather's weight in favor of the view that the Cubomedusæ are descendants of an attached Lucernaria-like form.

Two more diagrams, Figs. 33 and 34, are added in order to give a more complete understanding of a gastric ostium and its neighboring structures, the mesogonial pocket and the valve. Fig. 33 is a view of the gastric ostium and valve from the stomach side, and represents the appearance that would be given by a thick section through the arrow *x–y* in Fig. 32, in a plane at right angles to the paper. The heavy lines outlining the gastric ostium (*enr* and *enfl*) represent the place where the plane of the section has cut across the epithelium of the roof of the stomach above the ostium and the epithelium of the floor of the pocket-like depression internal to the valve. The continuation of the two heavy lines in either side of the ostium represents the region where the roof and floor of the stomach meet; *i. e.*, the edge of the lens-shaped stomach. The semilunar outline of the valve (*vg*) is shown by a light line just above the epithelium of the depression. As is seen by the reference arrow in Fig. 32, the valve lies a little external to the immediate plane of the section, and hence it is that its inner surface is seen in Fig. 33 and not a section of it. The vertical part of the suspensorium (*su*) is seen in section below the epithelium of the depression. The reference numbers 1, 2, 3 and 4 denote the same points in Figs. 32 and 33. Fig. 32 referred to Fig. 33 would lie in a plane at right angles to the paper through the reference arrow *x–v* of the latter figure.

Fig. 34 represents a horizontal section through the gastric ostium at the level of the arrow *a–b* in Fig. 32, or arrow *c–d* in Fig. 33. The reference numbers 5, 6 and 7, 8 denote similar points in the two figures 33 and 34. Fig. 32 as referred to Fig. 34 is through the arrow *e–f*; Fig. 33 is through the arrow *c–d*. In the series of cross-sections, Fig. 9 is taken at a level a little below that of Fig. 34, and passes through the basal part of the valve (*vg*).

(b) *Marginal Pockets.* The part of the peripheral portion of the gastrovascular system in each quadrant which is called the stomach pocket extends downwards as far as the sensory niche. Here by the coming together of the walls of the exumbrella and subumbrella the space between them is obliterated (Fig. 15) in the immediate perradius. From the sensory niche downward to the margin each stomach pocket is thus divided into two smaller pouches, the marginal pockets (*mp*). In each side of the Cubomedusan cube there are, then, in Charybdea two marginal pockets; or in all eight, a characteristic of the family Charybdeidæ. The marginal pockets as the name implies extend downwards to the bell margin, and are continued into the velarium as the velar canals. Of these (Fig. 3) there are two from each marginal pocket, or sixteen in all. The constancy in their number is one of the characteristics that distinguish C. Xaymacana from the very closely related C. marsupialis of the Mediterranean. (Compare Fig. 3 with the similar one by Claus for C. marsupialis, '78, Taf. I., Fig. 6.) The forked shape, while to be sure the common form in C. marsupialis, is an almost invariable characteristic in C. Xaymacana. It may be mentioned again that the presence of these canals is one of the chief features that distinguish the velarium of the Scyphomedusæ from the velum of the Hydromedusæ.

(c) *Canals of the Sensory Clubs and Tentacles.* The four interradial definitive tentacles and the four perradial transformed tentacles, the sensory clubs, are hollow, and their canals communicate directly with the peripheral part of the gastro-vascular system. The canal of the sensory club in each quadrant leads directly out from the stomach by a somewhat funnel-shaped opening formed by the approximation of the two walls of the stomach pocket. The relation of the canal of the sensory club to the stomach pocket is seen at a glance in Fig. 37. It is given by means of cross-sections in Figs. 12–14. Figure 12 shows the inner walls of the stomach pocket approaching the outer at two points, leaving between them a concavity freely open to the rest of the stomach pocket above and at the sides. Fig. 13, a little lower down, shows the two walls fused together at two points, making the interspaces a definite canal communicating with the stomach pocket above only. This canal lies directly over the sensory niche, and in the next figure (No. 14) the canal is seen to have passed through the roof of the sensory niche and to have entered the base of the stalk of the sensory club. In the enlarged end of the club, the part which bears the sensory structure, the canal widens into a terminal ampulla-like sac.

The endoderm lining the canal of the sensory club is specially differentiated. In the stalk it is more columnar than the epithelium of the stomach pockets, and is made up of cells containing a brightly staining nucleus with very little trace of cytoplasm. The cell bodies appear as if filled with a clear, non-staining fluid. Perhaps these cells give the stalk elasticity to act in connection with the thin layer of longitudinal muscle-fibres that are found just external to the supporting lamella. The epithelium of the terminal enlargement of the canal is composed of very high narrow cells, many of which show two nuclei of equal size and staining quality lying side by side.

In continuation of the specialized epithelium of the perradial furrows in the floor of the stomach the inner wall of the stomach pocket shows a strip of similar densely crowded columnar cells leading from the gastric ostium downwards to the canal of the sensory club. As in the other case, the strip probably represents a specially ciliated tract, and perhaps in it we see the reason why the canal of the sensory club is almost always found to contain either spermatozoa which are shed by the male reproductive organs directly into the stomach pocket, or else floating cells of the kind to be described in the next section.

The canals of the interradial tentacles arise from the peripheral gastro-vascular system much lower down than those of the sensory clubs, since these tentacles have preserved their primary positions with reference to the bell margin. Figure 16 represents a section taken at the level of the base of the pedalia which gives the connection of the tentacle canals with the gastro-vascular system. At the level below the sensory niche the four broad stomach pockets have been divided, as we have seen, into the right marginal pockets (*mp*). The figure shows that in the interradial corners the longitudinal septa (*ivl*, in the preceding figures), or lines of fusion between the two walls of the peripheral gastro-vascular space, which divide the primitively simple space into the four stomach pockets, have come to an end, leaving a connecting canal (*cc*) in each corner as all that remains of the primitive uninterrupted communication between all parts of the peripheral system. It is from these four connecting canals that the tentacle canals take their origin. From this point of origin each tentacle canal passes downwards, surrounded by the gelatine of the pedalium, into the tentacle proper.

The connecting canals are of morphological importance in that they are supposed, with much reason, to represent in the Cubomedusæ the circular canal of the Hydromedusæ.

9. *Reproductive Organs.* The sexes are separate in Charybdea. In both sexes the reproductive organs consist of four pairs of long leaf-like bodies, each leaf attached along one edge to the wall of the subumbrella in an interradius (see Fig. 1, *r*), and hanging free in the stomach pockets. From this position in the stomach pockets it is evident that the reproductive organs are endodermal. The lines of attachment of each pair is just internal to the longitudinal vascular lamella that fuses the outer and inner walls of the stomach pockets together in the interradius (*ivl*), and the reproductive organs are therefore structures belonging to the subumbrella. It is interesting to note how careful examination of the medusan organization takes away from the importance of the outer cup, the exumbrella, and adds to that of the inner, the subumbrella. We have seen that the phacelli and the sensory clubs, from whose position it would be supposed that they belonged to the exumbrella, are organs of the subumbrella, and that there is no muscle-tissue in the exumbrella; we find now that the reproductive organs belong to the subumbrella, and it will be shown later that the tentacles, like the sensory clubs, are structures of the subumbrella also. To the exumbrella are left only the functions of support and covering.

The mature reproductive organs extend very nearly throughout the entire vertical length of the bell, and are therefore found in the series of cross-sections in all but the uppermost and lowermost (Figs. 7–15 *r*). The organs consist of germ cells within, covered by an epithelium of columnar cells that shows here and there nettle cells. The ova are found with different amounts of yolk, according to age, surrounding a large nucleus almost devoid of chromatin and an intensely staining nucleolus. In young ova there appears very plainly in every case at least one small deeply staining body inside the nucleus, which very much resembles the nucleolus. These are probably so-called yolk nuclei, and while I have not made a special study of the ovogenesis, I infer that the constant presence of at least one, points to an origin of the ovum from a syncytium (of at any rate two cells), similar to that which has been recently shown by Doflein ('96) to occur in the formation of eggs in Tubularia. In the nearly mature ovary each ovum is surrounded by a layer of gelatine, which comes from the gelatinous sheet that enters the leaf-like ovary for its support along its line of attachment just internally to the interradial septum. It seems as if the ova, arising in the epithelium on the surface, pushed their way into the gelatine inside and there completed their development entirely surrounded by a slight investment of gelatine, which grows thinner around each ovum as it increases in size. In males the testes always show a similar division into compartments by gelatinous meshes, the compartments thus mapped out being filled with the small brightly staining spermatocytes. Ova and spermatozoa when mature are set free in the stomach pockets.

10. *Floating and Wandering Cells.* In the stomach pockets, the canals of the sensory clubs, and even in the stomach itself, are found in varying numbers freely floating cells having the appearance of young ova. They vary in size, the smallest being of the size and having the general aspect of the small ovocytes found in the ovary. The largest (Fig. 70) have exactly the same structure as the young ovarian eggs before they have begun to accumulate yolk. The granular deeply staining cytoplasm, the clear non-staining nucleus with its bright nucleolus and the nucleolus-like yolk nucleus, all show beyond doubt that these freely floating cells originate in the ovary.

In some of my preparations these cells are found not only floating free, but wandering through the tissues. Fig. 70 shows two such wandering cells fixed just as they were making their way either through the digestive epithelium into the gelatine of the floor of the stomach, or from the gelatine into the epithelium. The former seems the more probable, though why they should want to get into the gelatine is not very easy to conceive.

Perhaps there is some connection between this and the appearance that the young ovarian eggs have of pushing their way from the epithelium into the gelatine of the ovary. And of course it is not impossible that the whole phenomenon is abnormal, due to rupture of the ovaries which sets free young ova to exhibit their amœboid tendencies under new conditions. Against such an explanation, on the other hand, might be urged the fact that what seem to be the small floating cells are found occasionally in males as well as females, and that in the females a series can be traced with a good degree of certainty between the small floating cells like those found in the walls, and the larger ones which have all the characteristics of young ova.

However that may be, this amœboid action of cells having the structure of ova brings to mind the remarkable form of asexual reproduction described by Metschnikoff for Cunina proboscidea, under the name of "Sporogonie." Unfortunately Metschnikoff's original paper was not accessible to me, so that I was unable to obtain more particulars on the subject than those given in Korschelt and Heider's text-book (p. 33). The reproductive organs of both males and females of Cunina proboscidea are said to produce, besides the usual distinctively sexual elements, neutral amœboid germ cells, which wander into the endoderm of the stomach and circular canal, and also penetrate into the gelatine of the subumbrella. These amœboid cells divide parthenogenetically. One of the two cells of the first cleavage continues to divide and eventually forms an embryo of Cunina; the other remains amœboid and serves for movement, attachment and nourishment of the embryo.

Charybdea, however, has shown no sign of any such reproductive process on the part of its floating and wandering cells. The only indication that I get as to their use points to a possible nutritive function. The enlarged terminal portion of the canal of the sensory club almost invariably contains a number of the small-sized floating cells. These have a vacuolated, half disintegrated appearance, with the nucleus always compact and brightly staining. Now, examination of the high columnar cells that line the enlargement of the canal shows the presence in the cells of bodies of exactly the same appearance as those in the lumen. In one case a floating cell was found just at the end of an epithelial cell, to all appearance half ingested. The identity of the bodies inside the cells and those in the lumen is shown very clearly in some sections of material fixed in formalin, which preserves nuclei, cell walls and general outlines well enough, but does not retain the cytoplasm, and hence is useless for most purposes of histology. In the endodermal cells of the terminal enlargement thus preserved are found all the more distinctly the bright, compact, degenerated nuclei of the ingested cells, while in the lumen are seen other bright, compact nuclei with the poorly preserved remains of cell substances around them. In addition to the evidence from the appearance of the floating cells themselves and their ingestion by the endodermal cells, a little collateral evidence may perhaps be brought in from the Tripedalia about to be described. From the ovaries in this form are detached masses of cells (Fig. 71) which float free in the stomach pockets among the developing embryos, and to judge from the vacuolation that appears, are used up in their favor. These cell masses are described more fully in the part on Tripedalia.

B: Tripedalia cystophora.

a. *Habitat.*

The species upon which the new family was founded was obtained in great abundance in one locality in Kingston Harbor in the summer of 1896. The environment was even more unlike that in which Cubomedusæ have been found heretofore than in the case of Charybdea Xaymacana. On the west side of the Harbor there is a part more or less cut off from the main body of water, and so from the ocean, by a peninsula. This sheltered bay is dotted with small mangrove islands which toward the head of the bay become so numerous as virtually to convert it into a mangrove swamp. The water is shallow and discolored with organic matter, showing that the tide does not exercise much influence here, and the bottom is for the most part a black mud, deep enough to make wading very uncomfortable but not impossible near shore. The islands rise but slightly above the level of the waters, and the thick vegetation that covers them, for the most part mangroves, grows out into the water on all sides, forming a fringe of overhanging boughs. It was here in the shelter of the boughs, among the roots and half-submerged stems of the mangroves, that the small Cubomedusa was found to thrive. It could be obtained in great abundance almost any day, and of all sizes from the largest adults with stomach pockets filled with eggs or embryos down to small specimens only about two millimeters in diameter. In but one other place was Tripedalia found, and that was a similar region of half landlocked water skirted with mangroves, situated near Port Royal, across the harbor from the locality just mentioned. It would be hard to find places in which the conditions of life were more strikingly different from those of the pure deep sea in which the Cubomedusæ have been generally found before. The slight brownish yellow pigment made the small medusæ a little difficult to see in the discolored water, but like the pellucid Charybdea in the clear water of the harbor, their active movements gave away their presence. The swimming was very vigorous and was effected by quick, strong pulsations (as many as 120 per minute were counted), very different from the slow, rhythmic contractions of the

Discomedusan Cassiopea which was found in the same region over by Port Royal. Whether or not the animal made intentional efforts to escape capture could not be decided satisfactorily, but certain it was that they did escape often enough by swimming quickly below the surface of the semi-opaque water.

Tripedalia endured captivity much more hardily than the Charybdea, and would live in aquaria happily enough for a number of days—no attempt was made to see how long. Specimens with their stomach pockets filled with ripe spermatozoa, or with young at any stage from egg to planula, were taken in plenty from the latter part of June to the latter part of July. In each female the young were all at the same stage. The embryos were thrown out in the aquaria as free-swimming planulæ, which settled down on the bottom and sides of the glass in a day or two, and quickly developed into small hydras with mouth and typically with four tentacles (and four tænioles, W. K. B.), though three and five were by no means uncommon. In this condition they lived for three weeks without essential change, and they were still giving no promise of further development when the laboratory broke up and the jars had to be emptied.

b. *External Anatomy.*

The structure of the Cubomedusæ seems to be that of a type well established, and accordingly offers no very wide range of diversity among the different genera. The Charybdea that has just been described is a very typical form and will serve well as a standard with which to compare our species of Tripedalia. The resemblances are so close that a detailed account of the anatomy of the second form would involve much needless repetition. It is hardly necessary to do more than merely point out in what points Tripedalia resembles Carybdea and in what points it differs.

The form of the bell is less pyramidal than in Charybdea. Some measurements even gave the breadth greater than the height. The external surface is divided, as typical for the Cubomedusæ, into the four perradial sides and the four convex interradial ridges, and the furrows that separate these areas are with one small exception exactly the same as those of Charybdea, as may be seen by comparing the series of sections of Tripedalia (Figs. 21–30) with those of Charybdea (Figs. 6–15). The exception is almost too slight to mention. The adradial furrow in each octant which sets off the corner rib from the perradial surface in the lower part of the bell is not directly continuous, as in Charybdea, with the corresponding furrow in the upper part of the bell—that is, the *afr'* of Figs. 24–27 is not continuous with the *afr* of Figs. 22 and 23, as is seen by both being shown in Fig. 24. The upper furrow (*afr*) is continued only a short distance, however, below the starting point of the lower (*afr'*).

The pedalia conform entirely to the description given those of Charybdea, except that there are three attached to the bell margin in each interradius instead of one, and that the blade of each pedalium is much narrower.

The sensory clubs also show exactly the same relation to the bell and exactly the same structure.

In the bell cavity the proboscis has a longer and better defined stalk than that of Charybdea, and has the further and more important difference of possessing special sensory organs, to the number of fifteen or twenty. The suspensoria are much more developed than in Charybdea, so that the interradial funnels lying between are more marked. In a corresponding way the frenula are larger and stouter (Figs. 28, 29, *frn*). The musculature shows no new features and differs only in being comparatively more strongly developed and having a more pronounced striation. The nerve ring follows the same looped course from the margin in each interradius up to the level of the sensory clubs in the perradius.

c. *Internal Anatomy.*

The stomach offers no peculiarities, and the phacelli also agree with those of Charybdea except in having a smaller number of filaments in each tuft. The stomach pockets are not guarded by such well-developed valves as those described for Charybdea, though the valvular nature of the lips of the gastric ostia is indicated and the valvular functions undoubtedly performed. The gastric ostia are smaller (cf. Figs. 7 and 22), and this makes highly developed valves less necessary. No trace of anything corresponding to mesogonial pockets was noticed.

In the matter of the marginal pockets, however, we find that the agreement with Charybdea is no longer continued. The regions that correspond to the eight marginal pockets of Charybdea are formed, as in that genus, by the coming together of the exumbrella and subumbrella at the sensory niche (Figs. 25–28), but each of these regions is subdivided, as it is not in Charybdea, into two marginal pockets, a larger (*mp*, Figs. 28–29) and a smaller (*mp'*). In this way sixteen marginal pockets are formed as in the Chirodropidæ. Furthermore, as happens in the latter family but does not in the Charybdeidæ, the marginal pockets extend into the velarium. From each of the larger marginal pockets are given off two velar canals, while each of the smaller gives rise to but one short one (Fig. 18). Fig. 30 represents one of the last sections of a Tripedalia cut transversely, in which nothing but the pedalia and the velarium appear, and in it are shown the velar canals (*vc*), which come from the larger marginal pockets. The velarium appears in four segments because it is drawn upwards in the four perradii by the frenula (see Fig. 20). That the canals from the smaller pockets do not appear in the section is due to their shortness and to the fact that they are pulled upwards above the level of the sections by the frenula, together with that portion of the velarium.

The smaller velar canals, a pair in each perradius, seem to have in the males some function in connection with the storing of matured spermatozoa. In specimens with ripe testes they are very often found crowded to distension with spermatozoa, while the other velar canals may or may not contain them, and generally do not. The epithelium lining them is, like that of the others, composed of columnar cells higher on the wall turned toward the bell cavity than on that turned towards the exterior, but otherwise not specially differentiated. I searched in vain for any trace of opening by which the spermatozoa might gain the exterior. Fig. 29 shows another point which may be mentioned in passing, namely, that the canal of each of the three tentacles opens into the peripheral gastro-vascular system independently. The central tentacle of each group is the homologue of the single tentacle of Charybdea, and is formed in Tripedalia before the two lateral tentacles appear. Its communication with the peripheral pocket system is higher up than the openings of the lateral tentacles, so that in the section drawn the latter are just beginning to be indicated (*ct'*).

It remains only to speak of the reproductive organs of Tripedalia. The sexes are separate in this form also, and ovaries and testes have the same structure as is found in other Cubomedusæ. The development of floating masses of cells in the females, however, is a feature which, so far as I know, has not been observed before. These masses, of which a small one is represented in section by Fig. 71, are apparently developed along with the eggs, and repeat the structure of the ovary to all intents the same as if they were various-sized fragments of it broken loose. They consist mostly of high, columnar epithelial cells surrounding a few central cells and showing here and there a nettle cell just as the reproductive organ does. The epithelial cells differ from those of the ovary in containing one or more large vacuoles, and this vacuolation increases as the embryos, among which the masses float, develop. The idea naturally suggests itself, therefore, that they serve for nourishing and perhaps for protecting the embryos while they are developing in the stomach pockets of the mother individual.

PART III: DESCRIPTION OF SPECIAL PARTS OF THE ANATOMY.

A: THE VASCULAR LAMELLÆ.

In Medusæ it is a common thing to find that in certain definite places of the gastro-vascular system two endodermal surfaces that were primarily separated by a space have come together and fused into a single lamella or plate. Such a structure is called indifferently a cathammal plate, an endodermal lamella, or a vascular lamella. In the adult animal the vascular lamellæ are by virtue of their very nature formations "with a past." They are scaffolding left in the completed structure, giving us clues as to the way in which that structure was brought about; and in the Cubomedusæ, whose development is as yet unknown, they therefore afford an unusually interesting subject for special consideration.

The vascular lamellæ that are found in Charybdea and Tripedalia may for convenience be described as forming two systems, the internal and the marginal. The former comprises the endodermal fusions that separate the stomach from the stomach pockets (except for the spaces of communication left free, the gastric ostia) and those that separate the stomach pockets from one another. The marginal system consists of the lamella that connects *endoderm* of the gastro-vascular system with *ectoderm* of the surface in a ring all around the bell margin, and with it also the vascular lamella of the sensory niche, which has already been referred to in the general description of Charybdea. The lamellæ of the internal system have been described by previous writers, and especially by Claus in his paper on Charybdea, but they are still in need of comprehensive and clear treatment. The lamellæ of the margin and of the sensory niche have also been described by Claus, but not thoroughly or with entire accuracy, nor did he recognize the vascular lamellæ of the sensory niche as originally a part of the lamellæ of the margin. This last was first determined by H. V. Wilson upon specimens of Chiropsalmus quadrumanus obtained at Beaufort, North Carolina. Professor Wilson's unpublished notes on Chiropsalmus were very kindly placed in my hands, and so far as the vascular lamellæ are concerned my own work is only a confirmation and amplification of his, since Charybdea and Tripedalia in this respect agree with Chiropsalmus.

The vascular lamellæ of the internal system are the most prominent and morphologically the most important. They comprise the four vertical strips of fusion that separate the four stomach pockets in the interradii (*ivl* in the figures of the series of cross-sections of Charybdea and Tripedalia, Nos. 6–15 and 21–29), and four curved horizontal cross-pieces at the top of these which separate the stomach from the stomach pockets, and would make the separation complete did they not leave in each perradius a free space between their ends, which makes possible the gastric ostia.

The arrangement of this internal system of vascular lamellæ is simple. What they amount to is a certain definite number of linear adhesions between the two walls of an originally undivided gastro-vascular space, by which that space is divided up into a central stomach and a peripheral portion, and the peripheral portion thus further divided into the four stomach pockets. Perhaps the idea may be conveyed by likening the whole medusa to a couple of bowls fitting closely one within another and plastered together at the margins. The exumbrella then would correspond to the outer bowl, the subumbrella to the smaller inner bowl, and the original undivided gastro-vascular space to the space between the two. If now the walls of the space be cemented together in four horizontal curved lines just in the plane where the bottoms are bending round to become the sides of the bowls, leaving four interspaces between the ends of the lines, we should have the original space divided into a central horizontal somewhat lens-shaped region between the bottoms of the two bowls that would correspond to the central stomach, and a peripheral vertical portion between the sides of the bowls that would correspond to the peripheral gastro-vascular system; central and peripheral portions would communicate by the four interspaces between the lines of fusion, which would correspond to the four gastric ostia. If, further, the vertical peripheral portion be subdivided by four more lines of fusion running vertically at equal distances apart, each connecting above with the middle point of the corresponding horizontal line of fusion, we should have the simple peripheral portion divided into four parts, corresponding to the stomach pockets, by four vertical lines of fusion, corresponding to the four interradial vascular lamellæ, the *ivl* of the figures.

These mutual relations of stomach, stomach pockets and lamellæ will perhaps be made clearer if a comparison is drawn between them and the similar structures of a Hydromedusa. Liriope, one of the Trachomedusæ, is a good form to take for such a comparison, since by reason of its direct development from the egg it is free from the complications of hydroid medusæ. The young medusa has at first a simple, undivided gastro-vascular cavity which later is divided up into the central stomach and the typical radial to circular canals of the Hydromedusæ by means of fusions between the two endodermal surfaces. Diagrams *a*, *b* and *c* of Fig. 35 represent very schematically this process of division into stomach and canals. In *a* we have a projection upon a plane surface of the primary, undivided gastro-vascular cavity, as seen from above; *b* shows the first four points of fusion in the interradii; *c* represents those four points expanded by growth in all directions into broad cathammal plates in such a way as to leave the stomach in the centre, the radial canals in the perradii, and the circular canal in the periphery as all that remains open of the primary simple cavity. These broad plates of vascular lamella, separating the narrow radial canals, persist in the adult Liriope to tell the tale of the formation of the definitive gastro-vascular system. It seems to me that we are justified by analogy in drawing a similar conclusion for the Cubomedusæ. In *d* of Fig. 35 is represented a projection of a Cubomedusa, in which the homology of the stomach pockets with the radial canals of the Hydromedusa, and of the narrow strips of fusion with the broad cathammal plates, is shown at a glance. To make the comparison more perfect we have only to remember that in the Cubomedusæ there exists below each interradial vascular lamella a connecting canal (Figs. 16, 29 and 35 *d*, *cc*) uniting the two separate adjacent pockets. This, as has been pointed out by other writers, is the representative of the circular canal of the Hydromedusæ. Practically the only difference between the structure of the gastro-vascular system of the Cubomedusæ and that of a form such as Liriope, is that in the latter the fused areas have broadened out at the expense of the radial canals, while in the Cubomedusæ on the contrary they have become long and narrow.

One is strongly tempted by the foregoing comparison to speculate a little as to whether the reproductive organs of the Cubomedusæ, which lie *in* the stomach pockets and are generally supposed to be endodermal, may not bear some closer relation to those of the Trachomedusæ, which lie "in the course of" the radial canals (Lang's Text-book) and by common consent are ectodermal. And while we are being led by facts such as those just mentioned above to wonder just a little whether after all the position of the Cubomedusæ among the Acraspeda is so firmly assured—doubting some, yet in the frame of mind of one who "fears a doubt as wrong"—the velarium suggests itself as another point in question. Haeckel does not hesitate to state emphatically that the velarium of the Cubomedusæ and the velum of the Craspedote medusæ are only analogous, but the reasons that he gives (sie sind unabhängig von einander entstanden, und ihre Structur ist zwar ähnlich, aber keineswegs identisch; namentlich das Verhalten zum Nervenring ist wesentlich verschieden: System, p. 426) somehow do not produce so much impression upon one as the very velum-like appearance of the velarium itself. The origin from the fusion of marginal lobes is not as yet a matter of observation, and the relation to the nerve ring is not essentially different from that of the velum to the lower (*i. e.* inner) nerve ring in the Craspedotæ. The four frenula and the diverticula from the gastro-vascular system seem to be the chief differences in structure after all, and these Haeckel evidently did not think worth mentioning. This speculation, as to the possible relation of the Cubomedusæ to such forms of the veiled medusæ as Liriope, though it may be very tempting, is scarcely fruitful enough to repay much effort on the part of either reader or writer. The whole subject must remain uncertain until the facts of the development of the Cubomedusæ are known.

If the structure of the vascular lamellæ of the internal system has been made clear, the appearances of the vertical and horizontal components in the figures will be understood without much further explanation. The four vertical strips in the interradii (*ivl*) have been already referred to in the figures of the cross-sections of both Charybdea and Tripedalia. In the longitudinal sections of the two jelly-fish through the interradii, the vertical lamellæ are cut throughout their entire length from stomach to connecting canals (Figs. 5–20, *ivl*). The horizontal cross-pieces at the tops of the vertical lamellæ also appear in several of the figures. Fig. 36 represents the appearance that would be given by a longitudinal section taken through any portion of the upper part of the bell except in the interradii, or in the perradii, through the gastric ostia. The horizontal vascular lamella (*hvl*) is shown connecting the endoderm of the stomach (*ens*) with that of the stomach pocket (*enp*). In a longitudinal section directly through an interradius (Fig. 5 or 20) the horizontal lamella is cut just at the point where it joins the vertical, so that the two are not differentiated. In a section through the region of a perradius (Fig. 4 or 19) the horizontal lamella is of course not cut, since the section passes through the gastric ostium, whose existence is conditional upon fusion not having taken place between the endodermal surfaces.

The first figure in each of the series of cross-sections (Figs. 6 and 21) also shows the horizontal vascular lamella, cut across slantingly twice in each quadrant as it passes between the gelatine of the ex- and of the subumbrella to connect the epithelium of the stomach with that of the stomach pocket. The fact that more of the lamella does not appear in such a cross-section only shows that its course is not perfectly horizontal.

The region in which the same lamella lies is indicated in the surface view of the top of the bell of Charybdea (Fig. 2) by the bent line *hvl* in each quadrant. The figure manifests the appropriateness of Claus's name for the horizontal lamella—"bogenförmige Verwachsungs-Streifen." Haeckel calls the same structures "Pylorus-Klappen," and in his account of Charybdea Murrayana in the Challenger Report, speaking of the three divisions of the stomach (buccal, central and basal) which he traces upwards from the stalked forms of Scyphomedusæ, he says: "The central stomach in this Charybdea, as in most Charybdea, is joined to the basal stomach, as the pyloric stricture between the two is not developed and only faintly indicated by the slightly projecting pyloric valves." Again, in speaking of the valves of the gastric ostia, he says: "These four perradial 'pouch valves' alternate with the interradial pyloric valves." It is difficult to understand, however, how the "bogenförmige Verwachsungs-Streifen" of Claus, which are undoubtedly the same structures as those which I have called the horizontal lamellæ, and are only strips of endodermal fusion, can be "projecting pyloric valves," or indeed can properly be spoken of as valves at all. Possibly Haeckel was not quite able to understand Claus's description, and in his desire to find something in the stomach of Charybdea which would serve to set off a central from a basal part, such as is found in the Lucernaridæ, hit upon Claus's "Verwachsungs-Streifen." I have elsewhere given it as my opinion that in such of the Cubomedusæ as I have studied there is no structure in evidence that would properly serve to mark a limit between a basal and a central portion of the stomach.

We have next to describe the marginal system. The vascular lamellæ mentioned above in every case connected endoderm of one cavity with endoderm of another; those of the margin have the noteworthy difference that they run from endoderms of some part of the gastro-vascular system to *ectoderm of the surface.* The outermost cells of the endodermal lamellæ make direct connection with the ectodermal cells, without the usual intervention of a layer of gelatine.

The marginal lamella of Charybdea lies, as the name implies, just on the bell margin where the edge is curving round into the velarium. All around the whole circumference of the bell it is found (in Charybdea) at this same horizontal bend, except in the eight principal radii, where the tentacles and the sensory clubs have brought about modifications. In any place except these a vertical section through the margin will show the marginal lamella connecting the endoderm of the marginal pocket with the ectoderms of the surface, as represented by *vlm* in Fig. 38, which is a vertical section through the sensory niche a little to one side of the perradial axis.

In the interradii the marginal lamella undergoes modifications due to the fact that the bases of the pedalia are situated a little upwards from the exact margin, and that the lamella follows the outline of the bases. Fig. 1 shows one of the interradial corners of the bell margin looked at directly from the surface, so that the curved outline of the junction of the base of the pedalium with the exumbrella is seen. The trace made by the lamella where it meets the surface ectoderm follows this outline. The lamella is also shown in the vertical section through the interradius (Fig. 5 or 20, *vlm*), where it is seen running from the connecting canals (*cc*), which joins the two adjacent marginal pockets, upwards and outwards to meet the surface ectoderm. Its course from canal to surface is not in a direct line, but curved with the concavity upwards. Hence, in cross-sections at certain levels through the interradial corner it is met more than once and gives rise to appearances that seem at first sight too complicated for it to be just the same structure as the simple marginal lamella described above. That it is the same, and that the complication is only due to the insertion of the pedalia above the margin, can be determined by following through a series of cross-sections, the essential ones of which, as I hope, are given in Figs. 40–43. The levels of these are shown on Fig. 5 by the letters *w*, *x*, *y* and *z*, respectively. Fig. 40 shows the lamella cut but once, just below its highest part. The section is above the level of the connecting canal and hence still shows the vertical interradial lamella *ivl*. Fig. 41, at the next lower level (*x*), shows the same portion of the lamella intersected a little nearer the interior, while the junction with the endoderm of the connecting canal is shown still further inside. Fig. 42 is at level *y*, just through the bend of the loop, so that in part of its course the lamella is cut almost horizontally, *i. e.* in its own plane. Fig. 43 finally shows the lamella as it appears below the level of the connecting canal, cut twice, each portion joining endoderm of marginal pocket with ectoderm of surface. It thus bears exactly the same relations that it had when we first met it in Fig. 38 (*vlm*), except that here in Fig. 43 one finds that a cross-section cuts it at right angles instead of a vertical as in Fig. 38, as a result of its being pushed upwards from its former position on the margin by the insertion of the pedalium above the margin.

The vascular lamella of the sensory niche has already been alluded to as part of the marginal system, and brief reference has been made to it in the section on the sensory clubs. Like the rest of the marginal lamella, it connects endoderm with ectoderm. The line that its fusion with the ectoderm traces on the surface frames in a shield-shaped area at the bottom of the sensory niche, which is seen in the drawing of the outlines of the niche, Fig. 44 (*vls*). This lamella was observed by Claus, and was figured by him both in surface view and in cross-section through the niche. Apparently, however, he omitted vertical sections through the niche, so that he supposed that the outline traced by the lamella was not continuous above, *i. e.* over the stalk of the sensory club ('78, Fig. 41; text, p. 28). That the outline is closed above, though masked in surface view by the roof of the sensory niche, is seen at once in vertical sections, such as Figs. 37 and 38, one of which is directly through the perradius, the other a little to one side. Both show the vascular lamella of the sensory niche (*vls*) intersected twice, above and below the sensory club, and completely cutting off the exumbrella from any share in the bottom (or inner wall) of the sensory niche. Fig. 39, which is a cross-section through the upper part of the niche, and is essentially like the similar figure of Claus, shows in like manner that the bottom of the sensory niche belongs to the subumbrella. H. V. Wilson was the first to point out, in his unpublished notes, that the lamella of the niche is complete all round.

In the adult structure of Charybdea and Tripedalia the lamella of the niche is connected with that of the margin by a vertical strip of endodermal fusion that does not come to the surface like the rest of the marginal system, but remains just internal to the gelatine of the exumbrella, connecting the two adjacent marginal pockets. In the cross-sections of Charybdea it is seen in Fig. 16 (*vlc*); in those of Tripedalia it is seen in Figs. 28 and 29. In vertical section it is found in Figs. 4, 19 and 37. In Fig. 44, which represents the bell margin and velarium of Tripedalia arranged as if the velarium were vertical and pendant from the margin (instead of suspended by the frenulum so as to be at right angles to the vertical plane), the connecting lamella is shown as a dotted line (*vlc*)—dotted because it does not come to the surface—joining the lamella of the niche with that of the margin (*vlm*).

The same figure (No. 44) shows a characteristic difference between the marginal lamella of Tripedalia and that of Charybdea. While in Charybdea, as Claus points out, the marginal lamella keeps at one level, just a little above the bell margin, all the way round (except where disturbed by the special modifications of the tentacles and the sensory clubs), and never descends into the velarium, in Tripedalia on the other hand it describes a sinuous course, following the outlines of the marginal pockets, as is indicated in the figure by the light parallel line *vlm*. The course as it would be seen in a surface view is obscured just at each side of the interradius by the overhanging of the bases of the two lateral pedalia. This is why the lamella is not indicated at these points in the diagram. The course is seen to lie almost wholly on the velarium, that is, in the figure below the line which represents the bell margin proper, the line at which the angle comes when the velarium is in its normal position, horizontal to the vertical side of the bell.

In this sinuous course of the marginal lamella we have another point of resemblance between Tripedalia and the Chirodropidæ. H. V. Wilson worked it out in his sections of Chiropsalmus, and the reconstruction which I have given in the figure under discussion is in all essentials similar to his for Chiropsalmus. The differences lie only in the fact that Chiropsalmus has more velar canals, and that the chief marginal pocket in each quadrant is not forked peripherally, as is that of Tripedalia (*mp*), but presents its distal margin parallel to the edge of the velarium. The two smaller marginal pockets in the perradii (*mp'*) are on identically the same plan in both.

Tripedalia, having three tentacles joining the umbrella in each interradius, shows a disturbance of the course of the marginal lamella in these regions by just so much the more complicated than in Charybdea. The plan, however, is exactly the same. The lamella is pushed upwards from the margin by each of the bases of the three pedalia just as is done by the base of the single pedalium of Charybdea. Fig. 29 shows the lamella in the same relation to the canal of the central tentacle (*ct*) that it has in the similar sections of Charybdea (Figs. 16 and 43); and in addition the first appearances (as the series is traced downwards) of the arches of the lamella over the two lateral tentacles (*cl'*), which are inserted a little lower down than the middle one of the group. As concerns these lateral tentacles, the relations of the vascular lamella at this level are the same as that in the level of Fig. 40 for Charybdea.

It has been stated more than once already that the vascular lamella of the sensory niche is a part of the lamella that runs round the margin, and so far the only evidence given has been the strip of endodermal fusion running from the marginal lamella to that of the niche. This strip, however, as has been described, does not come to the surface and consequently seems at first sight to be a different structure from the lamella of the margin. That it is not, however, I found very prettily shown in a series of sections of one of my youngest Tripedalia. In this the lamella of the niche as it was traced in successive sections downwards, was found not to form a closed ring at the bottom of the niche, but each side was continued directly and separately downwards to the margin, where it passed into the corresponding part of the marginal lamella. A reconstruction of the condition, similar to that of Fig. 44, is given in Fig. 45, and I think explains itself at a glance. Evidently the vascular lamellæ that connect the lamella of the sensory niche with that of the margin at first come to the surface, like the rest of the marginal system, but as the animal grows older come to lie within the gelatine. In this way the condition found in cross-sections just through the margin of my very small Tripedalia, and represented in Fig. 46, becomes that of the adult seen in the corresponding portion of Fig. 29. It is as complete a demonstration as could be required that the lamella of the sensory niche is at first only a loop of the marginal lamella, a conclusion that had been already reached by H. V. Wilson on theoretical considerations, based upon the facts of the adult structure as he found them in Chiropsalmus.

As Wilson pointed out in his notes, these facts have a close bearing upon the question of the origin of the velarium. Sixteen marginal pockets are found in both Chiropsalmus and Tripedalia, and all of them extend into the velarium. It is not unnatural to suppose that these belong to sixteen marginal lobes, and that these lobes have fused together to form the velarium. In the Chirodropus figured by Haeckel (Taf. XXVI) in his "System" gelatinous lobe-like thickenings are shown in the velarium, corresponding to the sixteen marginal pockets. In Tripedalia no special gelatinous thickenings are found, but the arrangement of the marginal pockets is the same as that of the Chirodropidæ, and perhaps I ought, when treating of the systematic relations of Tripedalia (p. 5, Fam. III), to have recognized the analogy to the extent of saying that marginal lobes may not be completely absent from the velarium of Tripedalia. At any rate the gelatinous lobes in the case of Chirodropus on the one hand, and on the other hand the sinuous outline of the margin still mapped out by the lamella in Chirodropus, Chiropsalmus and Tripedalia, are certainly very suggestive of an ancestral Cubomedusa in which there was no velarium, but sixteen free marginal lobes instead. Two more indications favor slightly the same view. In both Charybdea and Tripedalia a small notch is seen in the edge of the velarium in the perradius (Fig. 44). Its constancy suggests that it may not be a chance or meaningless feature. The second point is the small size of the two marginal pockets adjoining the perradius. These are in the position of the ephyra lobes of the Discomedusæ, which always lie on either side of each sensory club, and which do not keep pace with the other marginal lobes in development.* In the Rhizostome jelly-fish especially they are found much smaller than the other lobes, as will be seen by a glance at such figures as Haeckel's for Lychnorhiza (System, Taf. XXXIV, Fig. 2), or for Archirhiza (Taf. XXXVI, Fig. 5), or Hesse's figure of the margin of Rhizostoma Cuvieri ('95, Taf. XXII, Fig. 22). The resemblance between such margins and that of Tripedalia (Fig. 44), with its simple, unbranched velar canals, is very suggestive. On the other hand it must be remembered that in considering the vascular lamellæ of the internal system we found the indication pointing rather more to Hydromedusan affinities than to any other. Charybdea throws no light on the question, since it has no marginal lobes on the velarium and the marginal pockets end strictly at the margin, so that the only diverticula of the gastro-vascular system in the velarium are the velar canals.

Before leaving the subject of marginal lobes and pockets I must answer a possible objection that may occur to some careful reader. It may seem that I am wrong in holding that there are two marginal pockets in each octant instead of three, that just as there is one velar canal from each of the smaller perradial pockets (*mp'*, Fig. 44), so each prong of the forked larger pocket (*mp*), since it is continued into a velar canal, ought to be called a marginal pocket likewise, the whole number of marginal pockets then being twenty-four instead of sixteen. Such a revision of the terminology would not be without some reason in its favor, and perhaps a study of more forms would show it to be correct. But for the present, at any rate, it seemed to me best to abide by the analogy of

Chiropsalmus, in which the peripheral edge of the larger marginal pocket in each octant is not bow-shaped, but runs parallel to the edge of the velarium. A revision of the terminology of the marginal pockets such as implied in the suggestion above would also give rise to complications when applied to Charybdea, since the latter has no marginal pockets in the velarium.

As to the functions of the vascular lamellæ, there is too little known to say much. It is rather improbable that structures retained so definitely should be mere scaffolding left over from a previous stage of usefulness. Claus has found in Chrysaora that the lamellæ form a kind of capillary network in communication with the gastro-vascular system, and he with others supports the view that they perform an accessory function in the nutrition of the tissues they penetrate. Upon this point I have no observations of my own to add.

The marginal vascular lamella is regarded by Claus as perhaps the vestige of a circular canal around the bell margin. On this subject, too, I have nothing to add. A lamella of endoderm that connects directly with the ectoderm of the surface along its whole course is a structure whose meaning I am wholly unable to understand or even to guess at. A similar lamella is described by Hesse ('95, p. 430) as occurring in the ephyra lobes of his Rhizostoma, and he mentions Eimer as the first to discover this structure, probably meaning the first to discover it in the Discomedusæ. Whether the lamella is found all around the margin is not stated. Hesse refers it to the ephyra, and remarks that the investigation of it in the ephyra would undoubtedly give interesting results.

I will close this part upon the vascular lamellæ with a very pertinent suggestion made by Professor Brooks to the effect that the usual way of speaking of the sensory clubs as having moved up from the margin is looking at the matter in the wrong way. The level of the sensory clubs undoubtedly represents the original margin, which elsewhere has grown down and away from its former level, leaving the sensory clubs like floatage stranded at high-tide mark. Only in this way can the lamella of the sensory niche have any meaning.

B: The Nervous System.

The nervous system of the Cubomedusæ is the most highly developed that is found in any of the jelly-fishes. If the position of the group among the Acraspeda is established, it alone is ample to prove that the Hertwigs had not sufficient evidence when they stated in their monograph on the nervous system of the Medusæ ('78) that the Acraspeda show a much lower nervous organization than the Craspedota.

The system naturally groups itself under three heads, the nerve ring, the sensory clubs, and the motor plexus of fibres and ganglia that underlies the epithelium of the subumbrella. The general relations of the nerve ring and of the sensory clubs have been given before in the description of Charybdea Xaymacana, so that we may pass at once to the consideration of the finer details of the nervous tissues.

In the structure of the nerve ring I have found myself unable to come to the same results as those given by Claus, who so far as I know is the only one that has studied the nerve with special reference to its histology. Our difference amounts to this, that he finds two distinct types of cells in the epithelium of the nerve, sensory and supporting, which would make it a receiving as well as transmitting organ, while I have not been able to demonstrate satisfactorily the sensory cells, and, therefore, so far as my own observation is concerned, I am disposed to attribute to the nerve simply the function of conducting impulses. I do not know just how much weight to assign to my inability to find evidence in my sections of the sensory type of cells. Eimer (mentioned by Hesse, '95, p. 420), the Hertwigs ('78) and Claus ('78) have independently discovered the two types in one medusa or another, and the Hertwigs, at least, have demonstrated them by macerated preparations. So far as Charybdea is concerned, however, Claus had only preserved material and had to rely upon sections, as have I, since the material which I had preserved with especial reference to maceration did not turn out well. The results that we get from sections vary enough for me to believe that Claus interpreted his sections very much by analogy with other forms—as indeed, is suggested by his own words ('78, p. 22): "Da es mir nicht geglückt ist die durch die längere Conservirung in Weingeist fest vereinigten Elemente zu isoliren, habe ich das muthmassliche Verhältniss beider Elemente nach Analogie der mir für die Acalephen bekannt gewordenen Verhältnisse, welche O. und R. Hertwig so schön auch am Nervenring der Carmarina zur Darstellung gebracht haben, zu ergänzen versucht." There can be no doubt of our having the same structures to deal with, for C. Xaymacana is so much like C. marsupialis as to be perhaps more worthy of being called a variety of the latter than a distinct species.

The structure of the nerve as I conceive it is given in Figs. 47 and 48. The former represents a cross-section, and shows, as others have pointed out, that the layer of circular muscle fibres (*cm*) is interrupted by the nerve. It is evident that the tissues which elsewhere on the subumbrella were differentiated into muscle epithelium and muscle fibre have here become nerve epithelium and nerve fibre, a point that has not been remarked upon before, so far as I remember, and that may be of interest in connection with the neuro-muscular theory. The epithelium of the nerve (*scn*) is seen to be made up of cells whose inner ends narrow down into a kind of stalk or process that runs to the gelatine of the supporting lamella (*gs*) and there joins a little cone of the gelatine that juts out to meet it. The cells are smaller in general than those that overlie the muscle layer, especially on the two lateral margins of the nerve, where they are more crowded together and overarch the nerve-fibres. The fibres are seen in cross-section between the processes of the cells. They apparently must lie imbedded in some clear, watery fluid that does not show in the preserved material. The processes of the epithelial cells give the fibres the appearance of lying in alveoli, or being divided into strands, and one of these strands (*ax*) is always discernible among the others by reason of its more numerous or finer or more compactly massed fibres. This is the "axis" of Claus. Here and there in its course appear ganglion cells having their long axis in the longitudinal direction of the nerve. Elsewhere, in the nerve as well, and usually nearer to the surface, are found other ganglion cells, mostly bipolar, some multipolar, which are readily distinguishable from those of the axis by the fact that their long axis lies across the nerve. One of these cells is shown in the figure (*gc*). Here and there in the epithelium alongside the nerve are found mucous cells (*mc*), distinguished by their clear contents and by the small exhausted-appearing nucleus at the base with a few threads of protoplasm.

In Fig. 48 I have tried to represent the structure of the nerve by means of a series of five different views such as would be given by focusing at five successive levels. In the first (1) we have the epithelium of the nerve (*scn* in Fig. 47) in surface view, the cells appearing polygonal in outline, with here and there a mucous cell. In (2) we find a very slight layer of ganglion cells and fibres having a transverse direction (*gc* and *fp* in Fig. 47). These are continuous with the plexus of fibres and ganglion cells which lie above the muscle layer all over the subumbrella, and which represent the motor part of the nervous system. This connection with the nerve shows how co-ordination is effected. At the same level are found fibres of the axis also having a longitudinal direction. In (3) is seen the main body of fibres, divided in the osmic preparation from which the drawing was made into irregular wavy strands which are in all probability largely the result of preservation, but are in part also due to the separation by processes of the epithelial cells, as was seen in Fig. 47. The axis is seen with one of its longitudinally directed bipolar ganglion cells; and at the sides the fibres of the circular muscle of the subumbrella. These show a slanting direction to the nerve, due to the fact that the nerve, as mentioned before, has a sinuous course from the margin in interradius to the level of sensory club in perradius. At the next focus (4) we come to the gelatine of the subumbrella (*gs* in Fig. 47), and below this (5) to the larger polygonal outlines of the endodermal cells of the stomach pocket (*enp*, Fig. 47), which like the ectoderm show mucous cells at irregular intervals.

A comparison, now, with Claus's figures ('78, Taf. II, Figs. 19–21) will show that, except for the rather unimportant matter of the mucous cells, which he finds regularly and thickly disposed on each side of the nerve ('78, Fig. 21), our only essential difference lies in the matter of sensory cells in the epithelium. His figures show a multitude of spindle-shaped sensory cells whose central ends are continued in processes that bend around into the mass of fibres of the nerve. In his Fig. 20 a relatively small number of nuclei, just one-third as many, are seen attached nearer to the surface, which represent the supporting cells. The plan of structure (as shown in his Fig. 20) is an alternation of (1) supporting cells offering a broad peripheral end to the surface and having the central end continued as a supporting fibre to the gelatinous lamella, and (2) spindle-shaped sensory cells with nuclei at a lower level, which send their peripheral process up between the supporting cells to the surface, while the central process becomes continuous with the nerve fibres, often branching into two processes. In my sections I have not been able to see either a regular alternation of nuclei at different levels, or central processes which unmistakably bend round into the nerve fibres. In every case in which I could trace the central process of a cell clearly it ran to the supporting lamella, and this whether the nucleus of the cell lay near the surface of the nerve or deeper down, as in the somewhat spindle-shaped cell seen on the left of the centre of the nerve in Fig. 47. Of course in many cases the central process could not be traced in a section, and this leaves room for the supposition that such were always the sensory cells. From my inability to demonstrate sensory cells in the nerves of Charybdea, I by no means wish to deny their existence; for that remains to be proved, or disproved, by macerations. At any rate, they cannot be so numerous as has been supposed. The position of the nuclei shows that.

The epithelium of the nerve is said by Claus to be ciliated. It has been suggested by Schewiakoff that probably in such cases the sensory cells bear one long cilium, while the supporting cells have many smaller cilia. Unfortunately, I made no observations upon the ciliation of the nervous structures of the living animal, and the traces of cilia that are shown in preparations of preserved material are a poor basis to speculate much on. Claus considers the sensory cells of the epithelium of the nerve a special seat of tactile sensation.

The way in which the nerve reaches the sensory clubs is interesting. Under the topic of the vascular lamellæ it was explained that the sensory clubs and the bottom of the sensory niche from which they spring are parts of the subumbrella. Fig. 37 reminds at a glance better than any other one drawing how the bottom or inner wall of the niche is completely cut off from the exumbrella by vascular lamellæ above and below the stalk of the club. From this figure, now, it will readily be understood that the nerve in order to pass to the base of the stalk has simply to traverse the gelatine of the subumbrella. This fact, which seems surprising enough at first sight in view of the position of the clubs on the external surface of the umbrella, was correctly pointed out and explained by Claus, but one or two figures will serve perhaps to give a clearer idea of it.

Fig. 49 is a diagram of the nervous structures in the region of the sensory niche, as they would be seen on the surface of the subumbrella turned toward the bell cavity. The outline of the sensory niche as it is seen through the tissue of the animal is represented by the line *osn*. The sensory club (*scl*), and its stalk with a conical basal portion are given by the lightly dotted outline and are also imagined as seen through the animal. The nerve (*n*), being on the surface of the subumbrella, is shown as a heavy line describing an arch over the outline of the niche. In the middle point of the arch is a slight thickening of the nervous tissue (*rg*) which shows in section a large increase in the number of ganglion cells, and is the radial ganglion of Claus. The same is seen, exaggerated in size, in Fig. 12. From it there extends upward a slender strand of nervous tissue (*rn*), the radial nerve of Claus. In Charybdea this can be traced but a very short distance. In Tripedalia it is much more distinct and traceable for a longer distance, and I might say in passing that this and the sensory organs in the proboscis are the only differences I have noted between the nervous systems of Tripedalia and Charybdea.

Nerve ring, radial ganglion and radial nerve all lie on the bell cavity surface of the subumbrella. The way, now, in which the nerve ring reaches the base of the stalk is simply by sending two roots through the gelatine of the subumbrella to the conical base of the stalk. These roots are seen in the diagram at *rns.* After passing through the gelatine the roots come together on the inner side of the base—that is, the side turned toward the bell cavity—and then pass downwards (*nst*) on the inner side of the stalk of the club to the mass of nervous tissue at its end.

This passage of nervous tissue through the gelatine in order to reach the sensory club is a little hard to grasp at the first, and I have tried to render it more intelligible by a couple of drawings of sections. Fig. 50 is a transverse section through the upper part of the region of the sensory niche, not quite horizontal (*i. e.* parallel with the bell margin), but slanting so as to lie on the plane of the reference arrow *x–y* in Fig. 49. The plane passes just through the top of the niche, and in two areas has cut through the roof with its epithelium of ectoderm (*ece, ecs*) so that the space of the sensory niche (*sn*) appears. The vascular lamella of the sensory niche (*vls*) is shown, as in Figs. 13 and 14, running on each side from the endoderm that lines the canal of the sensory club (*enc*) to the endoderm of the adjacent stomach pocket (*enp*). By it the gelatine of the exumbrella is separated from that of the subumbrella, and one sees that it is only through the latter that the nerve has to pass in order to reach the base of the sensory club. It is also seen that one part of the roof of the niche which is cut through lies outside of the ring of lamella and is therefore lined with ectoderm of the exumbrella (*ece*) while the other lies within the ring and is lined with ectoderm of the subumbrella (*ecs*). Owing to the slanting direction of the cut only the root on one side is cut through. The other is indicated, however, on the right side of the drawing. In this method of passage of nerve fibres, together with the accompanying ganglion cells, directly through the gelatine to the stalk of the sensory club my work is only confirmation and explanation of Claus.

Fig. 51 is a vertical section through the base of the stalk in the plane of the reference arrow *w–z* in Fig. 49, and therefore passing through one of the roots of the nerve of the stalk. Here again the region is seen to be cut off from the exumbrella by the vascular lamella of the sensory niche (*vls*), and the nerve is seen passing through the gelatine of the subumbrella from the surface of the bell cavity (*sc*) to the base of the stalk hanging in the sensory niche (*sn*). One of the ganglion cells (*gc*) that accompany the nerve is seen to have two nuclei, a not infrequent occurrence which has been pointed out by others.

The same figure shows that the axis (*ax*) of the nerve has penetrated the gelatine with the other fibres. Here at the base of the stalk it takes a horizontal course and becomes directly continuous with the similar structure of the other root, as Wilson, I believe, first pointed out. This part of the nervous tract which runs horizontally along the base of the stalk between the two roots (Fig. 49, *rns*) has been considered by Claus the representative in Charybdea of the upper nerve ring of the Craspedota, which therefore exists in Charybdea in four separate portions. Seeing, however, that the region in which it is found belongs to the subumbrella, the homology seems very doubtful. Moreover, the fact that the axis of the nerve ring runs through this outer portion, instead of remaining on the inner surface of the subumbrella and passing to the radial ganglion, rather indicates that the outer portion is part of the original course of the nerve ring, while the portion that remains on the inner surface is perhaps a later formation.

A very interesting feature of the nervous system occurs in the same region in the form of a tract of fibres underlying the endoderm, and separated from the other fibres by the gelatine of the supporting lamella. It is seen in vertical section in Fig. 52 (*enf*), which is a section through the base of the stalk in just about its median plane, and, therefore, to one side of the arrow *w–z* in Fig. 49 and the corresponding drawing, Fig. 51. In cross-section it is represented also in Fig. 50 (*enf*). It varies in size and prominence very much in different specimens. Fig. 52 is a camera drawing of it in the case that showed it most developed. Ganglion cells are found in it, but comparatively infrequently. In some cases the tract itself can hardly be found with certainty. Hesse has described in a Rhizostome a much more highly developed tract in a corresponding position on the base of the marginal body. Fibres from the "outer sensory pit" pass through the gelatine to the sub-endodermal tract, which is described as surrounding the epithelium of the canal of the marginal body like a collar and is most thickly developed on the under surface of the canal, at the place that just corresponds with the point where, and where only, I find the tract in Charybdea. Hesse thinks that fibres then pass from this region to the nervous epithelium of the "inner sensory pit" lying underneath the base of the marginal body, which contains a rich supply of ganglion cells and is considered by him to be the centre of the nervous system of the medusa. A close comparison cannot be drawn with Charybdea in this matter, however, since Charybdea has nothing to correspond with the "outer" and "inner" sensory pits. Moreover, the endodermal tract is not found encircling the canal of the sensory club, nor could I trace fibres passing from it through the supporting lamella into the fibres of the nerves.

Claus has figured ('78, Taf. V, Fig. 45, *Fb*) a small bundle of fibres in the stock of the sensory club lying between the endoderm cells of the canal and the supporting lamella. The same bundle is found in both Charybdea and Tripedalia and can be traced in cross-sections up the stalk to a point which must correspond with that at which the endodermal tract is seen in Fig. 52. Downwards it can be traced only as far as the entrance of the stalk into the knob of the club where it invariably becomes lost to view. According to Hesse ('95, p. 427) Schäfer found under the endoderm cells of the whole stalk of the marginal body a fibrous layer like that under the endoderm cells which he refers to slender processes from the cells of the crystalline sac. Although Hesse, as we have seen, finds the layer more limited in extent than Schäfer gives it, and does not trace it to the same source, the observation of Schäfer seems to me worthy of mention here, inasmuch as the trend of the fibrous bundle under the endoderm cells of the stalk in Charybdea and Tripedalia suggests quite strongly that the fibres come from the crystalline sac, as Schäfer thought to be the case in his medusa.

Besides the radial ganglion situated in the course of the nerve ring at its four perradial points there are four other similar ganglia on the subumbrella. These lie in the interradii, at the four lowermost points of the nerve's course, and undoubtedly send off nerves into the pedalia at whose bases they are situated. F. Müller ('59), whose work was not accessible to me, is quoted by Claus as recording two ganglia opposite the base of each pedalium which gave off a great number of nerves partly into the velarium, partly into the tentacles. Claus observed nothing of the kind in Charybdea and states that even the interradial ganglia do not exist.

That they do, however, is shown without doubt in sections of both C. Xaymacana and Tripedalia, but nerves to the velarium or to the tentacles I was unable to find.

On the two sides of each frenulum and of each suspensorium are found sub-epithelial ganglion cells in greater numbers than elsewhere on the subumbrella, and I am inclined to ascribe to them also the importance of special ganglia controlling the musculature of the frenula and suspensoria. Certainly such ganglia would not be out of place.

It has been mentioned that the greater prominence of the radial nerve and the possession of special sensory organs in the proboscis were the only points of difference I had noted between the nervous systems of Charybdea and Tripedalia. These sensory organs remain to be described. They are simple ciliated cysts containing a concretionary mass, and are situated in the gelatine of the proboscis, irregularly disposed of at any level, from the lips to the beginning of the stomach, and in any radius. In one series of the adult animal fifteen were counted, of which seven were situated about interradially, four perradially, two adradially and two subradially. In another, twenty-one were counted, twelve in the perradii and nine situated between the sub- and perradii. The one shown in Fig. 24 is in the perradial position, often seen. In the sections of the very young Tripedalia in which the vascular lamella had not reached the adult condition the sensory organs of the proboscis were not found, although the sensory clubs showed practically no difference from the adult. Their structure is very simple—merely a round or oval sac lined with ciliated cells which bear up and keep in constant motion an irregular coarsely granular concretion. Fig. 53 is a sketch made in Jamaica from the living specimen. Sections were somewhat disappointing in that they added but little. Fig. 55 was drawn to show that now and then a mucous cell (*mc*) is found among the other cells of the sensory epithelium. An irregular-shaped mass (*rc*) was always found inside the cysts as the organic remains of the concretion. It gave no trace of cellular structure and offered no evidence whether the concretion was the product of one or few or of all the cells of the cyst. The latter would be unique among the medusæ. Even if the otocyst is the result of the activity of only one or a few cells, it is, so far as I know, the only case known for the jelly-fish of a free, unsuspended concretion.

As to whether the cysts are of ectodermal or endodermal origin could not be determined, but there was some evidence in favor of the latter. Fig. 56 is a drawing of one seen in optical section in a whole mount of part of a proboscis, and shows a definite connection with the endoderm of the proboscis. This was the only case when such connection was satisfactorily established, but in sections it was not uncommon to find what seemed to be the remains of the broken stalk, as in Fig. 54 (*rs ?*). No connection could be traced between the cysts and any other part of the nervous system. As to function, the idea that they serve to give perception of space relations suggests itself as readily as any other hypothesis.

We come now to the consideration of the terminal knob of the clubs, the sensory portion proper. A complete and detailed account of the complex structure of these organs would fill many pages and involve much useless repetition. Claus ('78) has described them with accuracy, but not in great detail, and since then Schewiakoff ('89) has given a careful general description and has supplemented Claus's work by observations upon the finer structure made with the aid of more recent technique. It seems in place for me, therefore, to give in the briefest possible way a general idea of their structure, and to pass then at once to the points in which my work has led me to different conclusions from those of Claus and Schewiakoff. In brief, then, the knob of the sensory club consists of a thick, complex mass of nerve fibres, more or less imbedded in which lie the special sensory organs, surrounding the ampulla-like terminal enlargement of the canal. The surface between the special organs is covered with less specialized sensory epithelium. The sensory organs are seven in number. Of these, four are simple invaginations of the surface epithelium arranged in two pairs symmetrically to the median line in the proximal end of the knob (the end where the stalk enters) and having pigment developed in the cells so invaginated, while the space of the invagination is filled with a gelatinous refracting secretion. These are considered simple eyes. Two more of the organs are complex eyes situated on the median line of the inner surface of the knob, the upper one smaller than the lower, but having almost exactly the same structure. Each has a cellular lens over which extends a superficial, corneal layer of cells; below the lens a refractive "vitreous body"; and below this a retina with pigmented cells. The seventh organ is the crystalline sac, which lies almost at the end of the knob opposite to the stalk and contains a large concretion. In view of the fact that the sensory clubs *in toto* have been abundantly figured by Claus and Schewiakoff, it is my intention to give but one simple figure of the general relations, and I justify that one in that it was made from the fresh material. Fig. 57 is a camera sketch of the outlines given by a sensory club seen in optical section from the side. The smaller upper and the larger lower complex eyes which are situated on the mid-line, are seen in profile, while the two small simple eyes give the outlines that they would in a surface view of their side of the knob. Of course it is understood that two similar ones would appear on the other side, since the four simple eyes are symmetrically paired on either side of the mid-line. The sketch seems to show at least this much, that even in the living state the lens of the larger eye projects out beyond the other contours of the surface, so that the marked convexity ascribed to it in descriptions is not to be attributed to the preservation.

It is in reference to the structure of the retina and vitreous body of the complex eyes that I have found myself unable to come to the same conclusions as Claus and Schewiakoff. Since the work of the latter goes much further into the detail of the subject than does Claus's paper, it will be sufficient for me to compare my results simply with those of Schewiakoff.

The latter finds that the retina is composed of two kinds of cells, corresponding to the supporting and sensory cells referred to in the description of the nerve ring. These he figures ('89, Taf. II, Figs. 12 and 13) as alternating regularly. The two kinds of cells differ as follows:

(1) Shape. The supporting cells like those referred to before, are cone-shaped, having a proximal fibrous process that runs into the underlying stratum of nerve fibres, and on the surface of the retina a broad distal pigmented termination. The sensory cells are spindle-shaped, the proximal processes becoming continuous with fibres of the underlying nervous mass, while the distal process runs up to the surface of the retina (the part toward the lens) in between the ends of the supporting cell. The two kinds of cells are accordingly designated as pigment and visual.

(2) Position of nucleus. This comes in as a corollary of the shape. The nuclei of the visual cells lie in the enlarged central part of the spindle-shape, and, therefore, at a lower level than the nuclei of the alternating pigment cells.

(3) Processes in the vitreous body. The distal processes of the spindle-shaped visual cells are continued through the vitreous body to the cells of the lens as rod-like visual fibres which lie in canals in the (supposedly) homogeneous vitreous body. The pigment cells on the other hand have no fibres passing from them through the vitreous body, but in the latter are situated cone-shaped masses of pigment whose bases rest upon the broad ends of the pigment cells without, however, being a part of the cell.

(4) Pigment. The distal ends of the pigment cells in the retina are strongly pigmented, as the name implies. The processes of the visual

cells, which alternate with these, are pigmented likewise, but the pigment is not so abundant and lies in the periphery of the cell body, leaving free a highly refracting central axis.

If the relation of these cells to each other has been made sufficiently clear, it will be understood that, in accordance with Schewiakoff's scheme of the structure, sections that cut the retinal cells transversely give very different appearances at different levels. A section through the very tops of the retinal cells, that is, the last section of the retina before striking the vitreous body, would show large polygonal areas of heavy pigment (the ends of the pigment cells), in between which would lie the much smaller, less pigmented, highly refracting ends of the visual cells ('89, Taf. II, Fig. 19). A section lower down in the retina, that is, more toward the centre of the club, would strike the low-lying enlarged central portion of the visual cells with their contained nuclei, and the smaller, proximal ends of the pigment cells. It would, therefore, give the reverse appearance from the preceding section, namely, that of large unpigmented (or but slightly pigmented) areas (the swollen bodies and nuclei of the spindle-shaped cells), and in between them smaller pigmented areas, the ends of the proximally tapering pigment cells ('89, Taf. II, Fig. 20). A section on the other side of the one first described, that is, one of the first through the vitreous body, would show pigment areas of the same size as the large ends of the pigment cells (the cone-shaped streaks of pigment in the vitreous body which according to Schewiakoff are associated with the pigment cell), and in between them the cross-sections of the rod-like processes from the visual cells, lying in canals in the clear homogeneous ground-substance of the vitreous body ('89, Taf. II, Fig. 18).

Let me give a resumé of Schewiakoff's conception of the structure of the retina.

a. There is an alternation of pigment and visual cells, the nuclei of the spindle-shaped visual cells lying at a lower level than those of the cone-shaped pigment cells.

b. From the visual cells extend rod-like processes into the vitreous body, lying in canals in the latter.

c. In the vitreous body a cone-shaped streak of pigment overlies each pigment cell of the retina, which is not a part of that cell.

d. Apart from these pigment streaks and the rod-like processes of the visual cells the vitreous body is structureless, probably a secretion of the pigment cells.

My own work, now, has led me to a different conception, so that my conclusions on the same points would be as follows:

a. There is not good evidence of an alternation of cone-shaped pigment cells and spindle-shaped visual cells, with the nuclei of the latter at a lower level than those of the former.

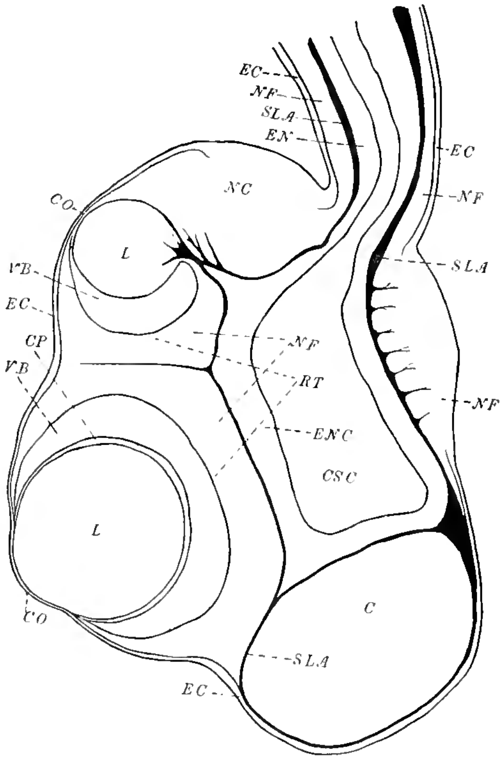
b. From some of the retinal cells otherwise not distinguished, there extend rod-like processes into the vitreous body, such as described by Schewiakoff.

c. The cone-shaped streaks of pigment in the vitreous body belong to the underlying pigment cells, in fact are direct continuations of them, and at their distal ends they are prolonged into fibrous processes lying in canals of the vitreous body exactly like the visual fibres of Schewiakoff.

d. The vitreous body is not a homogeneous secretion, but is composed of prisms of refracting substance, each with a denser central fibre.

Let us go over these four points in detail.

(a) As to the first, the question whether there is an alternation of pigment and visual cells, I am not prepared as yet to make a positive statement, since my not seeing both kinds as they are described has little evidential value against the fact that Claus and Schewiakoff both claim to have seen them. Perhaps proof could be obtained one way or the other by maceration of fresh or of specially prepared material, which none of us had. My evidence for not confirming alternation rests wholly upon sections. Fig. 58 represents a radial section through part of the larger eye of Charybdea, made from an osmic preparation which in this case showed two advantages over the material fixed in corrosive-acetic (usually by all odds the best), namely, that the vitreous body (*vb*) was not shrunken away from the retinal cells, as almost invariably happens, and that the retinal cells were contracted apart from one another in some places in such a way as to be almost equal to a macerated preparation. Now, in the figure it is seen that there is an apparent alternation of two kinds of cells, more regular than I usually find, but the ones that are undoubtedly the pigment cells of Schewiakoff are the ones that show the fibrous processes like his visual cells, and the pigment streaks in the vitreous body are seen to be integral parts of the cells, not cone-shaped masses lying in the vitreous body, merely associated with the pigment cells. If these *are* the pigment cells of Schewiakoff, the shorter cells in between must be his visual cells, yet they can by no means be said to conform to a spindle-shaped type, nor are their nuclei always at a lower level than (that is, internal to) those of the pigment cells. If the long cells with the fibres are, on the other hand, considered the visual cells of Schewiakoff, then again we find nonconformity to a spindle-shaped type, and nuclei not always at a lower level. The matter of alternation of nuclei at different levels seems to me any way too slight a distinction upon which to base a difference in function. It is a necessary mechanical consequence of the crowding together of many cells on one surface. And in many cases in perfectly radial sections through the retina I find the nuclei fewer in number and arranged in very nearly a single level. The retina of the smaller eye represented in Fig. 69 shows this. In sections further along in the same series the nuclei are found at different levels, due without doubt to the slanting cut.



[Dr. Conant did not complete Fig. 72, and the accompanying outline of Fig. 7 of Schewiakoff's memoir (Beiträge zur Kenntnis des Acalephenauges, Morph. Jahrb., Bd. XV, H. 1) has been substituted.—EDITOR.]

EXPLANATION OF LETTERS IN TEXT FIGURE.—*C*—concretion cavity; *CO*—cornea; *CP*—capsule of lens; *CSC*—cavity of sensory club; *EC*—ectoderm; *EN*—endoderm; *ENC*—endoderm of sensory club; *L*—lens; *NC*—network cells; *NF*—nerve fibres; *RT*—retina; *SLA*—supporting lamella; *VF*—vitreous body.

Fig. 72 is a horizontal section through the large eye, and shows that here, too, when the sections pass through the eye just radially, the nuclei are not found at different levels sufficiently definite to suggest two kinds of cells.

In the inner corner of the retina in the same figure (69) are seen cells without pigment which show nuclei undoubtedly at different levels. These cells in this position are a regular feature in the retina of the smaller eye. Schewiakoff considers them purely visual, because of the lack of pigment. In so doing it seems to me he forgets his own standard for discriminating beween pigment and visual cells. The pigment cells of the retina, according to him, are the same thing as the cone-shaped supporting cells found elsewhere in the nervous epithelium, and are, therefore, distinguished from the visual cells primarily by shape and by position of nucleus, secondarily by the greater development of pigment. When on the ground of pigmentation alone he calls the cells in the corner of the retina visual, he judges them by only the second test, and in so doing virtually admits, as it seems to me, that shape of cell and position of nucleus are matters of no great moment. His own standards place him in a dilemma. If on the other hand he judges by the lack of pigment, the cells are visual; if by shape of cell and position of nucleus, they are both visual and pigment cells without the pigment or supporting cells. What use there would be for simple unpigmented cells in one limited region of the retina is hard to see, so he naturally takes the other horn of the dilemma and calls them visual because they have little or no pigment.

The distinction, then, between pigment and visual cells is brought down to one of pigmentation only. Schewiakoff's test for this is that in the visual cells "Das Pigment durchsetzt aber nicht das ganze Protoplasma des centralen Zellenabschnittes, sondern ist auf seine Oberfläche beschrankt (Fig. 19, *sz*), so dass der innere, axiale, stark lichtbrechende Theil vollkommen frei von demselben ist." ('89, p. 37.) That is, in a section through the ends of the retinal cells each pigment cell will appear as a uniformly pigmented area, while each visual cell will appear as a light, strongly refracting spot with a ring of pigment around its periphery. This is the arrangement given in his Fig. 19.

An arrangement so definite ought to be easily made out in sections, yet I have not been able to find it so. My sections show considerable difference in the amount of pigmentation even in material preserved with the same killing agent. If the retina is heavily pigmented the ends of the cells have the appearance shown in Fig. 62, which represents a portion of a cross-section. The ends are seen as clearly defined polygonal areas differing among themselves in size, but not showing two types of size, or two kinds of pigmentation, the one uniform, the other a ring of pigment around a highly refracting central portion. If the retina is but slightly pigmented—and some were so light as to make depigmentation unnecessary—a difference is seen in the pigment, as shown in Fig. 63, but in no case were areas found that showed a highly refracting centre surrounded by a ring of pigment. (The unexplained structures in Fig. 63 will be referred to a little later.)

Figures 59–62 are a series of four successive sections drawn with the camera lucida for comparison with Schewiakoff's Figs. 20 and 19, and to show that the presence of two types of cells plainly marked within the retina by the position of the nuclei at different levels is at least not clearly demonstrated. Only the nuclei are drawn, since the cell bodies are not easily distinguished from the surrounding fibres. The eye is the same as that from which Fig. 72 was made. Fig. 59 shows a relatively small number of nuclei of slightly larger size than usual. These I take for two reasons to be nuclei of the ganglion cells that are found in the fibres at the base of the retinal cells (Figs. 58, *gc*, 69 and 72). They are the first nuclei struck in tracing sections toward the retina, and in the series from which Fig. 58 was taken similar nuclei appeared in both transverse and radial cuts through the retina stained brightly and clearly with hæmatoxylin, whereas the nuclei of the retinal cells proper were stained a diffuse brownish-yellow from pigment that had evidently gone into solution. Fig. 60 shows the closely aggregated, smaller nuclei of the retinal cells surrounded by the nuclei of the outlying ganglion cells. Schewiakoff's corresponding drawing ('89, Fig. 20) shows at this level a definite alternation of the bodies and nuclei of unpigmented visual cells, with the smaller, pigmented, proximal processes of the pigment cells. In the next section (Fig. 61) the pigmented ends of a few of the cells have been struck, and the following section (Fig. 62) shows that, in this heavily pigmented specimen at least, there is no good evidence within the retina itself of two kinds of cells, so that it is apparent that at any rate we cannot accept Schewiakoff's conception of the structure.

(b) Yet the fibres that Schewiakoff observed and associated with special visual cells occur beyond question. Fig. 64 is a drawing of the first cut through the vitreous body of Charybdea, and in among the sections of the pigment streaks are seen sections of processes lying within clear spaces exactly as Schewiakoff figures his visual fibres ('89, Taf. II, Fig. 18). That the fibres occur is indisputable, but as to the cells to which they belong I can say nothing except that from such evidence as I have given in the preceding paragraph I conclude that they come from pigmented retinal cells of not very different type within the retina from the others, if different at all.

(c) On the third point, that the pigment streaks in the vitreous body belong to underlying cells and are continued distally into fibrous processes like the visual fibres of Schewiakoff, the evidence is decisive. Fig. 58 has already shown it, and if this were not enough, a case of unusual stoutness of the fibres drawn in Fig. 67 is conclusive. The preparation from which the section is taken was one preserved with corrosive-acetic, and I have drawn the outlines with the camera in order to avoid exaggeration of the fibres as far as possible, and also to show the shrinkage of the vitreous body (*vb*). It is the shrinkage of the vitreous body that makes it so difficult to determine the exact relation of structures seen in the vitreous body to the retina. The fibrous processes run through the vitreous body to the "capsule" of the lens (*cp*) (see also Fig. 72), a layer of homogeneous substance much resembling that of the vitreous body, which is classed as a part of the vitreous body, but usually in the shrinking adheres to the lens. The capsule is therefore regarded by Schewiakoff as a secretion of the lens cells. Some fibres were found by him to have the appearance of branching upon reaching the surface of the capsule, others of passing through it and of seemingly ending among the cells of the lens. The same appearances were given in my sections. It is altogether impossible in the distal portion of the vitreous body to distinguish between the fibres of Schewiakoff and those that come from the long pigment cells. (Figs. 64–66 represent the appearance of the vitreous body at successive levels, and are from the same series of sections as Figs. 59–62 and 72.) In Fig. 64 the sections of the processes that Schewiakoff calls visual are easily distinguished from the sections of the long pigment cells. In Fig. 65, which is two or three sections nearer the lens, the pigment cells are shown by their cross-sections to be tapering down, and in Fig. 66, nearer still to the lens, the two kinds of processes are no longer to be distinguished from each other. In a few cases I have found pigment in a fibre which but for this would be called one of the visual fibres of Schewiakoff. Such considerations as these, the similar appearance in cross-section, the finding of pigment in a few cases, and the inability to trace to any readily distinguished special type of retinal cell, make me wonder whether the visual fibres of Schewiakoff are anything more than the distal processes of pigment cells, into which the pigment granules happened not to be produced at the moment of fixation.

Fig. 63, however, where the retina was only slightly pigmented, rather speaks against this view, for the number of darkly pigmented areas seen here (which are shown beyond question by radial sections to belong to the long pigment cells) is not great enough to account for the number of both pigment areas and visual fibres of Schewiakoff seen in such a section as Fig. 64. This would throw the visual fibres of Schewiakoff back upon some of the slightly pigmented cells of Fig. 63, otherwise not distinguished. I think the question cannot be settled without the maceration of fresh material, and experiments upon eyes killed in the light and in the dark.

In such cases as that of Fig. 63 it would seem conclusively shown that the long pigment cells must belong to a different type from the short, but as I have already said I can find no regularity in either their shape or in the position of their nuclei. And on the other hand Fig. 58 shows that the reverse relation may obtain and the long cells be less deeply pigmented on the edge of the retina than their shorter neighbors, so that it looks as if all the short cells had to do was to project half their pigment out into the vitreous body in order to become exactly like the long ones. This they could do if, as is possibly the case, they are prolonged into "visual fibres" of Schewiakoff that have escaped observation and so do not appear in the drawing.

Fig. 58 shows one more thing that is worthy of remark in passing. In the preparation in which the vitreous body (at this point at any rate) was not shrunken away from the retina, the fibre from each long pigment cell does not lie in a clearly defined space or "canal," such as is usually described as a constant structure of the vitreous body. Very likely these canals are formed only by shrinkage around the fibres, and the irregular shape of the spaces around the three fibres in Fig. 67 rather bears out the same supposition.

As to the structure of the vitreous body, apart from the fibres and pigment streaks already mentioned, I find it to be made up of prisms extending from retina to capsule of lens, each containing a central axis or fibre. Fig. 64 shows that the space around the pigment areas and "visual fibres," instead of being homogeneous, is wholly filled with the polygonal cross-sections of these prisms. In Charybdea they are generally more difficult to perceive than in my best material of Tripedalia which was killed in acetic acid. In this the polygonal areas stood apart from each other more plainly. Curiously enough I have been unable to demonstrate in Tripedalia the "visual fibres" of Schewiakoff. Here and there were found spaces that at first sight reminded of them (Fig. 68, *sh*), but they contained no central fibre, and were probably due to shrinkage. The polygonal areas themselves, however, often contained a clear spot in the centre, at one side of which would be found the cross-section of the fibre, as is shown in many cases in Fig. 68. The clear spot is here undoubtedly due to shrinkage of the gelatinous substance of the prism.

I think that these prisms and fibres are the direct continuations of retinal cells. In a section such as that drawn in Fig. 63, which takes just the very tops of the cells of a slightly pigmented retina, in the centre of the section just grazing the space that lies between the retina and the shrunken vitreous body, most of the cells toward the middle (where especially the extreme tips are taken) show in their centres a dot exactly corresponding to the dots in the polygonal areas of the vitreous body. In the exact middle of the section, where only the cell walls appear, slightly indicated, a dot is seen in each case. The size and shape of the ends of the cells correspond with those of the polygonal areas in the vitreous body, and I do not doubt that the latter are continuations of the former. The vitreous body, then, instead of being homogeneous, is composed of the clear highly refracting outer ends of retinal cells. The assumption lies near that these are the true visual rods, but of course it is assumption only.

To give a brief review, the points in which my conclusions differ from those of Schewiakoff are as follows: I find (1) that the long pigment streaks are parts of retinal cells continued into processes like his visual rods; (2) that the vitreous body is composed of prisms with central fibres proceeding from retinal cells; (3) that I am unable to get satisfactory evidence of two types of cell distinguishable within the retina, and at any rate find considerable evidence against the two types he distinguishes.

These results are not wholly satisfactory, for they leave us with three kinds of fibrous processes in the vitreous body which for the present we are unable to trace to three, or even two distinguishable types of cell in the retina. It would be more pleasing if we could confirm Schewiakoff's simple conception of the structure, with its one set of visual rods in the vitreous body referable to a clearly marked type of sensory cells in the retina, but I think the evidence that has been brought up justifies the conclusion that in some respects he saw too much, in other respects too little. This is not to be wondered at, since his material, to judge from a single statement, consisted of but twelve marginal bodies, and, moreover, the work on Charybdea forms but one portion of a paper that is excellent for the clearness of its descriptions and illustrations.

Before leaving the subject I must mention that Wilson suggested from his observations on Chiropsalmus that the vitreous body had a prismatic structure, but he was probably mistaken when he thought he found evidence of nuclei in it. Claus says that the retina is composed of pigment and rod cells alternating, and Wilson agrees with him, but under a sketch of a sense cell from the nerve he makes the express statement "not very well preserved." It seems very probable, therefore, that he followed Claus's interpretation rather than independent observations, and Claus interpreted his results very much by analogy of what had been found in other forms.

The smaller complex eye which is represented in Fig. 69 agrees in structure very closely with the larger. The chief differences are that sections do not show pigment extending into the vitreous body, that there is no "capsule" to the lens, and that the lens seems to be supported by a kind of stalk formed by a thickening of gelatine of the supporting lamella (*sl*). The gelatinous thickening lies between the lens and an outgrowth of endodermal cells (*en*) from the canal of the club. This outgrowth is a constant feature, figured by Claus and Schewiakoff for Charybdea, and by Wilson for Chiropsalmus, and found in Tripedalia also. The regularity of its appearance in all three genera leads one to suspect that it may have some significance not yet understood.

Just above the smaller eye there lies a mass of cells of peculiar structure (Fig. 69, *nc*). They are of a rounded polygonal contour, with a comparatively small circular nucleus in the centre, and are found in this region only. In and amongst them bundles of fibrous tissue are found in the sections, which pass from the surface cells to the supporting lamella. Claus describes the contents of these cells as coarsely granular protoplasm and says they cannot be taken for ganglion cells. He is inclined to believe that they play the part of a special supporting tissue. Schewiakoff, on the other hand, is convinced that they are ganglion cells, and finds processes passing out from them ('89, Taf. II, Fig. 22). I find, however, that the cell contours are perfectly regular and clearly without processes, and it is incomprehensible to me how, if his material was at all well preserved, he could for a moment have taken them for the same thing as the big multipolar ganglion cells with large nucleus and nucleolus which lie in about the same region and were correctly described and figured by Claus but are not specially mentioned by Schewiakoff. I cannot agree with Claus, however, that their contents are composed of coarsely granular protoplasm. That which appears such by low magnification shows itself under high powers to be a beautiful network with thickenings at the nodes of the meshes, which is brought out very plainly by a cytoplasmic stain such as Lyons blue. Around the nucleus is seen a more or less well-defined clear zone. What the function of the cell is remains as unknown to me as to Claus and Schewiakoff.

There is left one more point in reference to the nervous system upon which I wish to say a word. Claus and Schewiakoff both describe the wall of the crystalline sac as structureless, formed by the bare supporting lamella. The credit is due to H. V. Wilson of finding in Chiropsalmus that it has a special lining of epithelial cells, which he figures as a continuous, flattened layer. In both Charybdea and Tripedalia I find traces of the same in nuclei here and there, but whether they are the remains of a once continuous layer or not the sections do not show satisfactorily.

This ends the account of what it seemed worth while to say at present upon the nervous system. In concluding, the writer wishes to express his thanks for the help afforded by Dr. Wilson's notes, in particular on the subject of the vascular lamellæ, and desires to make especial acknowledgment of his indebtedness to Professor Brooks, whose suggestions, based upon many years of experience with the Medusæ, have been most welcome and helpful, and whose evidences of unfailing kindliness, both in Jamaica at the time the material was obtained and in Baltimore when it was being studied in the laboratory, take a most honored part in the pleasant memories associated with the work.

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TABLE OF REFERENCE LETTERS.

afr = adradial furrow.
afr' = furrow in Tripedalia that separates perradial from interrad. regions in lower half of bell. (In Charybdea the same furrow is directly continuous with *afr*.)
ax = axis of nerve.
c = concretion.
cc = canal underneath *ivl*, connecting the two adjacent marginal pockets.
ecl = circular canal.
ei = cilia.
cm = circular muscle.
co = cornea.
cp = capsule of lens.
cs = covering scale of niche.
csc = canal of sensory club.
cl = canal of tentacle.
ct' = beginning of canals of lateral tentacles in Tripedalia.
ec = ectoderm.
ece = ectoderm of exumbrella.
ecs = ectoderm of subumbrella.
ed = distal paired eye.
el = larger unpaired eye.
en = endoderm.
enc = endoderm of sensory club.
enf = tract of nerve fibres underlying endoderm.
enfl = endoderm of floor of stomach.
enp = endoderm of stomach pockets.
enr = endoderm of roof of stomach.
ens = endoderm of stomach.
ep = proximal paired eye.
es = smaller unpaired eye.
fc = funnel leading into canal of sensory clubs.
fp = fibre from subepithelial plexus of subumbrella.
fph = filaments of phacellus.
frn = frenulum.
ft = funnel-shaped depression in ectoderm axial to base of tentacle.
g = gelatine.

gc = ganglion cell.
ge = gelatine of exumbrella.
go = gastric ostium.
gs = gelatine of subumbrella.
hvl = horizontal vascular lamella.
i = interradius.
if = interradial funnel of bell cavity.
ifr = interradial furrow.
ivl = interradial vascular lamella.
l = lens.
lv = lip of valve.
m = bell margin.
mc = mucous cell.
mep = mesogonial pocket.
mo = mouth.
mp = marginal pocket.
mp' = smaller marginal pockets, in Tripedalia.
mst = muscle of stock of sensory club.
mt = muscle at base of tentacle.
n = nerve.
nc = network cells, in sensory club.
nf = nerve fibres.
nm = nematocyst.
nst = nerve of stalk of sensory club.
osn = outline of sensory niche.
p = perradius.
pe = pedalium.
ph = phacellus.
pr = proboscis.
r = reproductive organ.
rc = remains of concretion.
rcl = radial canal.
rg = radial ganglion.
rm = radial muscle.
rn = radial nerve.
rns = root of nerve of sensory club.
rs ? = remains of stalk (?) of sensory organ.
rt = retina.
s = stomach.
sc = bell cavity.
scl = sensory club.
scn = supporting cell of nerve.
se = sensory epithelium.
sh = shrinkage space.
sl = stalk of lens.
sla = supporting lamella.
sn = sensory niche.
so = sensory organ in proboscis of Tripedalia.
sp = stomach pocket.
sph = stalk of phacellus.
ss = stalk of sensory organ, in proboscis.
st = stalk of sensory club.

su = suspensorium.
sub = subumbrella.
tl = lateral tentacle.
tm = median tentacle.
v = velarium.
va = vacuole.
vb = vitreous body.
vc = velar canals.
ve = edge of velarium.
vfs = visual fibres, according to Schewiakoff.
vg = valve of gastric ostium.
vl = vascular lamella.
vlc = vascular lamella connecting *vls* with *vlm*.
vlm = vascular lamella of margin.
vls = vascular lamella of sensory niche.
vlst = vascular lamella of sensory niche at base of stalk.
wc = wandering cells.
w–x–y–z = successive levels of Figs. 40–43 on Fig. 5.

DESCRIPTION OF FIGURES.

Fig. 1. Charybdea Xaymacana, from one of the four interradial sides.

Fig. 2. The same from above.

Fig. 3. The same from below, the four tentacles cut off.

Fig. 4. The same cut in halves vertically (or radially) through a perradius.

Fig. 5. The same cut in halves vertically (or radially) through an interradius.

Figs. 6–16. Diagrams of horizontal (or transverse) sections through C. Xaymacana at successive levels.

Fig. 17. Tripedalia cystophora, from one of the four interradial sides.

Fig. 18. The same from below.

Fig. 19. The same cut in halves vertically through a perradius.

Fig. 20. The same cut in halves vertically through interradius.

Figs. 21–30. Diagrams of horizontal sections through T. cystophora at successive levels.

(The following are of Charybdea, except when specially stated otherwise.)

Fig. 31. Horizontal section through the suspensorium.

Fig. 32. Diagram of a gastric ostium seen from the stomach side.

Fig. 33. Diagram of a vertical section through a gastric ostium.

Fig. 34. Diagram of a horizontal section through a gastric ostium.

Fig. 35. Diagram to illustrate the formation of the central and peripheral gastrovascular systems of a Hydromedusa (*a*, *b*, and *c*) and a Cubomedusa (*d*).

Fig. 36. Vertical section through the upper part of the bell, adradial, to show horizontal vascular lamella.

Fig. 37. Vertical section through the perradius, to show vascular lamella of the niche of the margin.

Fig. 38. Vertical section a little to one side of the last, to show same structure.

Fig. 39. Horizontal section through the upper part of the sensory niche, to show vascular lamella of the niche.

Figs. 40–43. Horizontal sections through the base of a pedalium at successive levels, *w–x–y–z*. Fig. 5, to show marginal lamella.

Fig. 44. Diagram to show relations of sensory niche, of bell margin and velarium in adult Tripedalia. The velarium represented as pendant.

Fig. 45. To show the same structure in a young Tripedalia.

Fig. 46. Horizontal section through the last just at the margin, to compare with Fig. 29.

Fig. 47. Cross-section through the nerve ring.

Fig. 48. The structure of the nerve as seen by focusing at successive levels.

Fig. 49. Diagram to show the relation of the nerve ring to the sensory club.

Fig. 50. Horizontal section through the upper part of the sensory niche, to show passage of nerve root through gelatine of subumbrella to stalk of sensory club.

Fig. 51. Vertical section through base of stalk of sensory club, to show same passage.

Fig. 52. Similar section to last, but nearer to perradius, to show sub-endodermal tract of nerve fibres.

Fig. 53. Sensory organ in proboscis of Tripedalia, as seen from surface in living animal.

Figs. 54 and 55. Sections of same sensory organ.

Fig. 56. Vertical section through one side of proboscis, to show sensory organ attached to endoderm. (Tripedalia.)

Fig. 57. Diagram of the outlines of sensory club seen from the side, by camera lucida.

Fig. 58. Part of retina of larger complex eye cut radially.

Figs. 59–62. Four sections in direct sequence through retinal cells transversely, larger eye.

Fig. 63. Transverse section through the tips of cells of a slightly pigmented retina, larger eye.

Figs. 64–66. Three transverse sections through vitreous body at different levels. All from same series, but not in direct sequence ; larger eye.

Fig. 67. Radial section through retina, to show fibres from the long pigment cells ; larger eye.

Fig. 68. Transverse section through vitreous body of Tripedalia near retina.

Fig. 69. Vertical section through smaller complex eye.

Fig. 70. Wandering cells, Charybdea.

Fig. 71. Floating mass, from stomach pocket of Tripedalia.

Fig. 72. Horizontal section through larger complex eye. (See text figure, p. 50.)

VITA.

The writer of the foregoing dissertation, Franklin Story Conant, the son of Farley Franklin and Emily Wilbur Conant, was born in Boston, Massachusetts, September 21, 1870. His preliminary education was received in the public schools of Boston and the vicinity. In 1887 he entered the University of South Carolina, at Columbia, South Carolina, where he spent two years. In the fall of 1890 he entered Williams College and was graduated from there in 1893 with the degree of Bachelor of Arts. In the spring of 1894 he joined the Marine Biological Laboratory of this University at Beaufort, North Carolina, and in the fall of the same year entered upon a course of studies for the degree of Doctor of Philosophy, comprising Zoology as the chief subject, Physiology and Botany as the subordinates.

Two months of the summer of 1895 were spent at Beaufort again, chiefly in investigations upon the Chætognaths. In 1896 three months were spent with the Marine Laboratory in Jamaica. In June of 1895 he was appointed to a fellowship in Zoology, and in the following year was made a Fellow by courtesy.

Biological Laboratory, Johns Hopkins University.

Fig. 1.

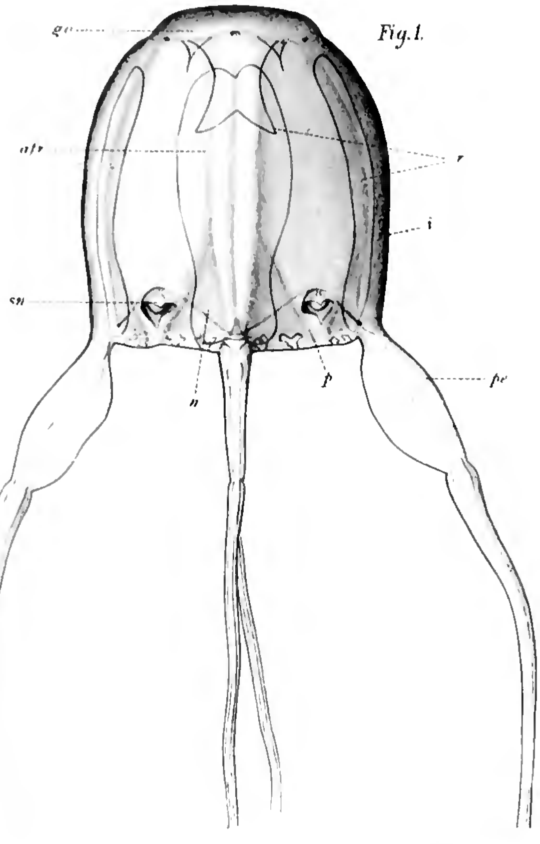
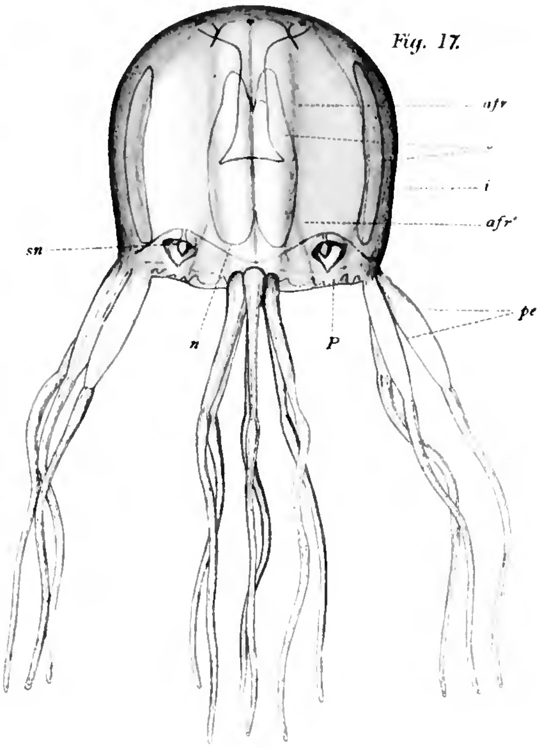


Fig. 17.



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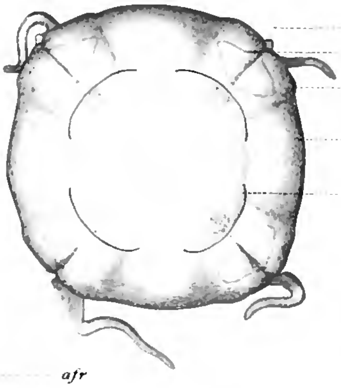

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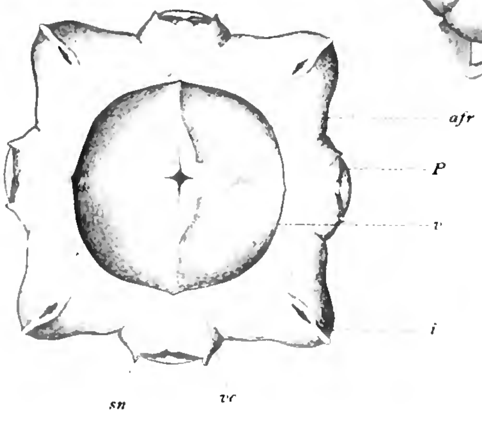

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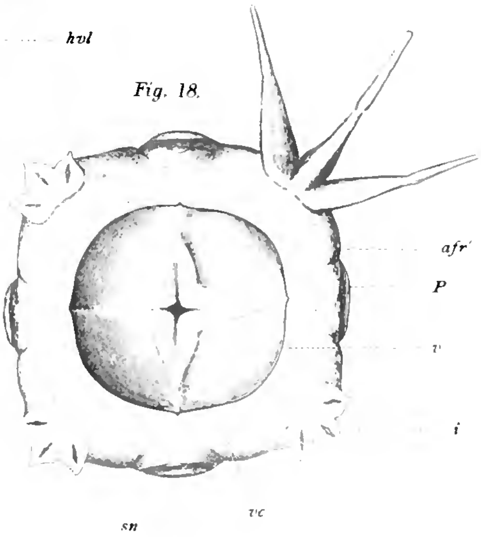

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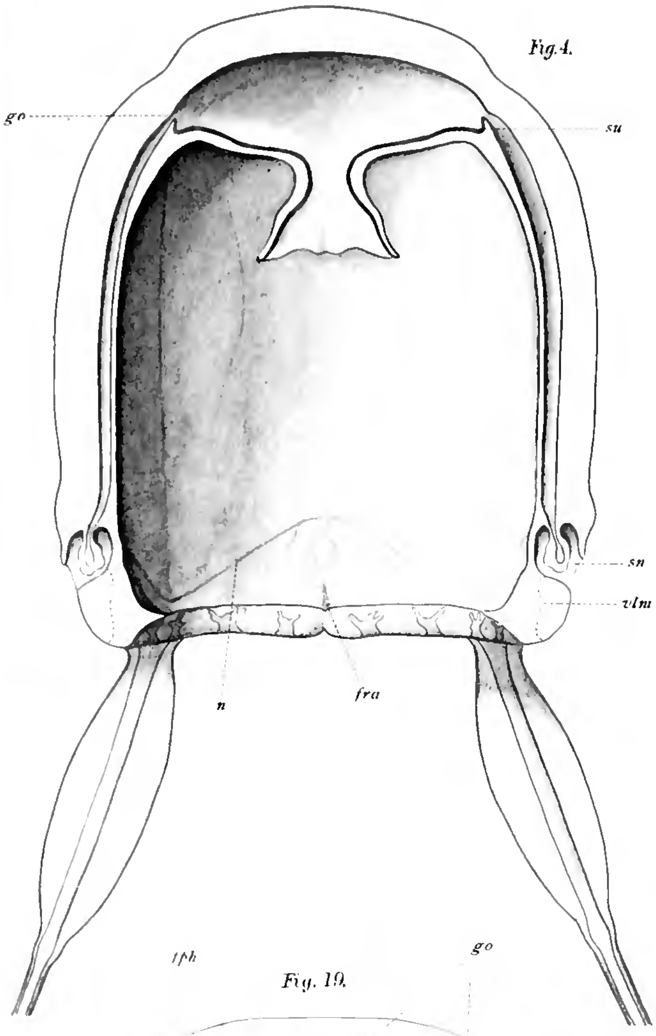
Fig. 4.



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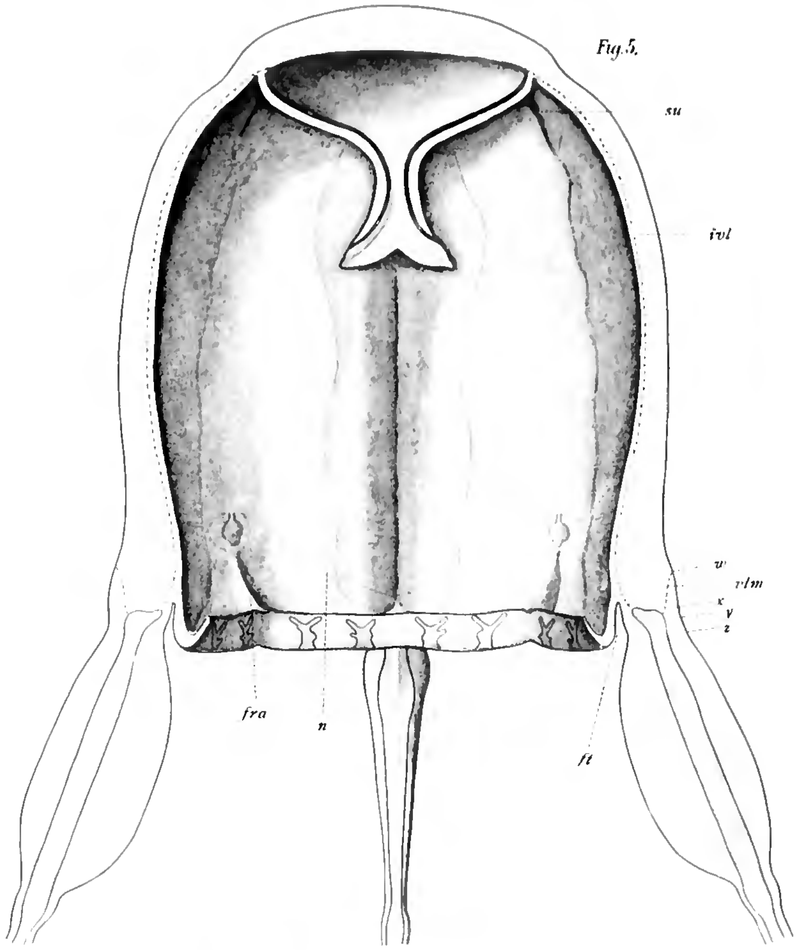

Fig. 19.

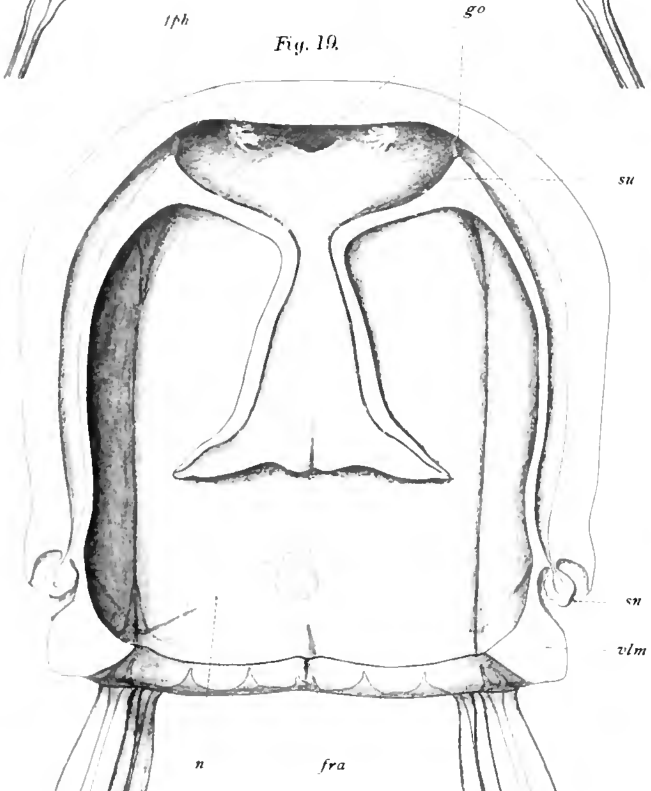

Fig. 20.

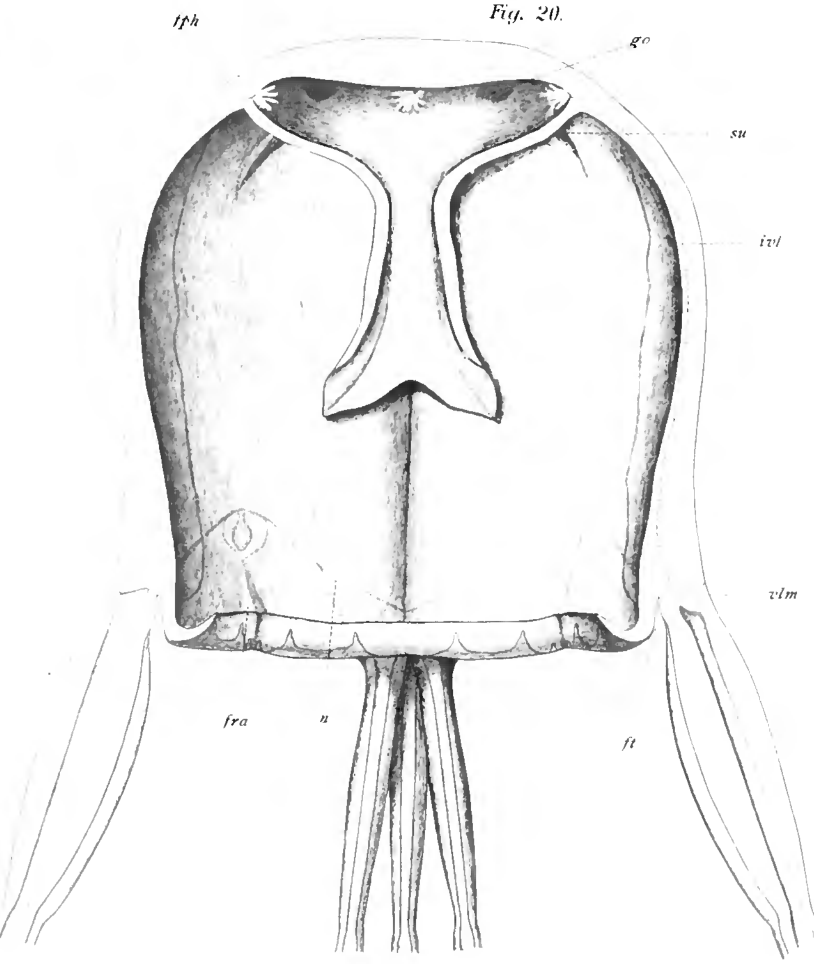

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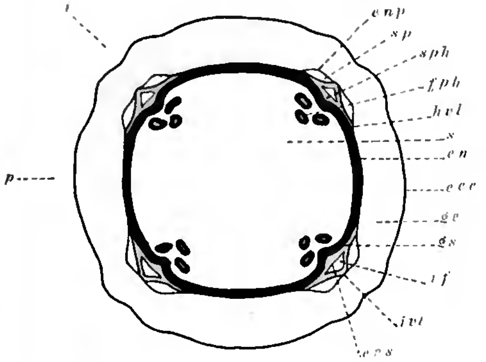
Fig. 6.



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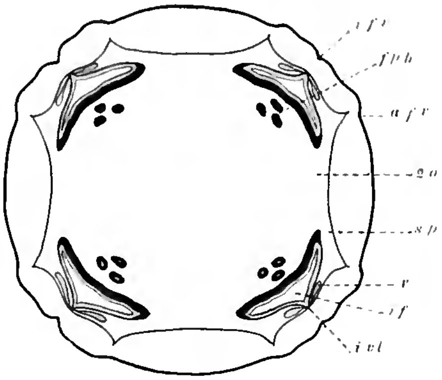

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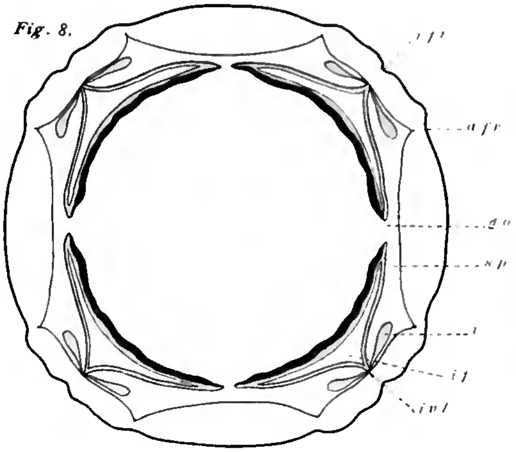

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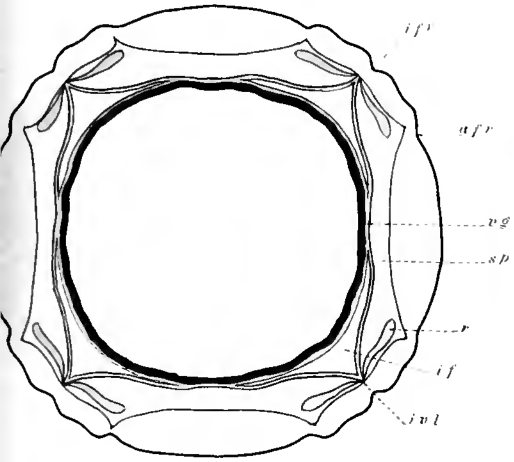


Fig. 10.

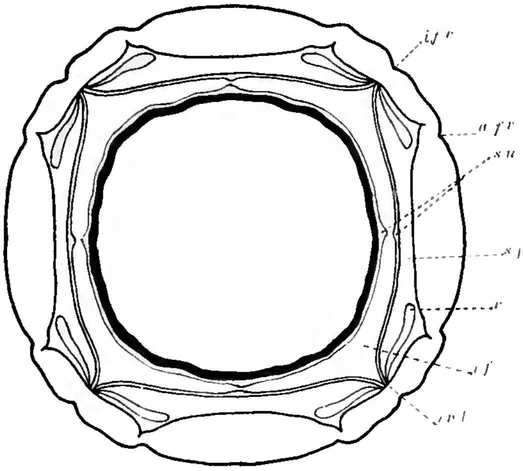
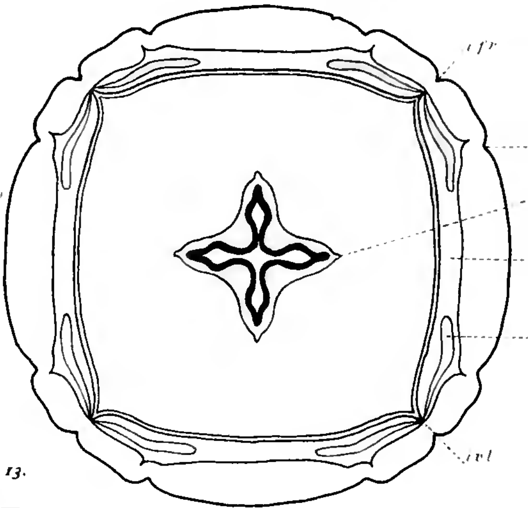


Fig. 11.



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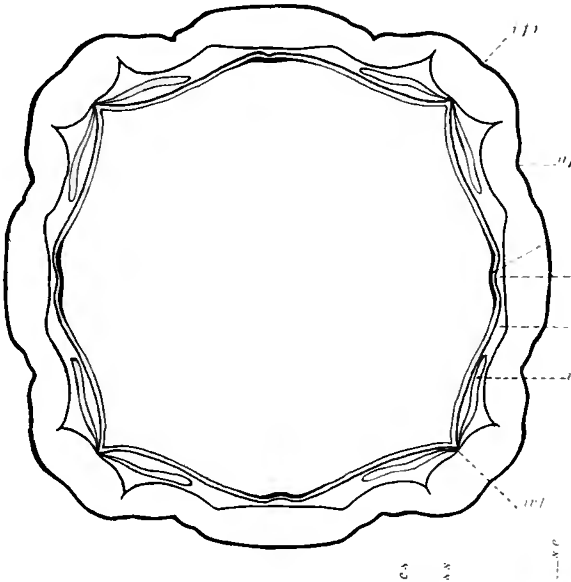

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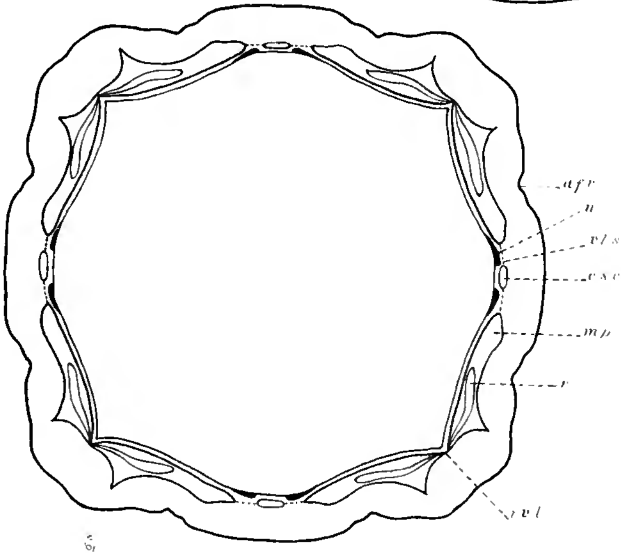

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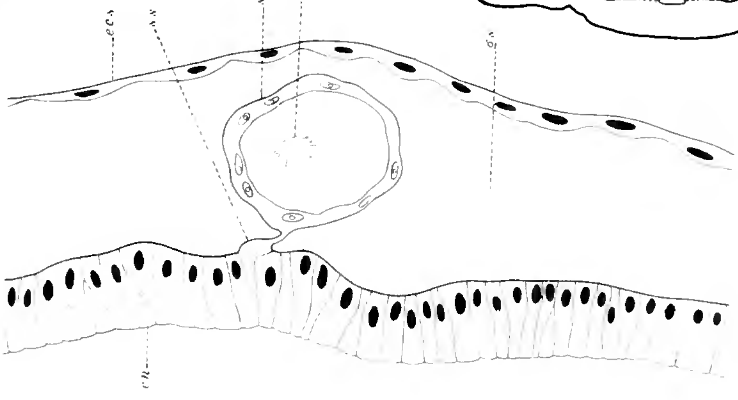
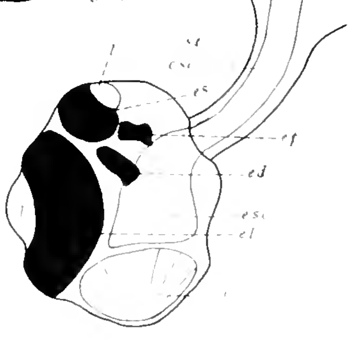


Fig. 57.



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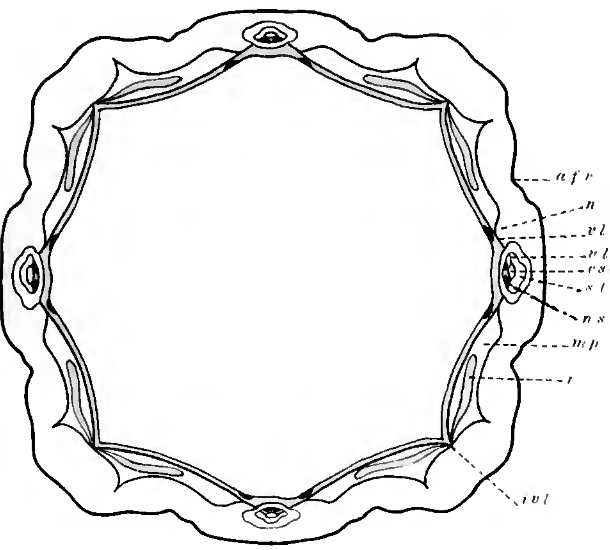

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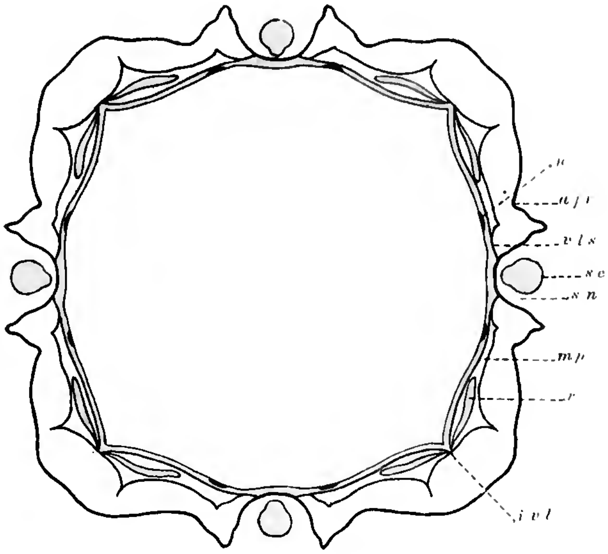

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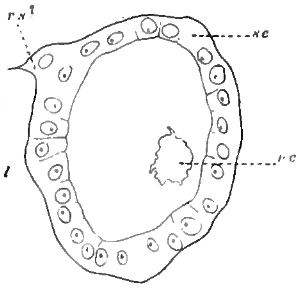

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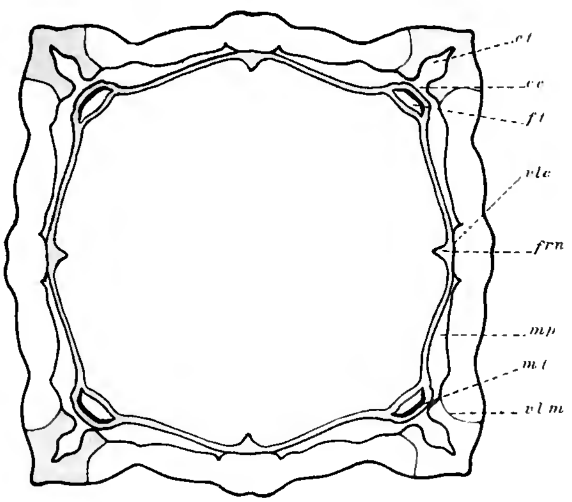

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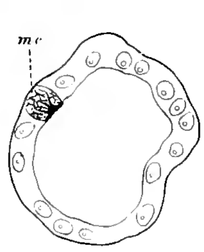

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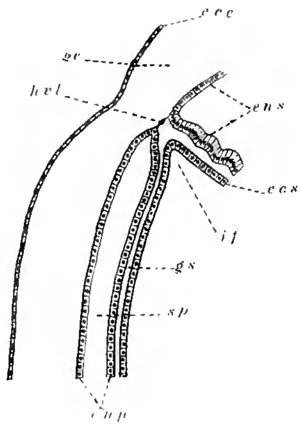

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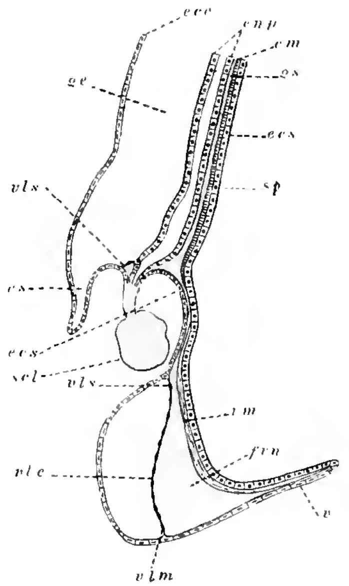

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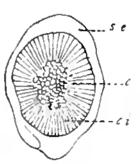

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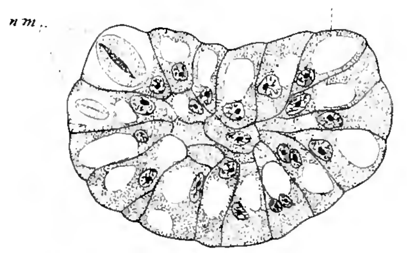

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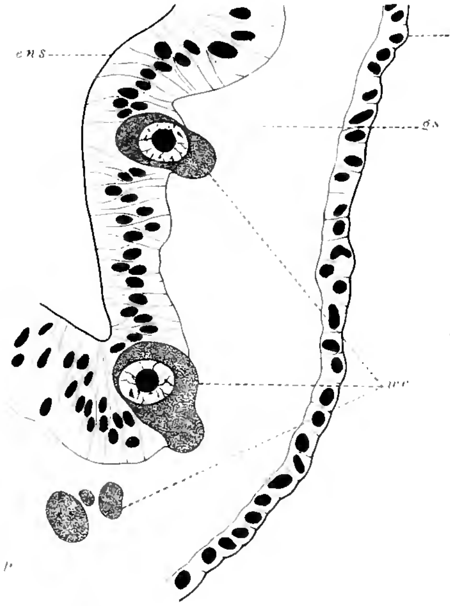

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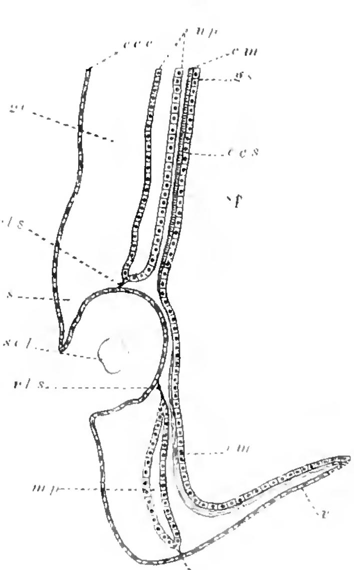

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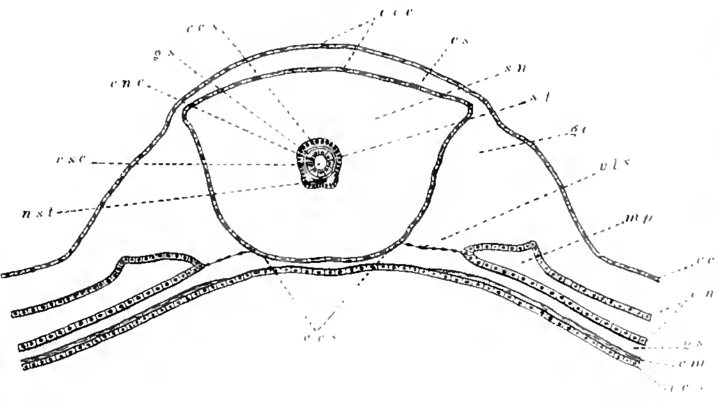

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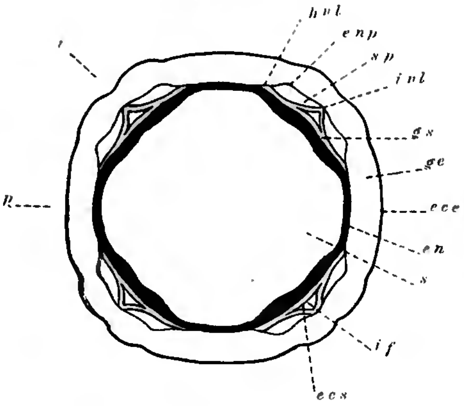

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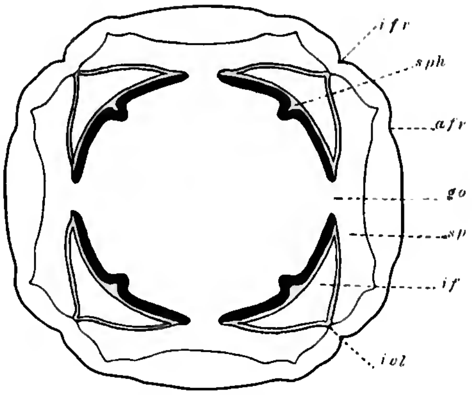

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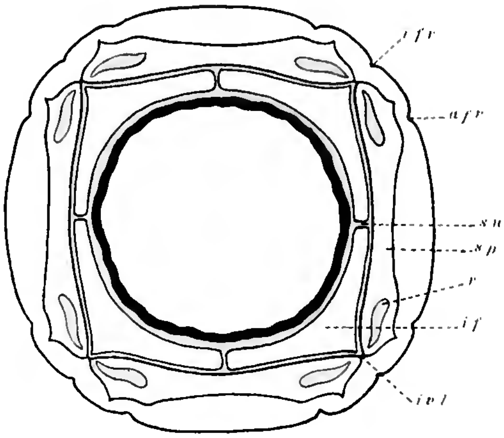

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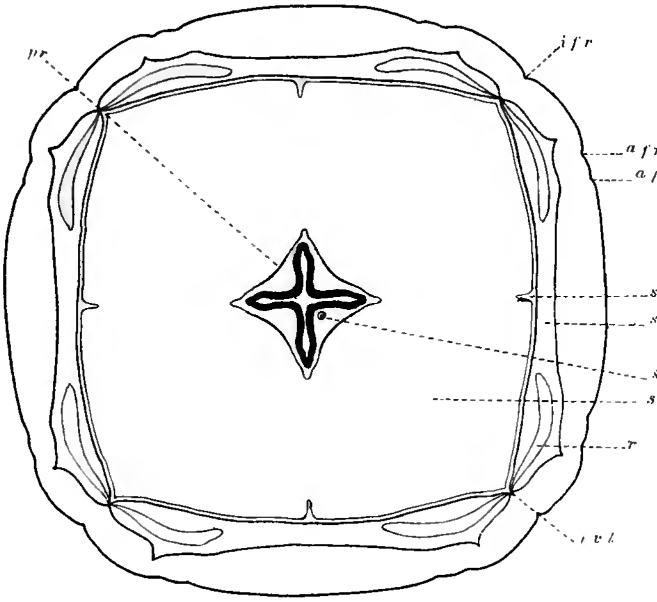

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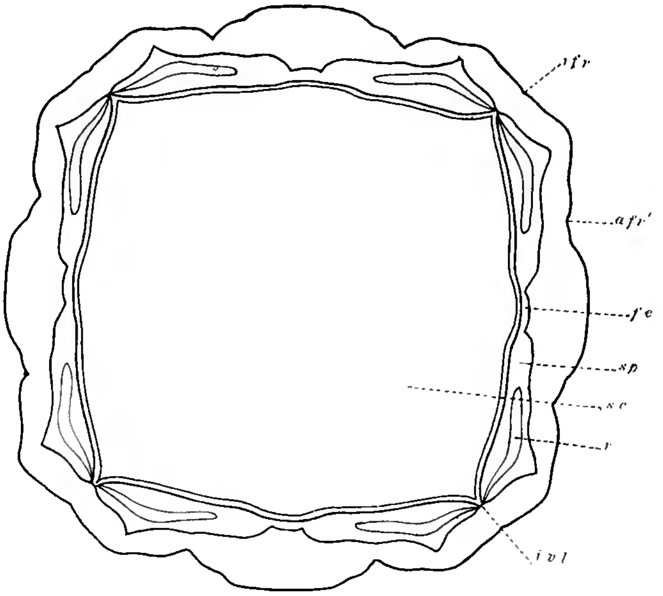

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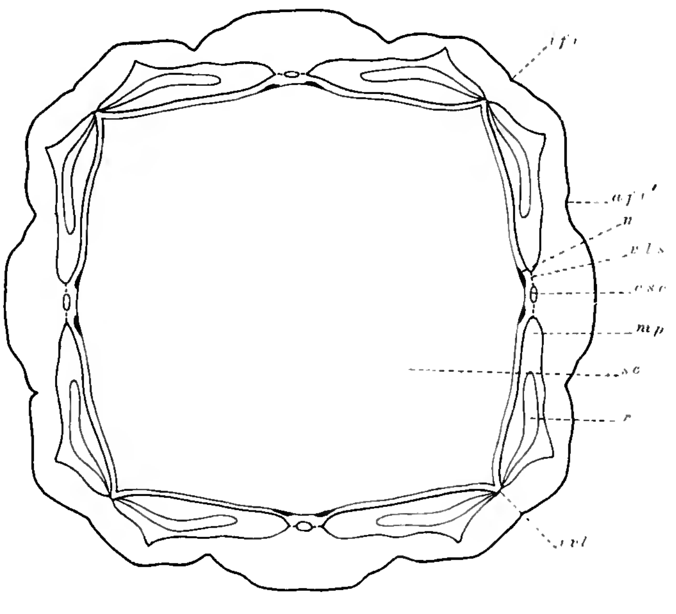

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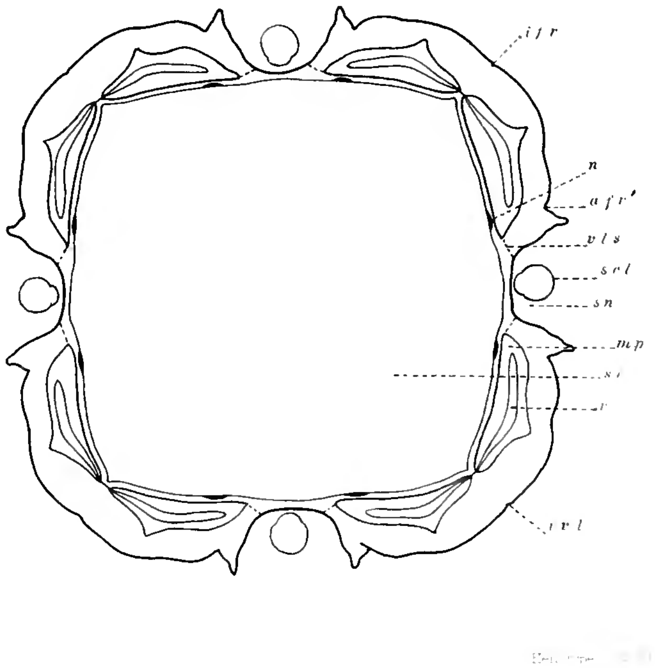

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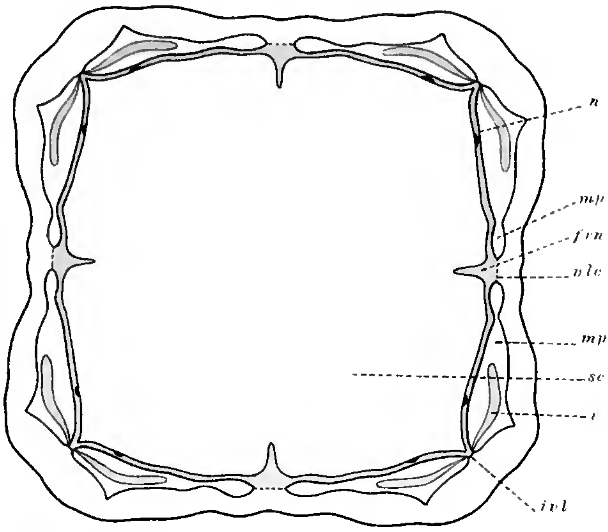

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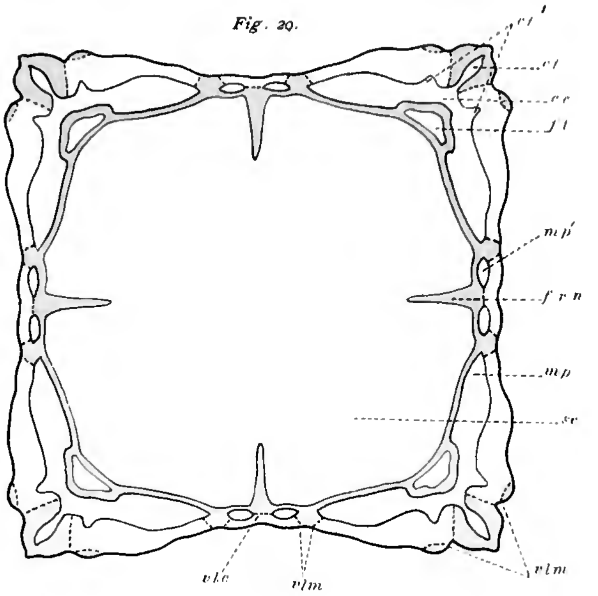

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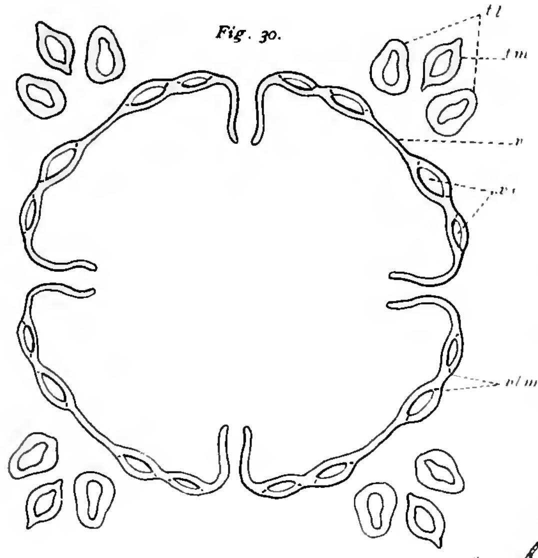

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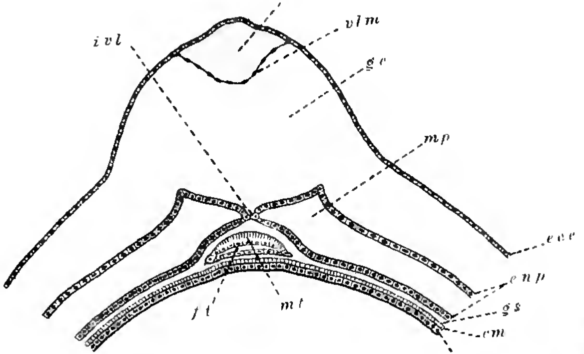

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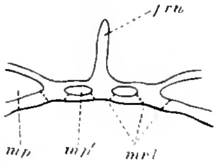

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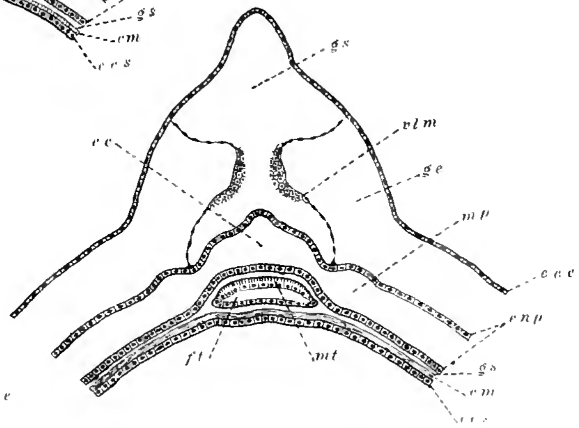

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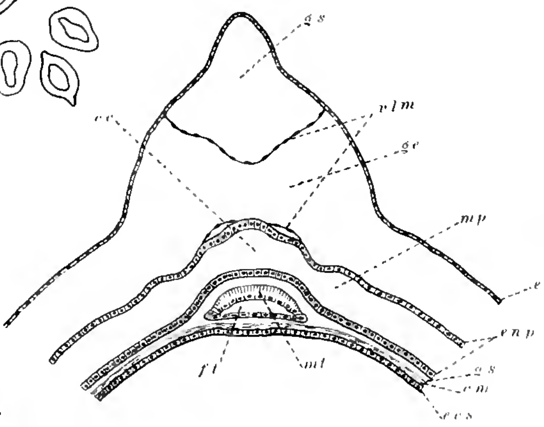

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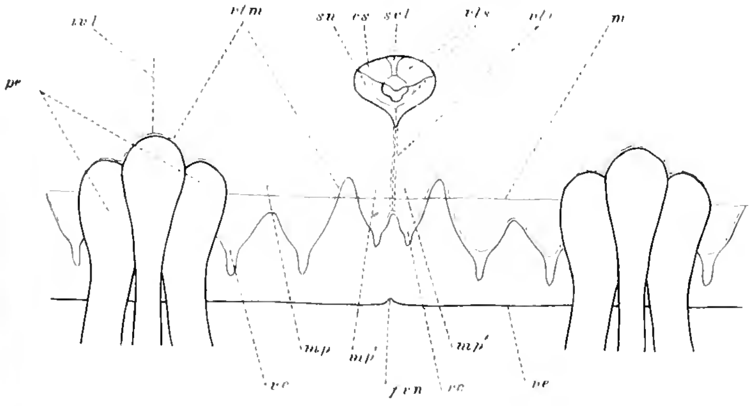

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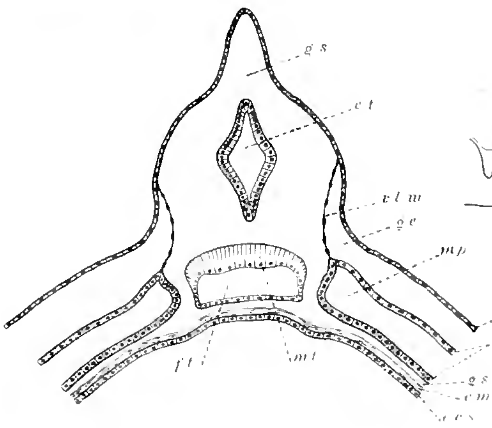

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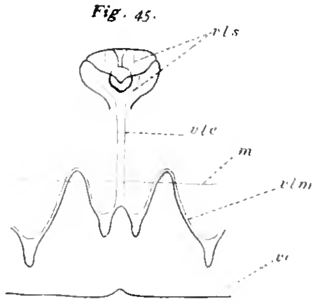

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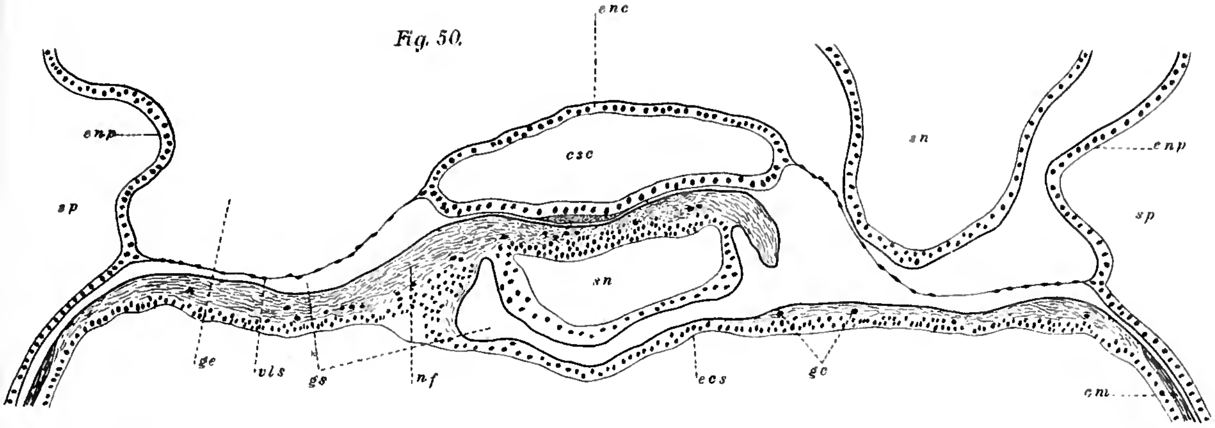

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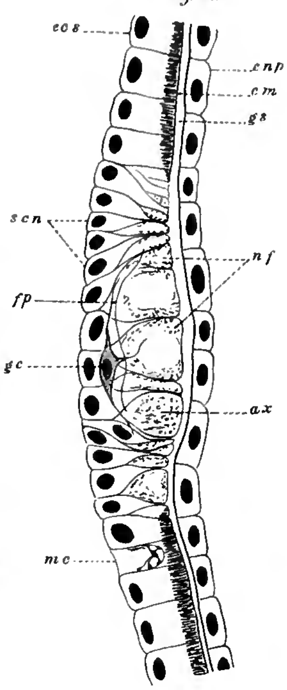

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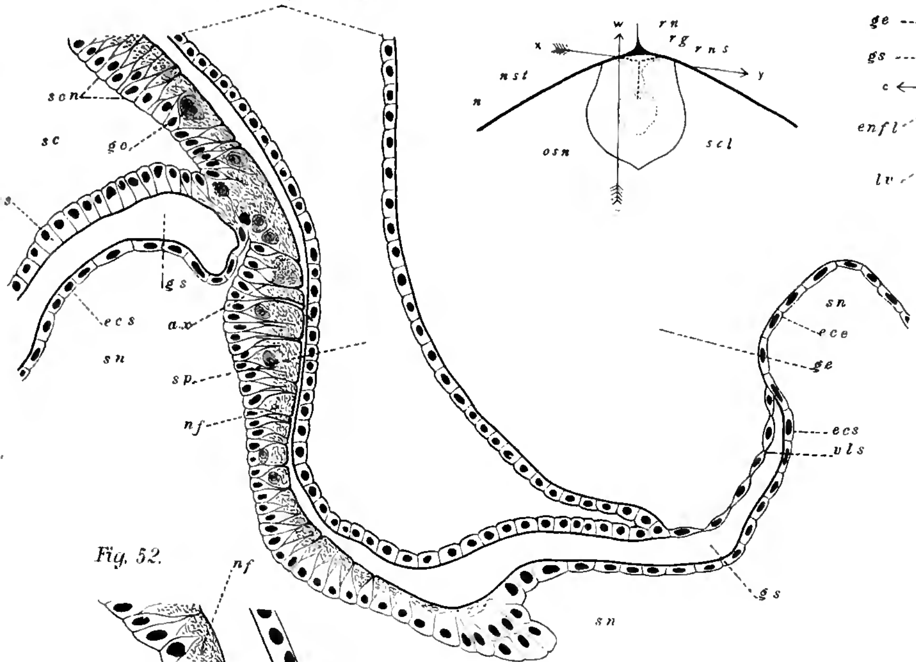

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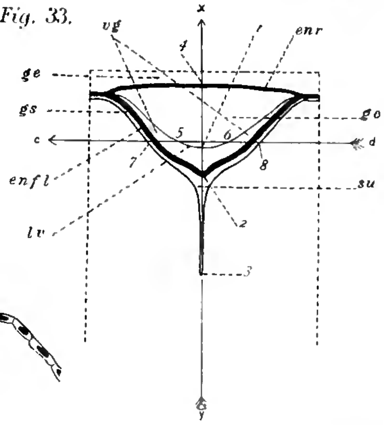
Fig. 33.



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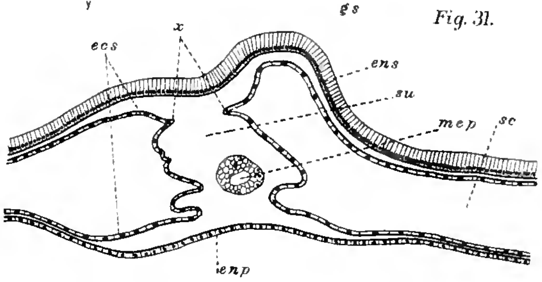

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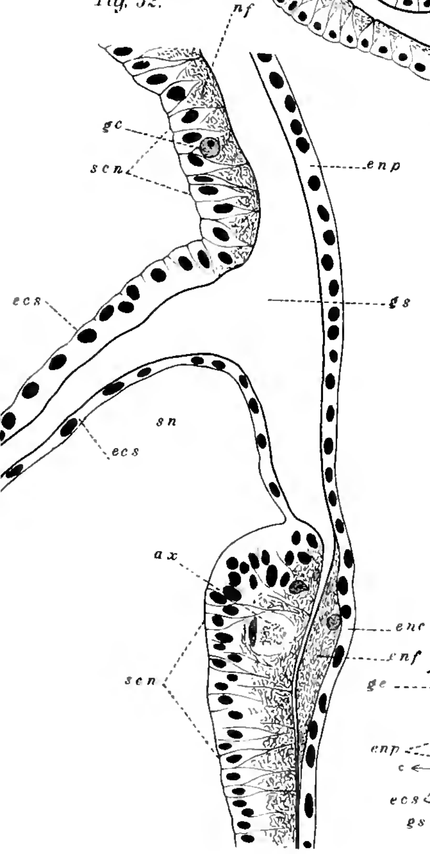

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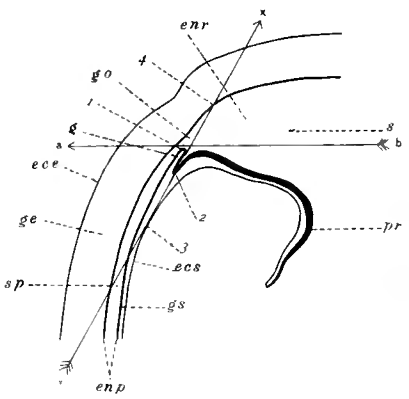

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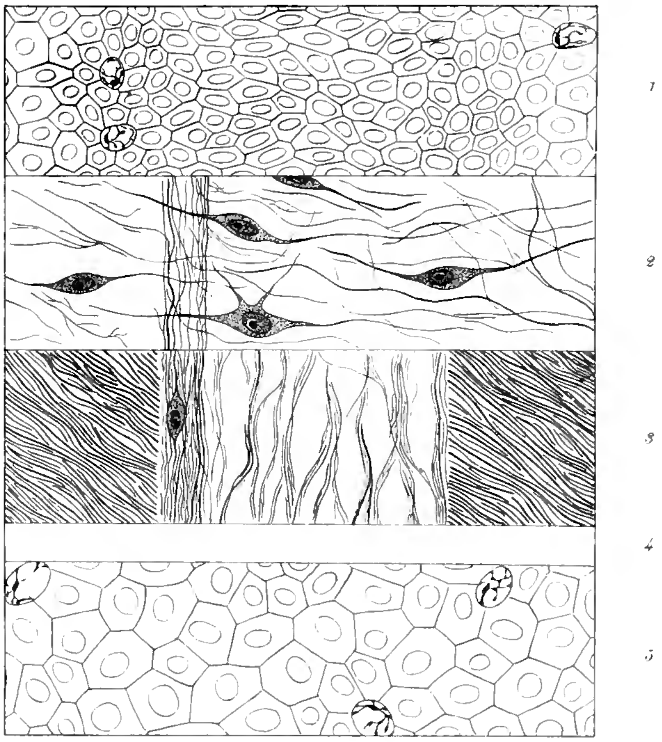

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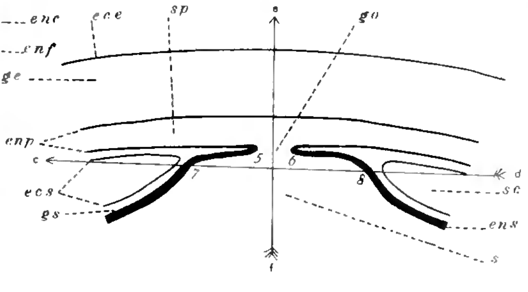

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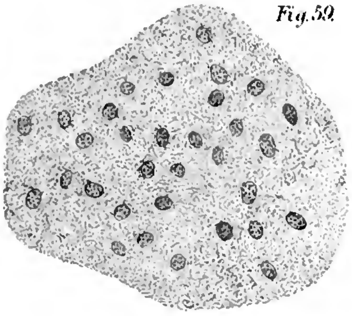

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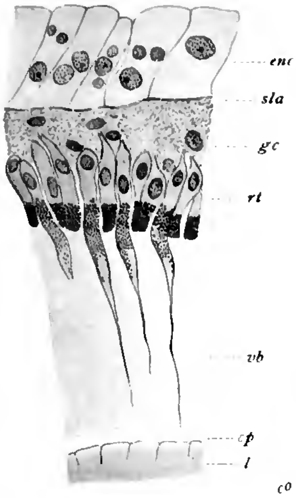

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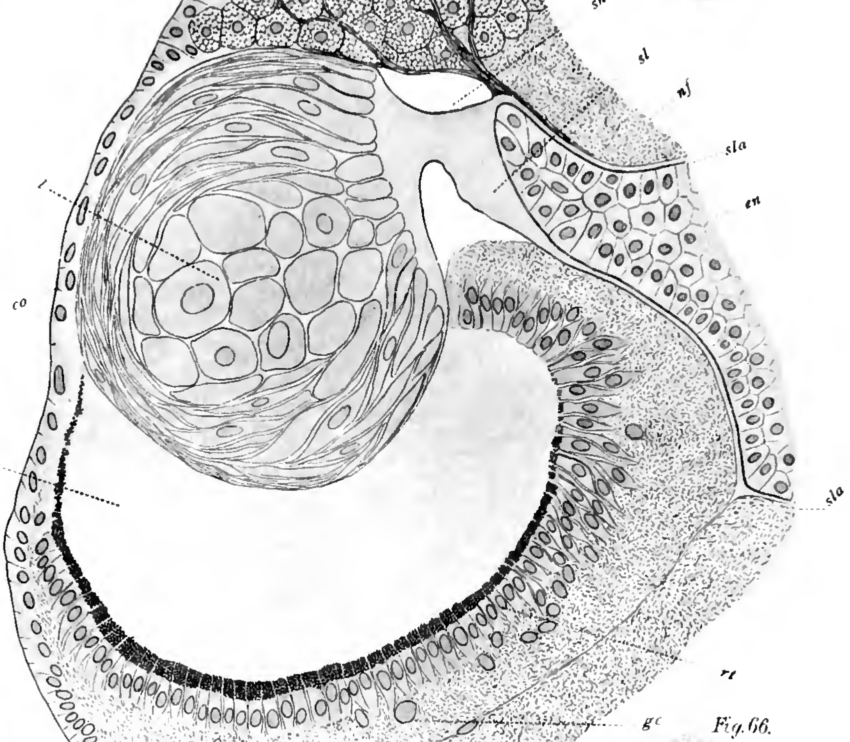

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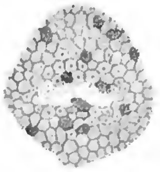

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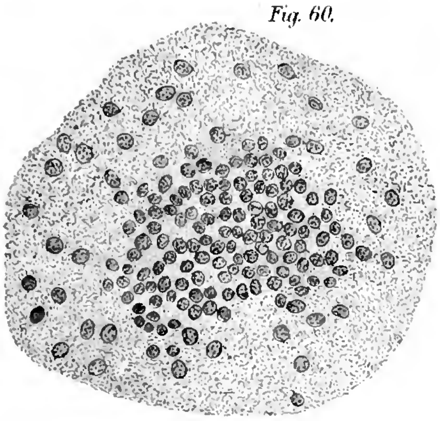

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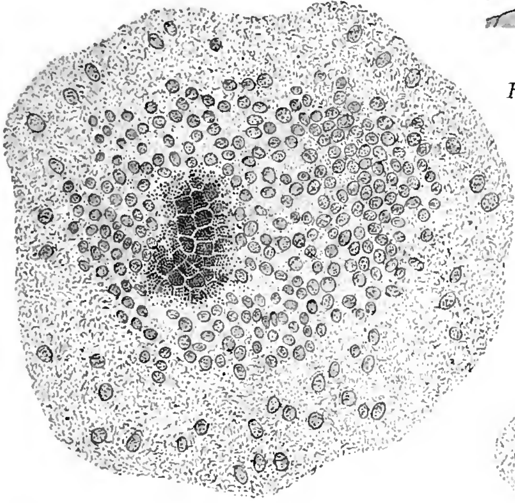
Fig. 61.



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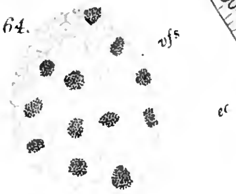

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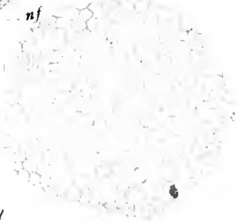

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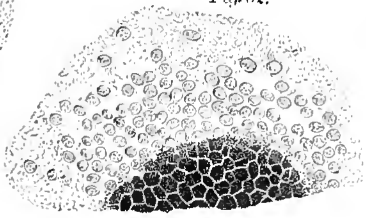

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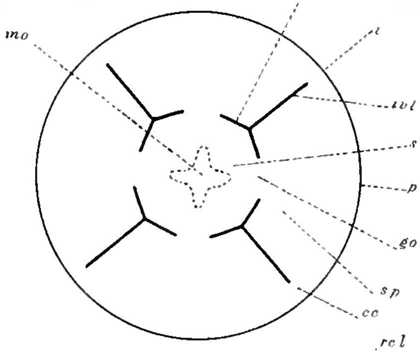

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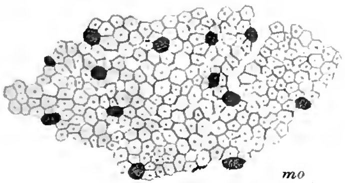

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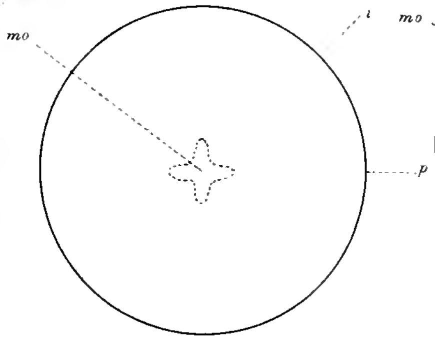

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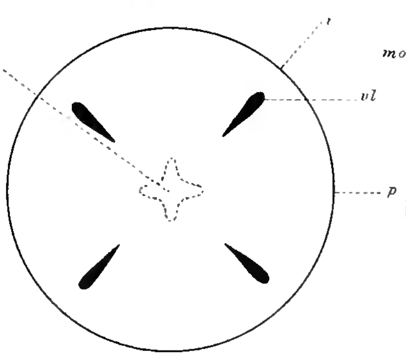
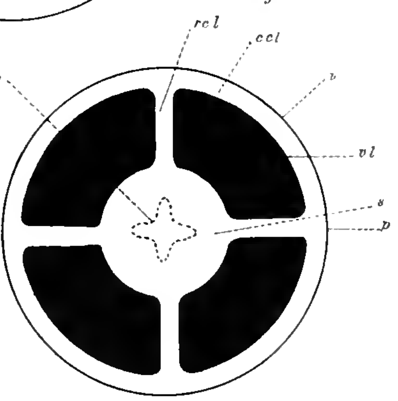


Fig. 35. c



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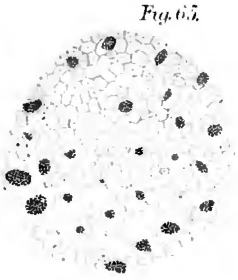

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Memoirs from the Biological Laboratory
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SYNAPTA VIVIPARA

A CONTRIBUTION TO THE MORPHOLOGY OF THE ECHINODERMS

BY

HUBERT LYMAN CLARK

(REPRINTED FROM THE MEMOIRS OF THE BOSTON SOCIETY OF NATURAL HISTORY)

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1898

3. SYNAPTA VIVIPARA: A CONTRIBUTION TO THE MORPHOLOGY OF ECHINODERMS.

BY HUBERT LYMAN CLARK.

(Read November 3, 1897.)

CONTENTS.

1. INTRODUCTORY.

In February, 1896, through the kindness of Dr. W. K. Brooks, there were placed in my hands for study a number of specimens of a small brown Synapta from Jamaica. In their body-cavities there were numerous young ones in all stages of development, so that an excellent opportunity was offered for working out the embryology. So interesting did this prove that I gladly availed myself of the privilege of spending the months of May, June, and July, 1896, at Port Henderson, Jamaica, in the marine biological laboratory of the Johns Hopkins University. For such a privilege I am under the greatest obligations to the authorities of that institution. During those months, I studied the segmentation of the egg and the early stages of development from living material and obtained an abundance of preserved material for further investigations. Since my return I have been engaged in a detailed study of the development and anatomy of the animal under the direction of Dr. Brooks, and it gives me great pleasure to acknowledge the debt I am under to him for his suggestions and help.

The young were easily procured by cutting off the heads of the adults and thus setting free the contents of the body-cavity. They could then be killed as desired, but young taken from the body-cavities of preserved adults were fully as satisfactory for all purposes. The best results were obtained by the use as a fixing agent of "corrosive-acetic" (four parts corrosive-sublimate and one part glacial acetic acid), but excellent preservation, especially for the adults, was secured by the use of picro-sulphuric or picronitric acid. Corrosive-sublimate alone gave poor results, while Perenyi's fluid proved very unsatisfactory, the material prepared with it showing only fair preservation, and staining very poorly. Very good material for the study of the calcareous bodies and the development of the calcareous ring was obtained by the use of absolute alcohol. In staining, it was found useless to try any solution which contained less than seventy per cent alcohol, collapse and distortion of the tissues always resulting. Kleinenberg's haematoxylin and eosin gave good results, but acid borax-carmine (70% alcohol) and Lyons blue (70% alcohol) proved the most satisfactory. The early stages of the larvae were oriented and imbedded in celloiden before imbedding in paraffine, and thus kept their shape very well. Although material was so abundant and easily obtained, it is impossible to tell the age of the different embryos, for none of the eggs obtained developed beyond the blastula, and later stages would live outside of the mother for only a very short time. Accordingly it cannot be determined how many days or weeks are required for the growth of the pentactula or older stages, though there is reason to believe that growth, at least early in life, is very rapid.

2. HISTORY AND SYSTEMATIC POSITION OF SYNAPTA VIVIPARA.

The Danish naturalist Orsted ('50) mentioned the discovery in the West Indies of a new genus of the Synaptidae, the chief characteristic of which was its being viviparous. To this genus he gave the name *Synaptula*, and the type species he called *vivipara*. In his very brief and unsatisfactory account, for which I am indebted to Ludwig's German translation ('81), he mentions the occurrence of the form in "shallow-water," describes the color as "greenish," and speaks of the presence of "eyes," "skin-glands," and "anchors." He never published anything further in regard to the species, and later writers, as Bronn ('60), Selenka ('67), and Semper ('68), accepted the genus *Synaptula* without comment. But Ludwig ('81), in describing a viviparous Chirodota (*C. rotifera*) from the coast of Brazil, suggested that it might be the species on which Örsted had based his new genus. This conclusion was adopted by Lampert ('85), and in his work we find *Synaptula vivipara* given as a synonym under *hirodota rotifera*. Théel ('86) placed *Synaptula vivipara* in the list of Synaptidae about which little or nothing is known, but he suggests in agreement with Ludwig ('81) that the stage of development which the eggs reach before leaving the mother, is not a satisfactory character upon which to base a new genus. Ludwig ('86) described a small *Synapta*, found in floating seaweed, west of the Abrolhos Reef, Brazil, which he regarded as identical with Örsted's species, since it contained young in the body-cavity and answered Örsted's description, except in color

In 1891, students of the Johns Hopkins University found at Port Royal, Jamaica, a viviparous Synapta, and, in 1893, another party from the same institution brought back a large amount of preserved material of this species, which they found abundantly about Port Royal. It was this material which came into my hands, and after examining it and studying the living animal at Port Royal, I had no difficulty in satisfying myself that it, as well as Ludwig's Abrolhos specimen, was indeed Örsted's *Synaptula vivipara*. A brief description to establish its position in the genus Synapta, was published by Clark ('96), and attention was there called to its similarity to *S. picta* Théel ('96). This species was described from a single specimen in the Challenger collection, from Bermuda, and the agreement of all its characters with those of *S. vivipara* was very striking. Dr. Théel writes me that he has specimens of a viviparous Synapta from Bermuda in his hands at the present time, which agree with *S. picta* and *S. vivipara* so completely that he has no doubt that all three are the same species; but the evidence is incomplete, owing to the absence of the anchors and plates in his Bermuda specimens, caused by the killing agent used. Although, as we shall see, *Synapta vivipara* differs in several important particulars from all other Synaptas hitherto described, they are not sufficiently obvious to warrant its separation, under the existing classification of the Synaptidae, as a distinct genus. Synaptula must therefore become a synonym of Synapta, and the synonomy of *S. vivipara* will be as follows: —

Synapta vivipara (Örst.) Ludw. Zool. Jahrbücher. Bd. 2, p. 28. 1886.
Synaptula vivipara Örsted. Vid. med. fra d. nat. For. i Kjöbenhavn for 1849–50, p. vii.
Synaptula vivipara Bronn. Klas. und Ord. d. Thier., Bd. 2, p. 403. 1860.
Synaptula vivipara Selenka. Zeit. für wiss. Zool., Bd. 17, p. 365. 1867.
Synaptula vivipara Semper. Reis. in Arch. Phil., 2. Theil, 1. Bd., p. 24. 1868.
Chirodota rotifera (in part only) Lampert. Die Seewalzen. Wiesbaden. 1885.
Synaptula vivipara Théel. Report on the Holothurioidea. "Challenger" Reports. Zool., Vol. 14, p. 32. 1886.
Synapta picta Théel., p. 10. Report on the Holothurioidea. "Challenger" Reports. Zool., Vol. 14, p. 32. 1886.

3. Distribution and Habits.

Örsted's specimens of *Synapta vivipara*, he tells us, were from the West Indies, and all of the specimens I have seen, came from Jamaica. Ludwig's single specimen came from the Abrolhos Reef off the coast of Brazil (18° S. lat.), while all of Théel's specimens are from Bermuda (32° N. lat.). We may therefore conclude that the species is pretty widely distributed throughout the eastern Atlantic ocean, wherever suitable conditions are found. In Jamaica, however, the species is extremely local and was found in only one place, the so-called "lakes" at Port Royal. These "lakes" are parts of the harbor which have been wholly or in part cut off by the growth of mangroves, so that they are very quiet bodies of water, though not at all stagnant or brackish. On the roots of the mangroves, which hang down in the water on all sides, is an abundant growth of vegetable and animal life. In some places, a particular sea-weed, one of the Florideae, crowds out all the other Algae. In this weed *Synapta vivipara* makes its home, and though carefully looked for elsewhere, it was found in numbers only in such situations. The late Dr. J. E. Humphrey kindly identified this alga for me, as *Acanthophora thierii* Lamouroux. This weed also grows in large bunches on the bottom in the shallow water of the harbor just outside the "lakes," and I was told that in 1893 the Synapta was found in great quantities there, but in 1896 it seemed to have entirely disappeared from that place. At Montego Bay, on the northwest coast of Jamaica, Acanthophora is very abundant on the mangrove roots, but a thorough search revealed no sign of Synaptas there. Even in the Port Royal "lakes," their distribution was very capricious, and only certain favored masses of Acanthophora contained them in any numbers. They seem to be quite social in their habits, and usually if one or two were found, there would be a whole colony of them. They are very sensitive to changed conditions, and I was unable to keep them alive in aquaria more than twenty-four hours. The anchors in the body-wall are so abundant and prominent that they cling very tenaciously to anything with which they come in contact, especially the hands, and it is accordingly no easy task to disentangle them from the sea-weed without injury. They seem to be able to swim very little, and it is doubtful if they ever leave the bunch of sea-weed, in which they have once settled. Their food consists largely of vegetable matter, diatoms being abundant in the stomach, but probably many small crustaceans and worms are also eaten. The tentacles are kept constantly in motion, and it was very common to find small amphipods caught among them, but I was unable to find evidence that these crustaceans ever served as food. Semon ('87) has called attention to what he considers a mimicry of coloration in *Synapta inhaerens*, in relation to the bottom on which it is found. In this connection, it is interesting to note that the reddish and greenish brown shades of *S. vivipara* are almost exactly those of the Acanthophora in which it lives. So close is the resemblance that it is very easy to overlook Synaptas, even when the sea-weed is in one's hand. Whether this coloration is actually protective or not is doubtful, for they seem to have few, if any, enemies. No internal parasites were observed; externally however a small brown calcareous sponge, like Grantia, was found firmly attached to the skin, just behind the circle of tentacles. When placed in aquaria, this Synapta does not break up by muscular contractions, like *S. inhaerens*, nor does it ordinarily eviscerate like many holothurians, but after crawling about restlessly for a while, it stretches out on the bottom and dies, almost without the contraction of a muscle. In a few cases, evisceration at the mouth took place, when they were thrown into a killing agent.

. Breeding goes on all through the spring and summer ; and there is no evidence to show that it does not go on all the year round. My earliest specimens, collected April 30, contained many well-developed young, and up to the end of July in all the specimens obtained, young were found, while Ludwig's specimen from Abrolhos was collected in September and contained very young embryos. The number of young in the body-cavity of a single adult varies greatly, depending more or less on the size of the individual. Specimens not over a centimeter long may contain a few, while some very large ones have scores. The largest number I have found is 176. It is a curious fact that the young are almost always in two broods ; that is, a certain proportion of them will all have reached a given age, say that of the pentactula, while the remainder will be much younger, say about that of the gastrula. When the young are very few, they will all be the same age, while if they are very numerous, they will sometimes show *three* different stages. This fact seems to indicate that the eggs ripen and pass into the body-cavity in lots of from six to a hundred, and that several days elapse before another lot is ripened. Regarding the length of time during which the young remain in the body-cavity, it is impossible to make even an estimate. Animals kept in aquaria frequently gave birth to young only five mm. long, and it was not usual to find much larger specimens in the adults examined, but sometimes a young one, fifteen or twenty mm. long, with all the characters of the adult, would be found still inside its mother. Observations made on the living animals showed that birth occurs normally at the posterior end of the body, apparently through the anus. Investigation showed that this was accomplished by a rupture of the body-wall, which may be through the skin some little distance from the anus (Fig. 29), or, as seems to be more generally the case, through the wall of the rectum close to the point where it joins the external body-wall, the young passing out through the anal opening. It may be that the openings in the wall of the rectum (Figs. 30 and 31), to be described later, are concerned in the birth of the young, but they seem to be too small to be of any service in this connection, except possibly as starting points for the rupture of the rectum wall. Under abnormal conditions, I found by experiment, rupture of the body-wall and consequent birth of the young may occur at other points than near the anus.

4. Fertilization and Segmentation of the Egg.

Like all other known Synaptas, *S. vivipara* is hermaphroditic. Ripe spermatozoa and ova are found in the same genital organ and even in the same branch, and to judge both from living material and preserved specimens, even at the same time; but this latter point could not be proven since it is impossible to determine simply by observation, when the egg is mature. The branches of the genital gland are nile-green in color in the living animal, while the fully grown ova are brownish yellow, and the spermatozoa, when in any quantity, appear to be white. In shape, the latter are like those figured by Jourdan ('83) for *Holothuria tubulosa.* The mature egg (Fig. 1) is about 200μ in diameter and before fertilization is not provided with any membrane. It is full of yolk material but comparatively transparent, so that the internal changes could be watched up to a late stage of development. Artificial fertilization proved unsuccessful, although attempted several times. Whether self-fertilization takes place or not could not be positively decided, but that it is at least very improbable seems clear from the structure of the genital organs and the probable manner of egg-laying. The genital gland of the adult Synapta lies just above the oesophagus, with one or two branches on each side of the dorsal mesentery and with the genital duct lying in that mesentery and opening to the exterior close to the base of one of the mid-dorsal tentacles. A cross-section of one of the branches (Fig. 40) shows that it consists of an external covering, the continuation of the epithelium, a very scanty connective-tissue layer consisting only of a few scattered mesenchyme cells, and a much folded germinal epithelium surrounding the lumen of the gland. Of the layer of circular muscle fibers which was found in the genital gland of *S. digitata* and *S. inhaerans* by Quatrefages ('42), Baur ('64), and Hamann ('84), I have found no trace in *S. vivipara.* The branches of the gland contract vigorously after being cut from the body, but so far as I could see, these contractions were always longitudinal. The germinal epithelium is more or less plainly made up of two or more layers of cells of which the external are the larger. As will be seen from figures 39 and 40, from this external layer of cells the ova arise and so come to lie between the germinal epithelium and the epithelium of the body-cavity, and do not pass into the lumen of the gland at all. This arrangement is quite the reverse of what Cuénot ('91) has shown to exist in *S. inhaerans*, and gives us a clue as to how the eggs get into the body-cavity of the mother. When the eggs are mature, they press so closely against the external epithelium of the gland that it bulges out sufficiently to be seen with the naked eye, in the living gland. Sections show that the epithelium over such ova is so stretched as to be thinner than elsewhere (Fig. 39), and probably the eggs enter the body-cavity simply by the rupture of the epithelium at that point. While this has never been actually observed, the theory is supported by a further examination of the genital gland. The smaller internal cells of the germinal epithelium give rise to spermatozoa, which are almost invariably to be found in the lumen of the gland, never on the outside with the ova. If we trace the lumen forward we find it passes directly into the lumen of the genital duct, the internal walls of the latter actually being formed by a continuation of the germinal epithelium, which has become of uniform thickness and ciliated internally (Figs. 36 and 37). The lumina of the two or three branches of the gland unite on entering the duct (Fig. 36) and pass through the latter upwards towards the body-wall. At no point is there any sign of communication between the genital duct and the space external to the germinal epithelium in which the ova lie. If we follow the genital duct upwards to where it comes in contact with the body-wall, we find it does not fuse with the ectoderm and open at once to the exterior, but simply lies in the connective tissue with its end against the ectoderm (Fig. 38), and although there are probably openings through which the spermatozoa pass out, they are so extremely small I have not been able to demonstrate them satisfactorily. In nearly all the specimens examined the genital duct contained large quantities of spermatozoa, but in no case was there any trace of an ovum. That the openings at the end of the duct are not directly continuous with openings through the body-wall is indicated by the occurrence of spermatozoa, sometimes in large quantities, in the connective tissue surrounding the terminus of the duct (Fig. 38). From all these facts I am convinced that the ova pass into the body-cavity by a rupture of the peritoneal epithelium, while the spermatozoa pass outward through the genital duct to the exterior. In *Cucumaria glacialis*, the only other viviparous holothurian concerning whose breeding we have any information, Mortensen ('94) thinks the eggs are laid on the bottom and taken up afterwards into the brood-sacks of the mother. But it is manifestly impossible that the eggs of *S. vivipara* could get into the body-cavity in any such way. The next question that arises is, how do the spermatozoa reach the ova inside the body-cavity of the mother, and the answer brings to light another interesting modification of structure, adapted to the viviparous habit. Careful examination of the rectum shows that through its wall there are direct channels of communication between the body-cavity and the exterior through the anus. The wall of the rectum is folded and ridged longitudinally, and at certain places, parts of these ridges have pushed out and fused with invaginations from the surrounding coelomic wall, forming distinct tubes connecting the interior of the rectum with the interior of the coelom (Figs. 30 and 31). No trace of valves or cilia was found in any of these tubes, but the passage of water in and out could be easily regulated by the opening and closing of the anus. With the anus open, each muscular contraction of the animal would tend to either force water out or draw it in through these openings, and in that way spermatozoa could easily get into the body-cavity and thus fertilization could take place within. This will appear more probable when it is remembered that the animals are very social, and that the water around a mangrove root on which there are hundreds of them, must contain countless spermatozoa. There is also a possibility that spermatozoa enter the body-cavity, through the water-pore and stone-canal, which, as we shall see, remain open in the adult, and also open into the body-cavity.

After fertilization a membrane forms around the egg and segmentation begins. It seems probable that the extrusion of the polar bodies occurs before the formation of this membrane, as Selenka ('83) found no trace of them in the segmenting eggs of *S. digitata*, and I could not find them in any of the eggs of *S. vivipara* which I examined, although they were looked for with special care. Segmentation and the formation of the blastula occur in practically the same manner as has been so well figured by Selenka ('83) for *S. digitata.* The first plane of division forms two blastomeres of equal size and appearance (Fig. 2). After a resting period of about twenty minutes, the second plane of division occurs at right angles to the first, giving rise to four similar blastomeres (Fig. 3). The third plane is at right angles to the first two, and we now have an embryo of eight equal cells with a segmentation-cavity between them (Fig. 4). The sixteen-cell stage (Fig. 5) soon follows, the division plane being at right angles to the preceding. The appearance of the embryo at this stage is very peculiar and characteristic, the cells being arranged in a band or ring and the segmentation-cavity being open at each pole. Another plane of division, again at right angles to the preceding, doubles the width of the band and decreases the openings at the poles, but it does not divide the cells exactly equally, so that the upper- and lowermost rows are of somewhat smaller cells than the two middle rows and have a less diameter (Fig. 6 and 7). The subsequent divisions occur with a fair degree of regularity in alternating planes, each division decreasing the openings at the poles until at last they are entirely closed. This occurs when the embryo consists of approximately 256 cells, and so the blastula is formed (Fig. 8). The cells of the four equatorial rows are somewhat larger than the rest, but the difference is not at all noticeable and apparently has no significance. The divisions have followed on each other with great rapidity so that the complete blastula is formed after about four hours, while in *S. digitata,* according to Selenka ('83), the blastula is the result of twelve hours' growth. It is for this reason, that I am inclined to think that the whole process of development in *S. vivipara* is very rapid.

5. GASTRULATION AND FORMATION OF THE HYDROCOEL AND COELOMIC VESICLES.

Invagination of one of the poles of the blastula soon forms the archenteron from the blind end of which the mesenchyme cells now begin to arise, some of the endodermal cells being simply crowded out into the segmentation-cavity. I could find no evidence at all of Selenka's ('83) two primitive mesenchyme cells, but on the contrary, I found cells all over the archenteron which were in various stages of passing into the segmentation cavity. On the other hand in not a single case were there found any of the ectoderma-cells forming mesenchyme, and I feel no hesitation in affirming that the mesenchymel arises exclusively from the endodermal cells, contrary to Ludwig's ('91) observations on Cucumaria. The number of mesenchyme cells is comparatively small, and they never become so numerous or play so important a part in larval structures as they do in *S. digitata*, judging from Semon's ('88) account and figures. The completed gastrula (Fig. 9) is covered with cilia which are easily seen in the living specimens, but in none of my preserved material has it been possible to demonstrate them. In a few cases gastrula were found free from the egg-membrane and moving about actively in the fluid of the body-cavity, but the great majority are still enclosed in the membrane within which they rotate by means of the cilia. The membrane may be retained, as preserved specimens show, until long after the coelomic vesicles are formed, and I am inclined to believe that there is no definite time when it is cast off, but that it ruptures and is lost whenever the larva has grown too big for it. As the archenteron increases in length it bends to one side and unites with the wall of what subsequently becomes the dorsal surface of the larva. Its lumen breaks through the surface, and thus the water-pore is formed, as described by Selenka ('83) for *S. digitata.* Meanwhile the gastrula loses its spherical shape and becomes more or less elongated (Fig. 10). The cells at the end opposite the blastopore are already somewhat different in form from those elsewhere and make a sort of plate of thickened ectoderm (Fig. 21) which may correspond to the so-called "neural plate" of other echinoderm larvae. This plate, however, does not lie exactly opposite the blastopore, but somewhat toward the ventral side of the larva, and as the gastrula increases in length, it comes to lie more and more on that side. At the same time, the archenteron continues to increase in length and grows forward and at the same time ventralward, thus drawing away from the water-pore. In so doing, that part of it which grows forward pushes by the part opening through the water-pore, on the right-hand side (looked at from the dorsal surface) so that the latter comes to lie on the left side of the larva (Figs. 11 and 12). As the archenteron grows it completely severs its connection with this vesicle, and pushing onward and downward against the thickened part of the ectoderm, becomes attached to it, and the mouth breaks through at that point. The mouth may be formed before the separation between the archenteron and the other vesicle is completed. Meanwhile the latter increases in size, and its walls become thinner. It grows backward toward the blastopore especially and soon becomes constricted and divided into two vesicles, the anterior of which is connected with the exterior by the water-pore, while the posterior is entirely closed and lies beside the posterior part of the stomach, if we may so designate the middle section of the archenteron (Fig. 13). Soon afterwards this posterior vesicle grows out laterally to the right, across the dorsal surface of the larval hind-gut, and forms on the right-hand side a vesicle like itself, which soon becomes entirely separate from it (Fig. 14). The anterior of these three vesicles is the rudimentary hydrocoel, while the pair of posterior pouches represent the right and left coelomic vesicles. Their mode of formation is essentially the same as that described by Selenka ('83) for *S. digitata*, but the relative size of the various organs is markedly different, so that the figures of the same stages show almost no resemblance. If figure 15 of *Synapta vivipara* be compared with the auricularia of about the same age which Semon ('88, Plate 6, Fig. 2) figures, this difference will appear in many ways. The rudiments of the two coelomic pouches and especially of the hydrocoel are very much larger relatively in *S. vivipara* than in *S. digitata*, while the difference in the digestive tract is even more noticeable. In the European species there is a well-marked differentiation into fore-, mid-, and hind-gut, while in the Jamaican form there is no such distinction evident. A remarkable difference is also to be seen in the external form of the larvae. That of *S. vivipara* has retained its elliptical shape and shows no trace of ciliated bands, while the other has assumed the familiar auricularia form. Furthermore, there is no trace of calcareous structures of any kind in *S. vivipara* to correspond with the plates at the posterior end of auricularia. In the latter also, Semon ('88) has figured and described a larval nervous system, but after careful investigation of this point, I am convinced there is none in the larva of *S. vivipara*. In external form, the latter is very regular, but with the growth of the coelomic pouches the ectoderm of the dorsal surface begins to become thinner and more flattened, while that around the mouth, especially posterior to it, shows a tendency to increase in thickness. This difference between the dorsal and ventral surfaces may sometimes be seen in very young larvae and is clearly shown in figure 22. Before the two coelomic vesicles have entirely separated, the hydrocoel has become considerably larger and begins to grow anteriorly and toward the right, while about the same time five outgrowths begin to appear on that side which is furthest from the fore-gut (Fig. 15). Soon after their appearance *five* other much smaller outgrowths arise, one at the right of each of the first five. The first series gives rise to the five primary tentacles, and the second series corresponds to those which in *S. digitata* give rise to the radial water-canals. In *S. digitata* however, there is a sixth outgrowth at the extreme left, the rudiment of the Polian vesicle, but in *S. vivipara* this vesicle is not formed until after the closure of the hydrocoel ring. The water-canal enters this ring at a point just between the fourth primary tentacle (counting from before backwards) and the fourth secondary outgrowth (Fig. 23). In this particular my observations confirm Bury ('89) in opposition to the statements of Semon ('88).

Before the outgrowths of the hydrocoel are very evident, that part of it which lies dorsally and in immediate connection with the water-canal bulges out, becomes thinner-walled than the rest of the hydrocoel, and gradually separates from it, but before the separation becomes marked, the outgrowth diminishes in size and with the increasing growth of the water-canal disappears. This structure, I believe, is the "anterior coelom" which Bury ('95) has shown to exist in the auricularia of *S. digitata*. It is very marked in some specimens of *S. vivipara* (Fig. 24), and I see no reason to doubt Bury's interpretation. He does not make very clear what the ultimate fate of this coelom is in *S. digitata*, but leaves the impression that it is connected with the subsequent formation of the madrepore plate, as Ludwig ('91) considers it to be in Cucumaria. In *S. vivipara* however, there is seldom any trace of it left after the hydrocoel ring closes, and there is no reason to suppose that it has any connection with the much later madrepore openings. About the time of the appearance of the primary tentacles, the larval anus, which was the original blastopore, closes entirely and the digestive tract ends blindly. Accordingly we now have a regular elliptical larva, about a third of a millimeter long, with the ventral ectoderm much thicker than the dorsal, without ciliated bands, calcareous particles, or nervous system, a mouth on the anterior ventral surface but no anus, a well-developed coelomic pouch on each side of the digestive tract, and a hydrocoel with five primary tentacles and five secondary outgrowths, opening to the exterior through the dorsal pore, by means of an *adradial* water-canal, upon which may still be seen the vestige of an anterior coelom.

6. THE DEVELOPMENT OF THE PENTACTULA.

In such larvae, the ectoderm of the ventral surface continues to thicken and before long is sharply set off from the ectoderm of the rest of the body, which consists of a single layer of cells. The thickened ectoderm forms a circular field around the mouth though the latter does not lie at its center, but nearer to its anterior edge. This circular disc gradually sinks below the level of the rest of the ectoderm, and the latter grows in over it from all sides, until the disc lies at the bottom of a shallow cavity, the so-called "atrium," which opens on the ventral surface through a small pore (Fig. 16). This pore does not lie directly over the mouth, but either before or behind or somewhat to one side. While these external changes are taking place, the hydrocoel has continued its growth, the anterior end passing across on to the right side of the larva where it bends downward and backward around the oesophagus to meet the posterior end near the middle line. The primary tentacles have increased considerably in size and are growing up around the floor of the atrium, while the secondary outgrowths also grow *upward* beside them. No Polian vesicle has yet appeared, and no marked distinctions between the different parts of the digestive tract are to be seen, but the latter has become very much arched toward the dorsal surface, and the lumen of the middle section is larger than at either end. A new anus may have been formed by the end of the hind-gut growing to the body-wall on the ventral side and an opening breaking through, but in some cases the definitive anus does not appear until the pentactula form is nearly attained. The most important changes have been going on meanwhile in the coelomic pouches, the growth of which has been very rapid. The left vesicle has grown more anteriorly than the right, and sends forward two finger-like processes, one of which passes across the median line into the right side of the larva, while the other grows up to the inner side of the hydrocoel ring, above the most posterior tentacle, and follows the course of that ring around the oesophagus (Figs. 26–28). These anterior prolongations of the left coelom were observed by Bury ('89 and '95) in *S. digitata*, but have apparently been overlooked by other investigators. The one which passes on to the right side of the body fuses so soon with the right coelom that I have been unable to confirm Bury's further observations regarding it, and in *S. vivipara* its appearance might easily be entirely overlooked. But the prolongation which passes to the hydrocoel remains distinct through all the later stages of the larva, and its subsequent changes are easy to trace. It soon loses its connection with the left coelom and forms a tube, lying on the oral surface of the hydrocoel ring. Meanwhile the right and left coelomic pouches have met and fused on the ventral side of the digestive tract, while dorsally they are still separate, the right pouch extending considerably further back than the left. The larva has now reached the condition shown in Fig. 16. In its subsequent growth the atrium, with its thick ectodermal floor and narrow opening to the exterior, moves to the anterior end of the larva, where it finally comes to lie, along with the mouth, oesophagus, and hydrocoel ring. The latter has now closed, without the formation of a Polian vesicle, somewhat to the left of the middle line apparently (Fig. 25), but I am not sure that the point of closure is always on the left side, for it is by no means easy to determine the exact mid-line. With the closure of the hydrocoel, occurs the union of the two ends of that coelomic tube which lies on its oral surface, so that we now have a circular sinus around the oesophagus just above the water-ring. This sinus is very evident in young Synaptas, and Bury's ('95) surmise regarding its origin from the left coelom is entirely correct. The primary tentacles are growing upward, not pushing the floor of the atrium out before them, as Semon ('88) says, but enclosing the atrium within their circle so that the thickened sensory epithelium, which they subsequently possess, does not arise as Semon describes. It is clear, from Figs. 16 and 17, that his description could not possibly apply to *S. vivipara.* The secondary outgrowths remain nearly unchanged in size and show no sign of bending backward to form radial canals. The Polian vessel is formed as an outgrowth on the inner side of the hydrocoel ring in the *left dorsal* interradius, as Ludwig ('23) found it to be in Cucumaria.

The digestive tract grows with greater rapidity relatively than any of the other organs. Accordingly, the oesophagus pushes upward toward the atrial opening, so that the thickened ectodermal floor of the atrium lies surrounding it, in the form of a poorly defined circumoral ring. Continued growth pushes the oesophagus against the upper ectodermal wall of the atrium, and with that it fuses, leaving the circumoral ring entirely cut off from the outer ectoderm of the body (Figs. 87 and 88). Meanwhile the growth of the primary tentacles has pushed this body-wall upward and outward, so that the narrow slit-like opening of the atrium is gradually widened until it finally disappears, leaving the ectodermal-covered, anterior end of the oesophagus to form the definitive mouth, in the center of the circle of tentacles. This process is not completed however, until the pentactula form is fully assumed. The differences between this development of the mouth and circumoral ring and that given by Semon ('88) for *S. digitata* are almost irreconcilable, but they are all dependent on the question, whether the five primary tentacles push up through the floor of the atrium or grow up around it. The latter is certainly the case in *S. vivipara.* While these changes are taking place anteriorly, the hind-gut has increased in length so that it has not only arched still more toward the dorsal surface but has bent on itself and formed a loop lying to the left of the stomach. The coelomic pouches already united and forming a single cavity ventrally, have met in, or close to, the mid-dorsal line and by the union of their walls have formed the dorsal mesentery. This mesentery follows pretty closely the curve of the intestine and attaches it throughout its course, to the body-wall. The water-canal lies in the anterior part of the mesentery, but whether that part was formed in a different manner, as Bury ('95) thinks probable, it is impossible to say from observations on *S. vivipara.*

Meantime most important changes are going on in the circumoral ring of ectoderm which we have seen was formed from the floor of the atrium. This ring is the beginning of the central nervous system, and from it the tentacle and radial nerves arise. As the primary tentacles push upward past the atrium, they lie closely appressed to its floor and wall. They retain this position even after the circumoral ring is pretty clearly defined, and before they have grown much above it, the radial nerves appear between each pair of them as outgrowths of the central ring. These outgrowths pass directly over the secondary outgrowths of the water-vascular system and bend backwards to run toward the aboral pole of the body. Very soon after they appear (not before them, as Semon ('88) describes for *S. digitata*), that part of the circumoral ring appressed to each primary tentacle begins to grow upward with it on its inner side, forming the tentacle nerves. As the tentacles continue to grow and press the anterior body wall outward, the ectoderm which covers them at the tip becomes noticeably thickened, especially on the outer side (Fig. 54), and apparently assumes a sensory function, probably in connection with the tentacle nerve. The formation of the otocysts of Thomson ('62), the "hörorgane" of Baur ('64), takes place as described by Semon ('88). They arise by evaginations from the outer side of the circumoral ring close beside the outgrowths which form the radial nerves. With the growth of the latter, the otocysts come to lie external to them at the point where they bend backward, and in this position the sense-organs remain throughout life. It is a very evident and noteworthy fact that the development of the radial nerves and otocysts does not take place at the same time in the five radii, but there is a marked difference between them. The first to appear is that nerve which subsequently indicates the mid-ventral radius, and with it appear its two otocysts. The two lateral ventral nerves appear next, and with them the otocyst which accompanies each one on its ventral side. The lateral dorsal nerves next appear (Fig. 1), and very soon afterwards the two other otocysts of the right and left ventral radii are formed. Last of all to develop are the otocysts of the right and left dorsal radii. This sequence in the appearance of these nerves and sense-organs is probably connected with the fact already mentioned, that the thickened ectoderm which made up the floor of the atrium did not lie symmetrically around the mouth, but the greater part of it was posterior or, when the mouth lies at the anterior end of the larva, ventral to it. What the significance of this condition may be, I am unable to suggest, but it is interesting to note that in Cucumaria Ludwig ('91) found the ventral radius the most advanced in development. Any possible similarity ends here however, for the development of the other radii was quite the reverse in Cucumaria of what it is in Synapta.

About the time of the completion of the pentactula form, there appear in the ectoderm of various parts of the body peculiar invaginations (Fig. 41) which are finally connected with the exterior only by a very narrow canal (Figs. 42 and 43, and Fig. 17, lgo.). These organs appear, from their structure and the great variation which they show in staining, to be of a glandular nature, and I am inclined to think they may be connected with the absorption of nourishment from the fluid of the body-cavity of the mother, for they never increase in size, are most abundant in the young with ten tentacles, and seem to have entirely disappeared in the adult, and finally, nothing of the kind has been described for any other holothurian. When fully grown they measure about fifty mikrons in diameter and somewhat less in depth. They consist of very long, clear cells, with nuclei at the extreme distal ends, surrounding a more or less spacious lumen which opens to the exterior by a narrow canal of ordinary epithelial cells. Sometimes the clear cells stained heavily, but often they did not stain at all.

Up to this time the mesenchyme cells have played no part in the development of the larva. In Fig. 16, they are shown as they appear scattered almost uniformly through the segmentation cavity. Shortly after this, however, they begin to gather around the lower and outer edge of the water-vascular ring, and by the time the pentactula stage is reached they have begun the formation of the calcareous ring. Contrary to Semon's ('88) views on *S. digitata*, and in accordance with Ludwig's ('91) observations on Cucumaria, I have found no evidence at all of any mesenchymatous musculature on the oesophagus. The first products of the mesenchyme cells to appear are five small straight rods between the primary tentacles but outside and somewhat below the hydrocoel ring. Soon after these, five more appear below the bases of the tentacles, so that there are now ten rods, five radial and five interradial, and they continue in this position so long as there are only five tentacles. I saw no evidence at all of any such shifting of position of the first five rods as Semon ('88) records for *S. digitata*, nor could I consider the position of the second series as agreeing at all with his description. Very soon after the appearance of the ten rods, they fork at the ends and begin to branch very irregularly. As will be seen from Fig. 46 a–i, the divisions occur at all sorts of angles and not only differ decidedly from Semon's figures of the same rods in *S. digitata* but show no sign at all of following his law ('87) for the formation of calcareous plates in Echinoderms. The much-branched ends of the rods come into very close contact but evidently never mingle, for the plates into which they develop are at all times easily separable and the line of division between them is practically straight. Very soon after the appearance of the first five calcareous rods, the radial nerves grow backward over them and before the completion of the pentactula, run to the posterior end of the animal.

We have now reached the complete pentactula form, a slightly older stage of which appears in Fig. 18. The pentactula is about half a millimeter long and its characteristics may be briefly summed up as follows: — Water-vascular system consisting of a closed hydrocoel ring or circumoral water-tube with five primary tentacles, between which are five very much smaller but equally erect secondary outgrowths; a water-tube in the mid-dorsal interradius connecting the circumoral ring with the exterior; and a Polian vessel in the left dorsal interradius. Nervous system consisting of a circumoral ring; five tentacle nerves on the inner face of the primary tentacles, the ectoderm of which is considerably thickened, especially on the outer side; five radial nerves bending backward over the secondary outgrowths of the water-ring and over the radial pieces of the calcareous ring, and running to the posterior end of the body; and five pairs of otocysts, lying external to the radial nerves, where they bend backward. Digestive system, consisting of a short oesophagus with the mouth opening anteriorly in the center of the circle of tentacles, a large stomach, a comparatively short intestine with a single loop in it, and usually an anus formed secondarily near or at the aboral pole. Digestive system attached to the wall throughout its whole course by a mesentery, formed by the union of the two walls of the right and left coelomic pouches. Calcareous ring consisting of five radial and five interradial pieces with much-branched ends. A few scattered glandular organs of doubtful function in various parts of the ectoderm.

7. The Development of the Adult Synapta.

Since there is no cessation of growth nor any resting period on the assumption of the pentactula form, it is impossible to draw any hard and fast lines which will always serve to distinguish that stage. For many larvae, which appear to have only five tentacles, show on careful examination the rudiments of new ones, and other larvae which show no tentacles externally show the perfect pentactula form, when sectioned. As soon as the five primary tentacles have pushed out so far as to entirely obliterate the original opening of the atrium, the secondary outgrowths of the water-ring, which have hitherto scarcely shown any indication of growth, begin to develop and push upward. As we have already seen, the radial nerves lie directly over them, so that they cannot grow straight up but push out to one side or the other of the nerve. The outgrowth which lies in the mid-ventral radius, however, develops very slightly and does not normally push out on either side of the nerve which overlies it. The outgrowths which lie in the right and left ventral radii take the opposite course, and broadening out laterally, grow up on both sides of the nerves which overlie them, to form accessory tentacles. The outgrowth of the right dorsal radius pushes out on the dorsal side of its overlying nerve and forms an accessory tentacle in the mid-dorsal interradius, while the outgrowth of the left dorsal radius shows as yet little tendency to develop either way (Fig. 85). Consequently we now have a larval form with ten tentacles, two in each interradius. As the accessory tentacles grow very rapidly they are soon equal in size to, and cannot be distinguished from, the five primary tentacles. It is hard to decide positively which of the five accessory tentacles develops first, for apparently they all begin to grow at about the same time. In *Chirodota rotifera,* Ludwig ('81) found the first two accessory tentacles in the lateral dorsal interradii, and he does not speak of finding any trace of additional tentacles in the other interradii. I have not found any stage similar to that in *S. vivipara,* and I think the five accessory tentacles appear at practically the same time. It is an important and interesting fact, however, that the five accessory tentacles are formed in precisely the same manner and from the same radii as the *second* series of five tentacles in Cucumaria, (Ludwig, '91). It seems to me that this fact proves satisfactorily that the radial canals in Synaptidae are homologous with those of the other holothurians or, more accurately, the secondary outgrowths of the hydrocoel ring in the Synaptidae are homologous with the five outgrowths of the hydrocoel ring in the true holothurians. In both cases, the ten-tentacled young has one primary and one accessory tentacle in each interradius. While this change is taking place in the number and arrangement of the tentacles, a corresponding change is going on in the calcareous ring. As the accessory tentacles push out into the interradii, the calcareous rod which lies at the base of the primary tentacle comes to lie between it and the accessory tentacle. I could not see that this came about by any actual movement of the rod itself, but was due simply to the increase of width in each interradius. In the further growth of the calcareous ring, the interradial pieces send up projections between the two tentacles (Fig. 46 h) and at the same time branch and divide so rapidly and irregularly that they soon become plates, with straight sides but pointed anteriorly and notched behind, made up of a very fine irregular network of calcareous strands (Fig. 44). The radial plates develop in the same way but send up two projections, one on each side of the radial nerve (Fig. 46 i), which finally fuse together above it and thus form the perforated plates of the ring (Fig. 45). About the same time, the mesenchyme cells lying between the ectoderm and the wall of the coelom begin to gather in groups close to the ectoderm and there give rise to anchors and anchor-plates so characteristic of the adult Synapta. The development of the calcareous bodies from a straight rod takes place as described by Semon ('87) for *Synapta inhaerans.* While these deposits appear in the body-wall as far anteriorly as the base of the tentacles, in the walls of the latter, lying parallel to the long axis, there appear numerous rather long, more or less, knobbed rods (Fig. 48) similiar to those described by Semon ('87) from the tentacles of various synaptids. These become very abundant in the older ten-tentacled larvae.

The digestive tract meantime has increased in length, and the stomach is more clearly marked off from the intestine and oesophagus. The nervous system has not undergone any marked changes, but each of the accessory tentacles is supplied with a nerve on its inner side, as in the case of the primary tentacles. In various parts of the skin, especially anteriorly, clusters of ectoderm cells are to be found which later form the so-called sense-papillae ("Tastpapillen" of Hamann, '83). I have been unable to find any connection between these spots and the nerves until a very much later period, and I cannot decide how or when this connection is made. The glandular organs previously described are very abundant at this stage, especially posteriorly. Soon after the pentactula form is complete, the walls of the coelom and of the hydrocoel begin the formation of muscle fibers, always on the side turned from the cavity which they enclose. The first to appear are the longitudinal muscles of the tentacles and radii. The former appear as fibers on the outside of the tentacle canals and they soon form quite a thick layer. The radial muscles arise within a fold of the coelomic wall, which appears along the inner side of the radial nerves. This fold begins anteriorly near the calcareous ring and runs backwards with the nerve, enclosing a considerable space between its walls. In this space the muscle fibers arise from the endodermal cells of the coelom. Later on, the circular muscles of the body appear, arising from the outer side of the coelomic wall also. They cross the space in which the longitudinal muscles lie, forming a layer between the latter and the nerve. At the same time, the longitudinal and circular muscles of the digestive tract, and the muscles of the water-ring, begin to appear, so that by the time the ten-tentacled stage is reached, the musculature is practically that of the adult. With the appearance of the longitudinal muscles of the tentacles, comes the development of the valves at the openings of the tentacular canals, close to the upper edge of the calcareous ring.

Before the accessory tentacles have begun to appear, there arises on the right hand side of the mesentery which fastens the intestine to the wall of the left interradius a longitudinal fold or evagination of the epithelium close to the intestine (Fig. 58). This fold follows the course of the intestine, with the mesentery on the dorsal side, and grows forward along the stomach and backward toward the anus. Later a similar fold appears in the coelomic epithelium on the opposite (ventral) side of the digestive tract and the two folds soon become connected around the intestine and stomach by numerous ill-defined lacunae between the coelomic wall and that of the digestive organ itself. These vessels are the first stages of the blood vascular system and into them cells from the coelomic epithelium pass to form the blood corpuscles. Theoretically the vessels ought to be lined with connective tissue of mesenchyme cells but these are so few in the early stages of the larva, that the connective tissue between the laminae of the mesenteries or even around the digestive tract is very hard to demonstrate. The main blood vessels appear to be purely entodermal in origin and their walls seem to be made up solely of the coelomic wall. At any rate, the dorsal vessel does not arise in *S. vivipara* in the way given by Semon ('88) for its origin in *S. digitata*, by a simple split in the mesenchyme where the two coelomic folds unite above the intestine to form the mesentery.

Very soon after the pentactula stage is reached the first rudiment of the genital system appears. It arises on the inner side of the right-hand lamina of the dorsal mesentery between the stone-canal and the oesophagus. The first appearance is simply the increased size of the cells at this point, resulting in a thickening of the wall (Fig. 32), but the cells soon multiply rapidly and form a more or less spherical mass within the mesentery (Fig. 33). As this mass increases in size, cavities appear within it (Fig. 34) and these increase in size and begin to unite together until they form one central lumen for the gland (Fig. 35). Meanwhile the right lamina of the mesentery forms an outer epithelium which soon becomes quite distinct from the central mass of cells. Between this epithelium and the remainder of the gland a few mesenchyme cells form an extremely scanty connective-tissue layer. In the full-grown ten-tentaculed larva, the genital gland is plainly seen (Fig. 19), lying entirely on the right-hand side of the mesentery, near the stone-canal.

The ten-tentacled larva (Fig. 19) is a more clearly defined stage in the development of *Synapta vivipara* than is the pentacula; that is, it seems to last longer, and the relative condition of development of the various organs is more constant. The changes which occur subsequently in the assumption of the adult form must now be considered. The most obvious of these is the increase in the number of tentacles which arises from the addition of another tentacle to the right and left dorsal interradii (Fig. 86). The extra tentacle of the left side arises from the left dorsal "secondary outgrowth" of the hydrocoel ring, which has hitherto remained in its original position beneath the left dorsal nerve but now pushes out on its lower or ventral side and forms the eleventh tentacle. At the same time, the extra tentacle of the right side arises from the lower or ventral side of the right dorsal "secondary outgrowth" which pushes out on that side of the right dorsal nerve and forms the twelfth tentacle. Not infrequently individuals are found with thirteen tentacles, and in these the extra tentacle is usually in one of the ventral interradii. In such cases it is probable that the mid-ventral "secondary outgrowth" has grown up on one side or the other of the mid-ventral nerve, although in normal specimens it does not develop at all. Occasionally the extra tentacle is in the mid-dorsal interradius, and in such cases it is probable that the left dorsal "secondary outgrowth," which normally develops only a single tentacle, has given rise to a second on the dorsal side of the left dorsal nerve. Corresponding to these changes in the number of tentacles additional plates appear in the calcareous ring, but these plates do not arise by interpolation of new rods. On the contrary, the plate of the same radius with the new tentacle increases its length and sends upward a new projection for the support of the tentacle (Fig. 47), and this subsequently forms the center of the new accessory plate. In specimens of the calcareous rings cleaned with caustic soda, it seemed to me that the calcareous plates of the right and left dorsal radii were less easily separated from those plates on their ventral side than from those on the dorsal, so I am inclined to think that for a time, if not throughout life, these two plates remain in closer union than any of the others. In specimens with thirteen tentacles, there is an additional plate in the calcareous ring corresponding to the extra tentacle. About this same time the miliary granules (Fig. 50) begin to appear in various parts of the body-wall and in the tentacles. Like all other calcareous concretions of Synapta, they are formed by mesenchyme cells. They usually appear in clusters of several hundred, which continue to increase in number afterwards until it may reach thousands. By the time twelve tentacles have appeared, the genital gland begins to push over on the left hand side, but it is not until long after the adult form is assumed in all other respects that the left branch of the gland equals the right in size. As soon as the left branch is well started, the germinal epithelium begins to push upward in the mesentery beside the stone-canal, and forms the genital duct, but does not reach the outer body-wall for some time. This account of the development of the genital duct accords with Mortensen's ('94) observations on *Cucumaria glacialis*, although his account of the origin of the genital gland itself differs considerably from my observations. Important changes are going on meanwhile in the nervous system. From the inner side of the circumoral ring nerves or bands of nervous tissue arise and pass inward to the oesophagus. These will be referred to more fully in describing the nervous system of the adult. Even in the ten-tentacled stage, before the remaining two tentacles have made a fair start, there arises on each side of the tentacle nerve at its base a knob-like outgrowth which becomes covered over with a peculiar mesenchyme layer, and these form the "eyes," which also appear at the base of the eleventh and twelfth tentacles, after they receive their nerves from the circumoral ring. With the appearance of these eyes, the first trace of pigment appears in the mesenchyme not only about them but in various parts of the body, especially around the calcareous ring. This pigment on its first appearance is bright green, even about the eyes, so that at this stage the eyes of the young Synapta are very conspicuous as large green spots at the base of the tentacles. Very soon, however, a dark reddish brown pigment appears, but this is probably an older stage of the green, and not a different pigment; for the pigment around the eyes soon loses its green color and turns brown, and there is no reason to assume that the pigment in other parts of the body is any different from that around the eyes. All of the pigment arises in the connective tissue, and is apparently a product of the mesenchyme cells. It is especially abundant at the anterior end of the body, and above all other places in and around the calcareous ring.

Before the number of tentacles is complete the ciliated funnels so characteristic of Synapta begin to appear on the mesentery, near the body-wall. These funnels arise from a large cell or group of cells in the endodermal epithelium of the mesentery (Figs. 61 and 62a). The multiplication of these cells soon forms a hemispherical outgrowth (Fig. 62d) which increases in size and becomes more and more spherical in shape, until it is finally attached to the mesentery by only a narrow stalk (Fig. 62e). It then begins to flatten on one side, and the cells of its outer layers become smaller and stain more heavily than those nearer the stalk (Fig. 62f). The flattened surface at last becomes concave and the funnel shape begins to be assumed. At the same time, the stalk becomes elongated and draws up within it some of the connective-tissue layer of the mesentery, which becomes the supporting layer of the funnel. Even during the ten-tentacled stage the digits of the tentacles begin to be formed, but they do not become prominent until the twelve tentacles are all developed. The digits arise as evaginations of the water-canal of the tentacle (Fig. 56) which very soon become shut off from the main canal and in the adult have no connection with it (Fig. 55). The earliest ones to appear are near the middle of the tentacle, and the later ones appear both proximally and distally to them. The digits form longitudinal muscles on the outer side of the central cavity in the same way as the tentacles themselves. They are also supplied with nerves from the main tentacle nerve. The peculiar glandular organs of the larva are no longer forming but seem rather to be disappearing, and the longitudinal rods of the tentacles reach their maximum number at this time. The circumoral sinus, which was entirely cut off from the rest of the coelom in the pentactula stage, has increased greatly in size (Fig. 89) but is now in open communication with the body-cavity, though strands of connective tissue traverse it, uniting the oesophagus to the water-ring and, higher up, to the coelomic wall. With the greatly increased size of the young Synapta, comes a considerable change in the relative position of the organs in the body-cavity. The body has grown much posteriorly, drawing out with it that part of the intestine which lies in the right ventral interradius. The nerve ring is drawn upward with the growth of the tentacles, so that it comes to lie very near the ectoderm at their base. The increased length of the tentacular canals has pushed the water-ring downward so that it lies some distance below the calcareous ring (Figs. 90 and 91), but it is still in open communication with the exterior by means of the water-canal (Fig. 66). Mesenchyme cells have formed a few calcareous rods about the latter (Fig. 49), especially near the point where it passes into the body-wall. Just within the body-cavity from this point, openings have appeared on it which place its interior in direct communication with the body-cavity, so that the water-vascular system combines the primitive external opening of the pentactula with the internal madreporitic openings of the other holothurians. The mesenchyme cells around the calcareous ring have formed on its posterior edge a connective-tissue ring, which later becomes so prominent in the adult as the cartilaginous ring.

In concluding this account of the embryology it may be well to summarize briefly the derivation of the different organs from the germ layers of the gastrula.

Ectoderm. From the gastrula-ectoderm arise the ectoderm of the adult, the sensory epithelium of the tentacles, the entire nervous system including all the sense organs, the larval glandular organs, and a small part of the oesophagus. Possibly the extreme posterior part of the rectum is also ectodermal.

Endoderm. From the gastrula-endoderm arise first of all the scattered mesenchyme cells which make up the mesoderm. Soon afterwards the hydroenterocoel is divided off. The remainder of the archenteron forms simply the lining of the digestive tract, including most of the oesophagus. From the hydroenterocoel, the coelomic pouches are constricted off, leaving behind the hydrocoel, from which the entire water-vascular system, and also the cavities of the digits, arise. The longitudinal muscles of the tentacles and digits come from the epithelium of the hydrocoel. The coelomic pouches form the peritoneal lining of the body-cavity and the epithelial covering for the various organs contained in it. All the muscles of the body-wall, gut, genital glands, water-ring, and Polian vessels are also derivatives of the endoderm. The genital organ, including the genital duct, and the ciliated funnels are likewise derived from the wall of the coelom. The haemal system is also covered by the epithelium of the coelom and apparently arises as evaginations of the same, while the blood-corpuscles certainly come from that layer.

Mesoderm. From the mesenchyme cells, arising from the archenteron of the gastrula, come all the connective tissue of the body, the pigment, the covering of the eyes, all the calcareous concretions (including the calcareous ring), and the cartilaginous ring. No trace of mesenchymatous musculature was found anywhere, and the part which the mesoderm takes in the formation of the haemal system is certainly inconsiderable.

8. The Anatomy of the Adult.

Although the anatomy of the European Synaptas is so well known, thanks to the investigations of Baur ('64), Semon ('87), Hamann ('83 and '89), Cuénot ('91), and others, there are so many points in which *Synapta vivipara* differs from the forms hitherto examined, it seems desirable to add a few words concerning these and other points. Except in the case of sense-organs, no attempt has been made to go into the histology, but my attention has been confined to the more general features of the minute anatomy. In the structure of the body-wall and the muscular system, there are no important features to mention, aside from the shape of the longitudinal radial muscle bands. Each of these bands is forked at its anterior extremity, and the two branches are attached to the radial calcareous plate, one on each side of the radial nerve. These branches soon unite as they pass backward, and form a single narrow band, which extends far out into the body-cavity. But still further back, it decreases in depth and increases correspondingly in width, and the epithelium which covers it tends to fuse at the outer edges with the epithelium of the body-cavity, so that at numerous points in its course the muscle has acquired secondary attachments to the body-wall. During the greater part of its course, it is a nearly flat band, but as it approaches the extreme posterior region of the body, it tends to become cylindrical, and where it ends near the anus the cross-section is circular. These changes in shape will be made clear from Figs. 94–100. The structure of the genital glands has already been given in detail, and the openings in the wall of the rectum have also been sufficiently described. The blood-vascular or haemal system is very simple, consisting of a dorsal and ventral vessel on the intestine and stomach with connecting lacunae in their walls. Posteriorly, both vessels end about half way down that section of the intestine which lies in the right ventral interradius (Fig. 92). Anteriorly, the ventral vessel ends a little in front of the stomach, on the oesophagus. The dorsal vessel runs forward to the water-ring and forms on its inner side a circumoesophageal ring, from which branches pass on to each tentacular vessel. The dorsal blood-vessel also seems to open out in the mesentery to form broad lacunae about the genital gland, such as Cuénot ('91) found in European Synaptas, but I never found coagulated blood there as in the dorsal vessel, and I do not feel sure that such lacunae actually exist. The ventral vessel of the stomach does not lie appressed to its wall, but entirely free from it and connected with it by several small branches. It is also connected by a large transverse vessel with the ventral vessel of the intestine (Fig. 92), and the two sections of the latter are also connected by a similar vessel. These transverse vessels do not appear until the animal is several centimeters long, when they arise by outgrowths of the coelomic epithelium of stomach and intestine which, lying close together as they do in the loops of the digestive tract, touch and fuse (Figs. 59 and 60) and with the increased growth of the intestine are finally drawn out to slender connecting vessels. Like the vessels of the young Synapta, these are supposed to be lined with connective tissue, but I have been unable to detect it in their walls.

The ciliated funnels of *Synapta vivipara* differ considerably in appearance from those of *S. digitata* or *S. inhaerans*, though they do not differ essentially in structure. Only one sort seems to be present and these are quite small but extremely numerous on all three of the mesenteries. They measure from 40μ to 75μ in length, and from 30μ to 40μ in breadth and depth, which is only about half the size of those of *S. digitata*. They are broad funnel- or cornucopia-shaped in outline and usually have a short stalk. Their general structure will be easily understood from Figs. 63–65. The water-vascular system consists of a circumoesophageal ring from which canals arise and pass to the tentacles, into which their entrance is guarded by well-developed valves. Each tentacle rests on the calcareous ring in such a way that the outer half of the base is on the outside of the calcareous plate, forming a sort of rudimentary ampulla (Fig. 90). There is not in the adult, any more than in any of the larval stages, the slightest trace of radia. water-canals. Dependent from the ring-canal there is always present in the left dorsal interradius a slender Polian vessel five or six millimeters long, and in nearly all adults additional Polian vessels, sometimes as many as six, are present in the ventral interradii. The stone-canal leaves the water-ring on the left-hand side of the mid-dorsal interradius and does not lie in the dorsal mesentery but clearly separate from, and to the left of it. It soon passes into it, however, on its outward course and runs to the body-wall close beside the genital duct (Figs. 66 and 67). It enters the body-wall on the right of the mesentery and bends upward more or less abruptly, opening finally to the exterior close behind the circle of tentacles (Figs. 66–70). In exceptional cases there are two openings (Figs. 71–73) or rarely the reverse happens and the canal closes before the exterior is reached. Besides this external opening, the stone-canal also opens into the body-cavity through a well-developed madrepore (Figs. 66 and 74). Throughout its course the canal is heavily ciliated, and especially so around these madreporitic openings, the whole arrangement being admirably adapted for keeping the body-cavity fluid well aerated.

The nervous system consists as in all Synaptidae of the central circumoral ring with the five radial branches and the smaller branches to each of the tentacles, but there are some additional nerves and certain of the sense-organs which have not been figured hitherto. Each of the radial nerves is divided longitudinally into an outer and an inner band as in other Synaptas, but, unlike them, there are no canals or vessels of any kind accompanying the nerves. There are, therefore, in the radii of *S. vivipara,* no spaces or lacunae in connection with either the blood, water, or nervous systems, but they are marked simply by the longitudinal muscles and nerves (Fig. 99). Each tentacle-nerve sends off branches to the digits (Fig. 55), so that almost the whole surface of the tentacle becomes sensory. On the base of the tentacles and in various parts of the ectoderm all over the body, there are numerous sense-buds or "taste-papillae," (Fig. 84), such as were first described by Hamann ('83). The structure of these organs has been well described by him and still more recently by Cuénot ('91). My observations support the opinion of the latter, that under each one of these sense papillae there lies a small ganglion. From the lower side of the circumoral ring, there arises between every two tentacles a broad band-like nerve (Figs. 75 and 76) which runs inwards towards the mouth, innervating the ectoderm of the oral disc as well as the muscles of the oesophagus. Hamann ('83) describes a single nerve to the oesophagus, and Semon ('88) speaks of it in *S. digitata,* but so far as I can learn no other nerves from the inner side of the ring have been described in holothurians. At the base of each tentacle, there are easily seen a pair of reddish brown spots, the so-called eyes (Figs. 77 and 78). Similar spots are mentioned in various Synaptas by Müller ('50), Baur ('64), and Semper ('68), but Semon ('87) and Hamann ('84) seem to doubt their visual function. There can be little doubt, however, that in *Synapta vivipara* these eyes are actually of service as light-detecting organs. In position and general structure they resemble those described by Ludwig and Barthels ('91) for *Synapta vittata.* They consist of a distinct, rather horny mesodermal layer, of a light brown color, containing scattered nuclei, overlying the swollen end of a large nerve which arises on each side from the base of the tentacle-nerve (Fig. 77). The ends of these nerves are made up of large nerve-cells with large nuclei, which are somewhat swollen and apparently vacuolated at their outer extremities. They are polygonal in outline, when seen in cross-section (Fig. 79), and the inner ends taper off into fibers which run out into the nerve (Fig. 80). The mesodermal covering, which also has the appearance of being vacuolated, is clearly a continuation of the thin mesoderm layer which surrounds all the nerves. The eyes are about 60μ in diameter, the mesodermal covering being six or eight mikrons thick. That this covering may be affected by light is probable, for its color is due to the pigment it contains. The other noteworthy sense-organs are the otocysts

(Figs. 81–83), already mentioned as lying external to the radial nerves at the point where they bend backwards over the calcareous ring. They are much smaller than those figured by Cuénot ('91) for *S. inhaerans* and differ from them in having only a single large vesiculated cell enclosed within them, instead of a number of small ones. The otocysts of *S. vivipara* measure only about 60–70μ in diameter, while the contained cell is almost a quarter as large. In no case have I found more than one cell enclosed in an otocyst of this species. Hamann ('84) suspected that they were larval organs having no function in the adult, but Semon ('87) has already proved that idea erroneous, as Hamann ('89, p. 308) has since admitted. If any further evidence were needed, it could be found in the increase of size of the organs during the development of the animal (Figs. 81–83) as well as in the very obvious connection with the radial nerves. But I am inclined to the view that these so-called otocysts do not function as hearing organs at all, but are of use to indicate the animal's position. Semon ('87) was unable to find any cilia in them, and his experiments on living Synaptas brought him to the conclusion that they were deaf to sound waves. If the enclosed cell is vesiculated, as it appears to be, it must float in the fluid with which the otocyst is filled and so presses on that part of the wall which is uppermost. Any change in the position of the animal would cause a corresponding change in the position of the enclosed cell and thus give rise to a changed sensation.

The fully grown *Synapta vivipara* (Fig. 20) measures from ten to fifteen centimeters in length and from four to nine millimeters in thickness; the size depending largely on the state of contraction of the muscles. In color they vary from a pale reddish brown to a very dark greenish brown more or less spotted and blotched with white. The ground color is due to the pigment in the connective tissue of the body-wall and varies greatly with the amount of that pigment, but the white spots and blotches are due to the aggregation of great numbers of the miliary granules, just beneath the ectoderm. The pigment is not affected to any extent by pure alcohol, but corrosive sublimate and all acids destroy or greatly modify it. Just posterior to the calcareous ring and in connection with it there is a ring of cartilage-like connective tissue (Fig. 90). This structure was described and figured by Théel ('86), who also figured the anchors and plates from the body-wall, in his account of *S. picta*. The anchors (Fig. 51) lie close under the ectoderm and parallel with it, at right angles to the main axis of the body. Each anchor is much curved or bowed inwards, while its arms or flukes are curved outward so that the points of the arms are always projecting. The vertex is not toothed but has five or six almost spherical knobs on its edge. The posterior end is broadened out into several short, very finely-toothed branches. Beneath the anchors lie the rounded, smooth-edged, somewhat arched plates, which normally possess seven large toothed holes

(Fig. 52) and two large and three small smooth holes. On the side of the plate next to the anchor and near the posterior end is an arched bow, which bears a few teeth on its anterior edge. Increased growth of the plate often increases the number of holes (Fig. 53), but as a rule they are very constant. The calcareous rods which were so abundant in the tentacles of the young larvae are so few that for a long time I was led to consider them entirely wanting. The tentacles (Fig. 57) of the adults are long and slender with from 12 to 18 pairs of digits, but the number varies greatly with the age and size of the animal. The glandular organs which characterize the young ten-tentacled stage seem to be entirely wanting now; at any rate, I have never found any trace of them in an adult.

A number of interesting monstrosities were found, chiefly among the older embryos. One of these is shown in Fig. 93, but some of the others were much more complicated, consisting of three, four, and, in one case, five young, which had grown together, or budded from each other in various ways. Among adults, besides the rather common addition of an extra tentacle, the only peculiar specimen found was one which had only three radial muscles and nerves and only eleven tentacles. There were three tentacles in the mid-dorsal interradius (indicated by the mesentery), and four tentacles in each of the lateral interradii.

9. Conclusions.

Probably no theory of echinoderm phylogeny has attracted more attention or seems more plausible than that upon which Semon ('88) determined, as the result of his studies on the development of the auricularia larva of *Synapta digitata.* Although it still finds supporters at the present time, the investigations of Ludwig ('91) on *Cucumaria* and of Ludwig and Barthels ('91) on the anatomy of the Synaptidae have shown the incorrectness of Semon's views, while the observations of Bury ('89 and '95) have cast doubt on his interpretation of some of the conditions in auricularia. It is not my intention to enter here into any discussion of the phylogeny of the echinoderms but only to suggest some of the points in the phylogeny of the holothurians, upon which the history of *Synapta vivipara* seems to throw some light, and to indicate some of the particulars in which my studies have apparently offered support to Bury's ('95) theory of the ancestral form of the echinoderms.

There are three possible opinions concerning the relationship of the Synaptidae to the other holothurians: first, Semon's ('88) view that Synapta represents a primitive form, from which the other holothurians have been derived; second, Cuénot's ('91) view that the Synaptas represent a more primitive branch of the echinoderms than and different from the true holothurians; third, Ludwig's ('89–'92) view that the Synaptidae are degenerate, pedate holothurians. Semon bases his opinion on the high development of the nervous system in Synapta, the absence of anything in their manner of life to cause degeneration, and the fact that no organs appear in the development of the young Synapta which are not present in the adult. His own observations on the nervous system of Synaptas as well as Hamann's ('83) and Cuénot's ('91) show that there is some tendency to diversity in the nervous system, especially as regards sense-organs, among the Synaptidae, and it also shows a considerable degree of adaptability to changing conditions. Moreover, I have found in *S. vivipara* that the sense-organs are highly developed, and there are additional nerves to the oesophagus, indicating modifications to suit the mode of life. It seems from these facts, that too much stress must not be placed on the opinion that the nervous system of *Synapta digitata* is primitive. As regards degeneracy and the absence of anything in the mode of life to cause it in Synaptas, it seems that Semon has expressed an erroneous opinion of the causes of degeneration. He says that we know of only three reasons for its occurrence, parasitic, fixed, or subterranean life, and, since none of these are characteristic of Synaptas, they cannot be degenerate. Had he given the matter more careful consideration he would have seen how untenable his position is. Certainly no one will deny that the loss of the power of flight in certain birds, as the famous New Zealand ground parrot, is degeneration, yet they are neither parasitic, fixed, nor subterranean. Any change in the mode of life, due to a change in environment, may result in degeneracy. The word has come to have a bad significance so that we think of it as indicating that the animal is on the down-hill road, whereas it strictly means that the animal has lost some organ or group of organs which its ancestors possessed and so has become less complex than they. Such a loss must necessarily, however, always be a gain to the species involved, otherwise it could never have come about. Now, it is entirely conceivable that in certain conditions of life on the ocean bottom, in shallow water near shore, the loss of numerous ambulacral appendages and the concentration of the water-vascular system in the circumoral tentacles would be a distinct advantage to the animal. Such has certainly been the case in Caudina (Gerould, '96), for instance, and it is probably true of all the Molpadiidae, although in these cases it may have been brought about by subterranean life. But Semon has by no means proved his point that the Synaptas are not, as a rule, subterranean. Whatever may be the condition at Naples, both on the New England coast and in Jamaica *Synapta inhaerans* and its allied forms are found normally buried deep in the sand, while the large Synaptas, like *S. lappa*, are found under stones, which is practically a subterranean mode of life. The absence of anything, therefore, in their manner of life to cause degeneration is by no means proven and will hardly stand as a good test for considering the Synaptas primitive. The statement that there is no structure developed in the young Synapta which does not appear in the adult is completely refuted by the careful observations of Ludwig and Barthels ('91) on the absence of radial water-canals in the Synaptidae. Since all observers are agreed that radial canals are developed in the embryo of *S. digitata*, it is clear that we have here a most important structure lost in the adult. For these reasons, it seems to me that Semon's view is no longer tenable. Cuénot's ('91) view is based chiefly on the important differences in the embryology of the Synaptidae and that of other holothurians, but it seems to me that he does not take sufficient account of the important evidences of degeneration in the Synaptas.

Ludwig's ('89–'92) view appears to be the one best supported by the facts, and the anatomy and embryology of *S. vivipara* offer no little confirmatory evidence. If we compare its ten-tentacled stage with the hypothetical ancestor which Ludwig describes for the Synaptidae, the resemblance is extraordinary, almost the only important difference being that the genital gland in *S. vivipara* is not equally developed on each side. In fact, the ten-tentacled stage of *Synapta vivipara* represents an actual step in the development of the Synaptidae from Ludwig's hypothetical ancestor. The Jamaican species is beyond doubt a highly modified form, and, though in some respects more highly organized than other Synaptas, in certain particulars, degeneration has gone further. Differing from other holothurians in its manner of life and its mode of reproduction, it has undergone various modifications to fit it for the changed conditions. Living in sea-weed near the surface of the water, it has developed pigment in its skin to a marked degree, and at the same time has acquired additional sense-organs in the eyes at the base of the tentacles, and an increased innervation of the oral disc. In conformity to its changed mode of reproduction, important changes have taken place in the structure of the genital gland, openings have appeared in the walls of the rectum to connect the body-cavity with the exterior, while the stone-canal has retained or has acquired secondarily its original connection with the exterior. During the progress of these specializations, the same causes have led to degeneration in other particulars. The changed mode of reproduction has modified the genital duct, so that its lumen is no longer open to the ova, and it no longer has an obvious opening to the exterior. The changed mode of life has caused a greater concentration of the water-vascular system around the mouth and a consequent *further* degeneration of the radial canals, so that they no longer appear as such even in the embryology, but tentacles develop directly from the secondary outgrowths of the hydrocoel. And, furthermore, the mid-ventral outgrowth has degenerated a step further and normally never develops at all, but disappears altogether, which is especially interesting as the mid-ventral radius is the first to develop its nerve and otocysts, and so seems to be the leader in modifications. The manner of life has also caused a modification of the tentacles in a way which we may consider as a degeneration from other Synaptas. Semon ('87) describes calcareous rods in the tentacles of all the Mediterranean Synaptas, and these appear abundantly, as we have seen, in the young stages of *S. vivipara*, but in the adult they seem to have almost entirely disappeared, the tentacles and digits being very delicate and flexible and containing no calcareous deposits, except some miliary granules. The changes in the larva due to the retention and development of the ova in the body-cavity of the mother, such as closing of the blastopore and absence of any true metamorphosis, must also be taken into consideration. For these reasons, we must consider *S. vivipara* as a highly specialized Synapta, but in its water-vascular system it has degenerated a step further than *S. digitata*, although it is neither "parasitic, fixed, nor subterranean" in its manner of life.

It is very clear from the examination of the literature on the subject that the study of any one form or class of echinoderms is entirely insufficient to fit one to determine on a theory of the phylogeny of the group. Notable examples of this may be seen in the speculations of Semon ('88), Bütschli ('92), and MacBride ('96). The *facts* added to our knowledge of echinoderm embryology by all these writers are of real value, but their hypotheses are for the most part of little importance. The same may be said of any attempt to determine the entire course of echinoderm evolution by the study of palaeontology alone, a notable example of which has recently appeared by no less an authority than Haeckel ('96). The only author who has carried on original investigations on all the classes of echinoderms and has formulated his views on the phylogeny of the group is Bury ('80 and '95), and I cannot conclude this paper without calling attention to the support which my observations give to him, on the questions involved in the development of the Synaptidae. Regarding all the points on which he lays particular stress, I have confirmed his work completely or in part. The adradial position of the water-tube, the rudimentary left anterior enterocoel, and the growth of the left body-cavity around the oesophagus are all very clearly marked in the development of *Synapta vivipara.* The only point on which I could not entirely confirm his views was on the formation of the mesentery of the stone-canal from the left coelom entirely, and on this point what evidence I did obtain indicates the correctness of his position.

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11. Explanation of Plates.

[All figures except 20 and 23 were drawn with the aid of a camera lucida.]

ABBREVIATIONS USED.

A. — atrium.
AE. — anterior enterocoel.
AN. — anus.
AO. — atrial opening.
AT. — accessory tentacle.
BC. — body-cavity.
BL. — blastopore.
BV. — blood-vessel.
CF. — ciliated funnels.
CH. — circumoesophageal ring of blood-system.
CM. —circular muscles of body-wall.
CR. — calcareous ring.
CT. — connective tissue.
Car.R. — cartilaginous ring.
Cir.S. — circular sinus formed from the anterior-prolongation of the left coelom.
DV. — dorsal vein of blood-system.
E. — enterocoel.
Ect. — ectoderm.
Epi. — epithelium.
Ey. — eyes.
GD. — genital duct.
GG. — genital gland.
H. — hydrocoel.
I. — intestine.
LC. — left coelom.
LGO. — larval glandular organ.
LM. — longitudinal muscles.
M. — mouth.
Mes. — mesenchyme.
MD. — madrepore.
MY. — mesentery.
NR. — circumoral nerve-ring.
O. — otocysts.
OE. — oesophagus.
OEN. — nerve-band to mouth and oesophagus.
PT. — primary tentacle.
PV. — Polian vesicle.
R. — rectum.
RC. — right coelom.
RN. — radial nerve.
SC. — stone-canal.
SO. — secondary outgrowth of the hydrocoel.
SP. — sense-papilla.
T. — tentacle.
TC. — canal of tentacle.
TN. — tentacle-nerve.
TV. — blood-vessel on inner side of tentacular canal.
V. — valves.
WP. — water-pore.
WR. — water-ring.

PLATE 11.

Fig. 1. Mature ovum. 225x.

Fig. 2. Two-cell stage of segmenting egg. 225x.

Fig. 3. Four-cell stage. 225x.

Fig. 4. Eight-cell stage. 225x.

Fig. 5. Sixteen-cell stage. 225x.

Fig. 6. Thirty-two-cell stage, seen from the side. 225x.

Fig. 7. Thirty-two-cell stage, seen from one of the poles. 225x.

Fig. 8. Blastula, seen from the side. 225x.

Fig. 9. Gastrula, seen from the side. 225x.

Fig. 10. Older gastrula, seen from left-hand side, to show formation of the water-pore.

Fig. 11. Still older stage, seen from left-hand side, to show the drawing away of the archenteron from the water-pore. 225x.

Fig. 12. Slightly older stage, seen from left side, to show the formation of the mouth. 225x.

Fig. 13. Older stage, seen from in front (ventrally), to show the formation of the enterocoel. 225x.

Fig. 14. Older stage, seen from in front (ventrally), to show the formation of the coelomic vesicles. 225x.

Fig. 15. Older stage, seen from in front (ventrally), to show the five primary outgrowths of the hydrocoel. 225x.

Fig. 16. Older stage, seen from left side, to show the hydrocoel, body-cavities, and atrium. 225x.

Fig. 17. Very young pentactula, from right side, to show the nerves and sense-organs. 225x.

Fig. 18. Older pentactula, seen from dorsal surface, to show the radial nerves, calcareous ring, and rudiment of accessory tentacle. 130x.

Fig. 19. Ten-tentacled young, seen from right side, to show genital gland and arrangement of organs. Twelfth tentacle just developing. 22x.

Fig. 20. Adult *Synapta vivipara*, seen from ventral surface. Nat. size.

PLATE 12.

Fig. 21. Vertical section of gastrula, to show the thickened ectoderm at apical pole. 225x.

Fig. 22. Transverse section of Fig. 13, at the line A. B., to show the thickened ventral ectoderm. 225x.

Fig. 23. Schematic outline of hydrocoel, to show the position of water-canal.

Fig. 24. Transverse sections of hydrocoels of three embryos, to show formation of anterior enterocoel. *a*, youngest stage; *b*, somewhat older; *c*, oldest stage. 225x. In *c*, only a very small part of the hydrocoel is shown.

Fig. 25. Transverse section of larva, somewhat older than Fig. 16, to show closure of hydrocoel ring, without the formation of a Polian vesicle. 225x. The section is very oblique, and takes in a part of the floor of the atrium (A), and only a portion of the hydrocoel.

Fig. 26. Transverse section of larva like Fig. 16, to show anterior prolongation of the left coelom. 225x.

Fig. 27. Transverse section of same larva, somewhat higher up, to show the left prolongations of the left coelom. 225x.

Fig. 28. Longitudinal section of larva like Fig. 16, very badly preserved, to show the anterior prolongation of the left coelom, *ant. l. c.* 225x.

Fig. 29. Posterior end of an adult, to show the rupture of the body-wall, caused by birth of the young. 35x.

Fig. 30. Transverse section of the posterior end of an adult, to show one of the openings from the rectum into the body-cavity. 65x.

Fig. 31. One of these openings more highly magnified. 500x.

Fig. 32. Part of a transverse section of a young pentactula, to show the origin of the genital gland. 500x.

Fig. 33. Similar section of an older larva, to show the increased development of the genital gland. 500x.

Fig. 34. Similar section of a still older larva, to show first appearance of lumen and covering epithelium of the genital gland. *l*, beginnings of lumen; *epi*, outer epithelium of gland, formed secondarily from right side of mesentery. 500x.

Fig. 35. Similar section of a young twelve-tentacled larva, to show the genital gland well developed on the right-hand side of mesentery and confined to that side. 500x.

Fig. 36. Part of a similar section of an adult, to show the formation of the lumen of the genital duct from the lumina of the glands. 200x.

Fig. 37. Longitudinal section of a part of genital duct, to show its structure and position in the mesentery. *l*, lumen of duct; *g. e.*, germinal epithelium; *m. e.*, epithelium of mesentery. 950x.

Fig. 38. Transverse section of dorsal body-wall of an adult, to show the termination of the genital duct. *sp*, spermatozoa. 225x.

Fig. 39. Longitudinal section of a small part of genital gland, to show the position of ovum, pressing against the epithelium of the gland. *epi*, epithelium of gland; *ov*, ovum. 500x.

Fig. 40. Transverse section of genital gland, to show its structure and the position of the ova (*ov*). 500x.

PLATE 13.

Fig. 41. Transverse section of the ectoderm of a pentactula, to show the invagination which forms the larval glandular organ. 500x.

Fig. 42. Transverse section of the same organ, fully grown, from the body-wall of a ten-tentacled larva. 500x.

Fig. 43. Longitudinal section of one of these organs, to show the peripheral position of the nuclei, and the lumen at the center. 500x.

Fig. 44. Interradial plate from the calcareous ring of an adult. 35x.

Fig. 45. Radial plate from the same ring. 35x.

Fig. 46. The development of these calcareous plates. *a*, youngest stage; *b-g*, successively older stages; *n*, older stage of an interradial plate; *i*, older stage of a radial plate. 225x.

Fig. 47. Part of the calcareous ring of an old ten-tentacled larva, to show the growth of the radial plate (*r.p.*) of the calcareous ring, in support of the developing eleventh tentacle. *ip*, interradial plates. 65x.

Fig. 48. Calcareous rods from the tentacles of a ten-tentacled larva. 225x.

Fig. 49. Calcareous rods from around madrepore. 225x.

Fig. 50. Miliary granules from the skin of an adult. 225x.

Fig. 51. Anchor from the skin of an adult. 120x.

Fig. 52. Normal anchor-plate from an adult. 120x.

Fig. 53. Abnormal anchor-plate from an adult. 120x.

Fig. 54. Longitudinal section of the tentacle of an old pentactula, to show the thickened ectoderm at the tip. 225x.

Fig. 55. Cross-section of a young tentacle, to show the entire separation of the canals of the digits from the central canal of the tentacle. 225x.

Fig. 56. Longitudinal section of part of a young tentacle, to show the origin of the digits, as outgrowths of the tentacle-canal. 225x.

Fig. 57. Tentacle of an adult. 22x.

Fig. 58. Transverse section of a mesentery and intestine of a pentactula, to show the origin of the haemal system from the right lamina of the mesentery. 500x.

Fig. 59. Loop of intestine in a small adult, to show formation of the transverse vessels of the haemal system. 35x.

Fig. 60. The same from an older specimen. 65x.

Fig. 61. Cross-section of the dorsal mesentery of a larva one mm. long, to show the beginning of the ciliated funnels. 575x.

Fig. 62. The development of the ciliated funnels. *a*, the first large cells seen from above looking down on the surface of mesentery; *b*, increased number of cells; *c*, slightly older stage seen from the side; *d*, older stage, surface view; *e*, older stage, seen partly from the side; *f*, older stage seen from the side. 575x.

Fig. 63. Longitudinal section of a funnel, to show its structure. 950x.

Fig. 64. Ciliated funnel of an adult, seen from in front. 575x.

Fig. 65. Ciliated funnel of an adult, seen from above. 225x.

Fig. 66. Surface view of stone-canal of an adult, to show its course from water-ring to the exterior. 35x.

PLATE 14.

Fig. 67. Cross-section of stone-canal and genital duct of an adult before they enter the body-wall. 225x.

Fig. 68. Cross-section of stone-canal and genital duct of same adult in the body-wall. 225x.

Fig. 69. Cross-section of same stone-canal as it approaches the body-wall. 225x.

Fig. 70. Cross-section of the same, where it opens to the exterior. 225x.

Fig. 71. Cross-section of the terminus of a stone-canal with two openings, to show the uppermost opening. 500x.

Fig. 72. Cross-section from the same series, two sections lower down. 500x.

Fig. 73. Cross-section of the same series, two sections further down, to show the second opening. 500x.

Fig. 74. Cross-section of a stone-canal of an adult, taken through the madrepore to show the openings. 225x.

Fig. 75. Longitudinal section of nerve-ring of an adult (transverse section of the animal), to show the nerve-band to the mouth and oesophagus in cross-section. 200x.

Fig. 76. Transverse section of nerve-ring (longitudinal section of animal), to show the same nerve in sagittal section. 200x.

Fig. 77. Longitudinal section of nerve-ring and transverse section of tentacle-nerve, to show the position of the eyes. 120 x.

Fig. 78. Cross-section of nerve-ring and one of the eyes, to show their relative position. 225x.

Fig. 79. Cross-section of the tip of one of the eyes, to show the vacuolated structure of the mesenchymatous covering as well as of the polygonal nerve-cells. 950x.

Fig. 80. Sagittal section of one of the eyes, to show the shape and structure of the nerve-cells. 950x.

Fig. 81. Cross-section of an otocyst and its single vesiculated cell from a pentactula. 500x.

Fig. 82. Cross-section of the otocysts and a part of the radial nerve from a twelve-tentacled young five mm. long. 500x.

Fig. 83. Cross-section of an otocyst of an adult, showing the single vesiculated cell within. 500x.

Fig. 84. Cross-section of a sense-papilla in the ectoderm of an adult, to show its structure and nerve connections. *ga*, ganglion ; *n*, nerve running to radial nerve. 500x.

PLATE 15.

Fig. 85. Transverse section of an old pentactula, to show the formation of the five accessory tentacles and the otocysts ; the secondary outgrowths of the left dorsal and mid-ventral radii have not developed at all as yet. The section is slightly oblique, more posterior on the left than on the right. 225x.

Fig. 86. Transverse section of an old ten-tentacled stage, to show position of the eleventh and twelfth tentacles. The section is somewhat oblique, more posterior on the right than on the left. 120x.

Fig. 87. Longitudinal section of the anterior end of a pentactula ; on the left through a radius ; on the right a little to one side of a radius. *f*, indicates the place of fusion between the oesophagus and roof of the atrium. 225x.

Fig. 88. Another section of the same series; on the right, through an interradius, just touching on the side of the Polian vesicle ; on the left a little to one side of an interradius. *f*, indicates the fusion of the oesophagus with the roof of the atrium. 225x.

Fig. 89. Longitudinal section of a ten-tentacled young, to show position of the various organs. 65x.

Fig. 90. Longitudinal section of an adult through one of the tentacles, to show the position of the various organs. 35x.

Fig. 91. Longitudinal section of an adult through a radius, to show position of the organs. 35x.

Fig. 92. Adult laid open in right dorsal radius, to show position of the organs and especially the blood-vessels on digestive tract. Nat. size.

Fig. 93. Larval monstrosity, a double embryo. 225x.

Fig. 94. Cross-section of longitudinal muscle of adult at the point of juncture with the calcareous ring. 65x.

Fig. 95. Cross-section of same muscle, lower down. 65x.

Fig. 96. Cross-section of same muscle, lower down. 65x.

Fig. 97. Cross-section of same muscle, lower down. 65x.

Fig. 98. Cross-section of longitudinal muscle of a smaller adult, somewhat anterior to the middle of the body. 200x.

Fig. 99. Cross-section of a longitudinal muscle in the middle of the body. 80x.

Fig. 100. Cross-section of a longitudinal muscle at extreme posterior end of the body. 200x.

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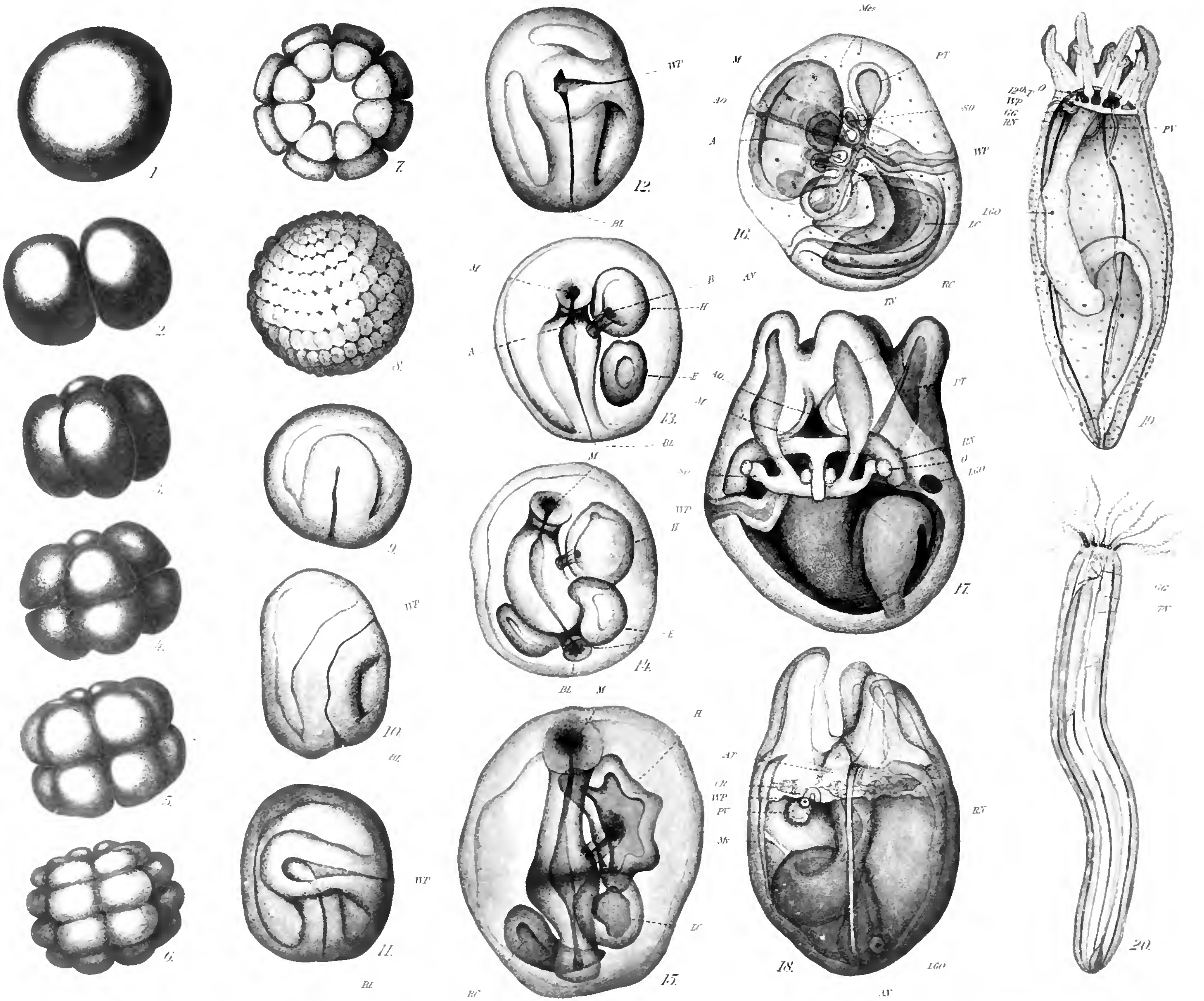

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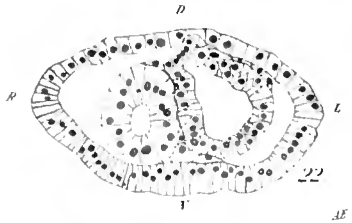

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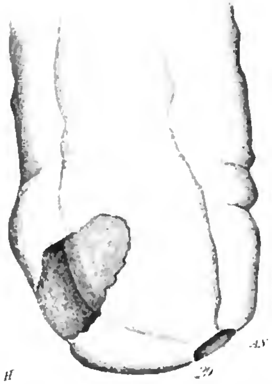

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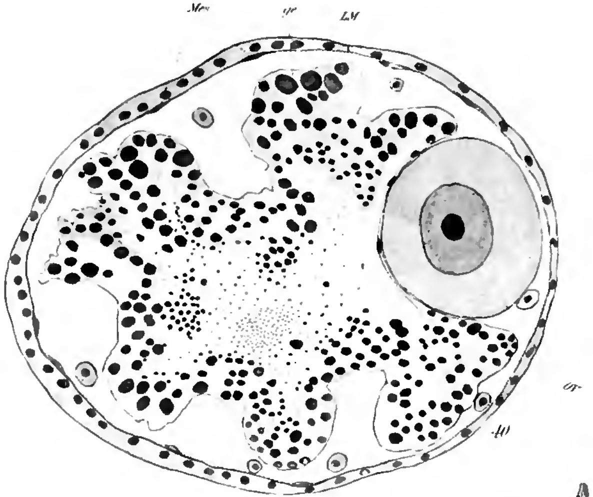

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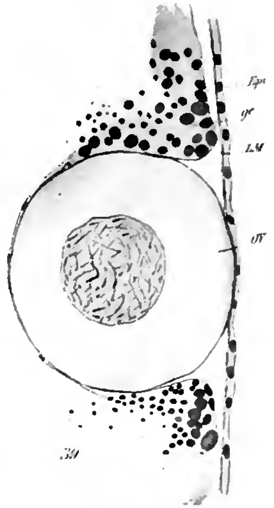

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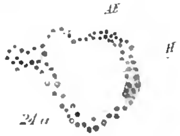

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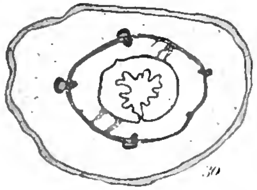
24 b.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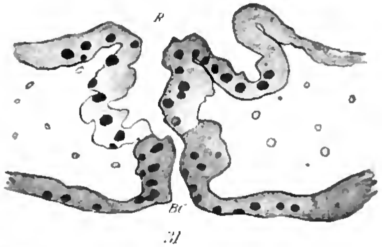

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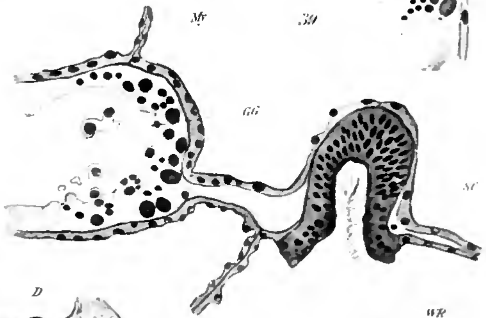

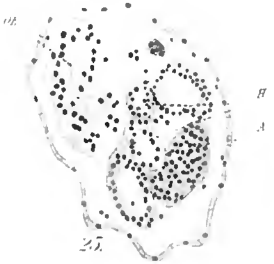

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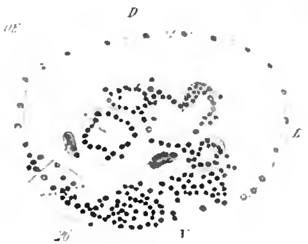

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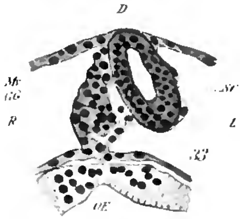

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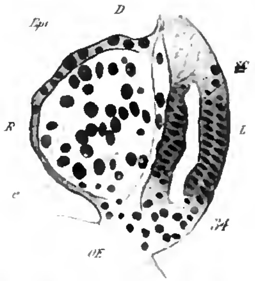

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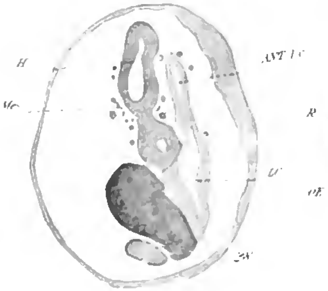

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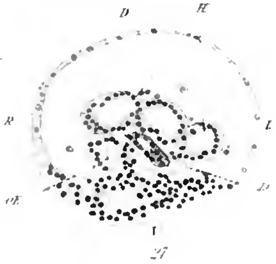

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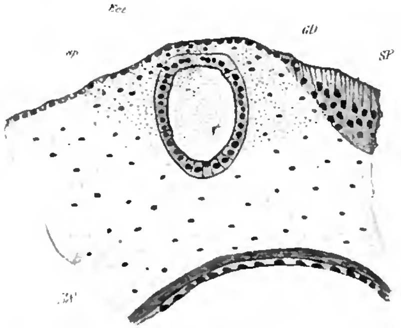

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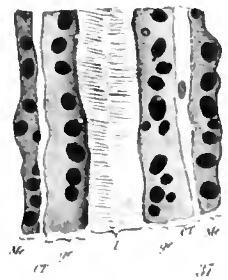

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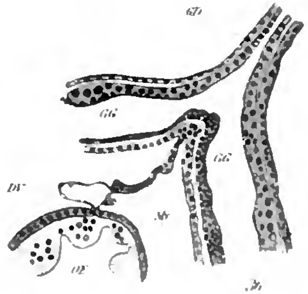

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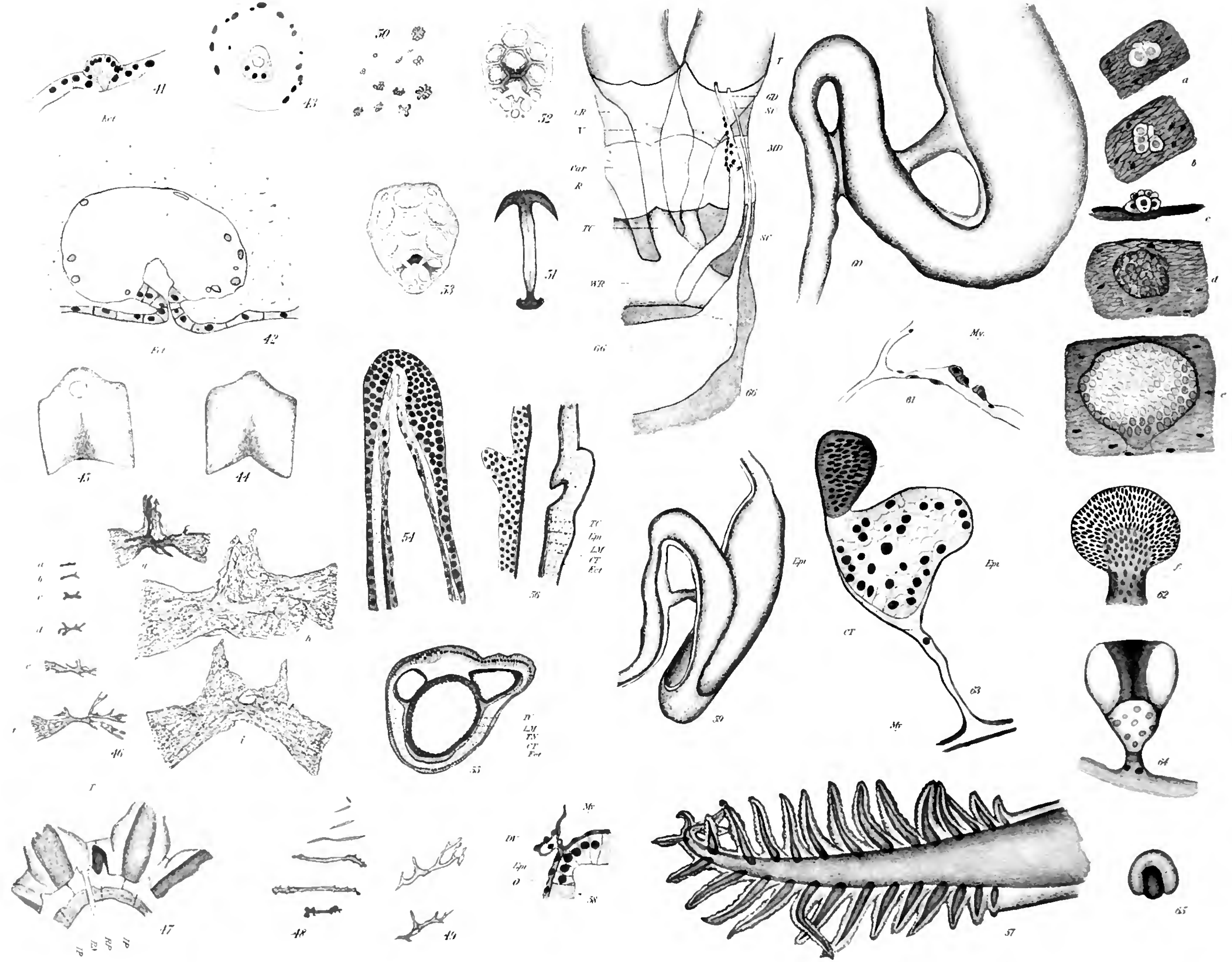

CLARK. SYNAPTA.

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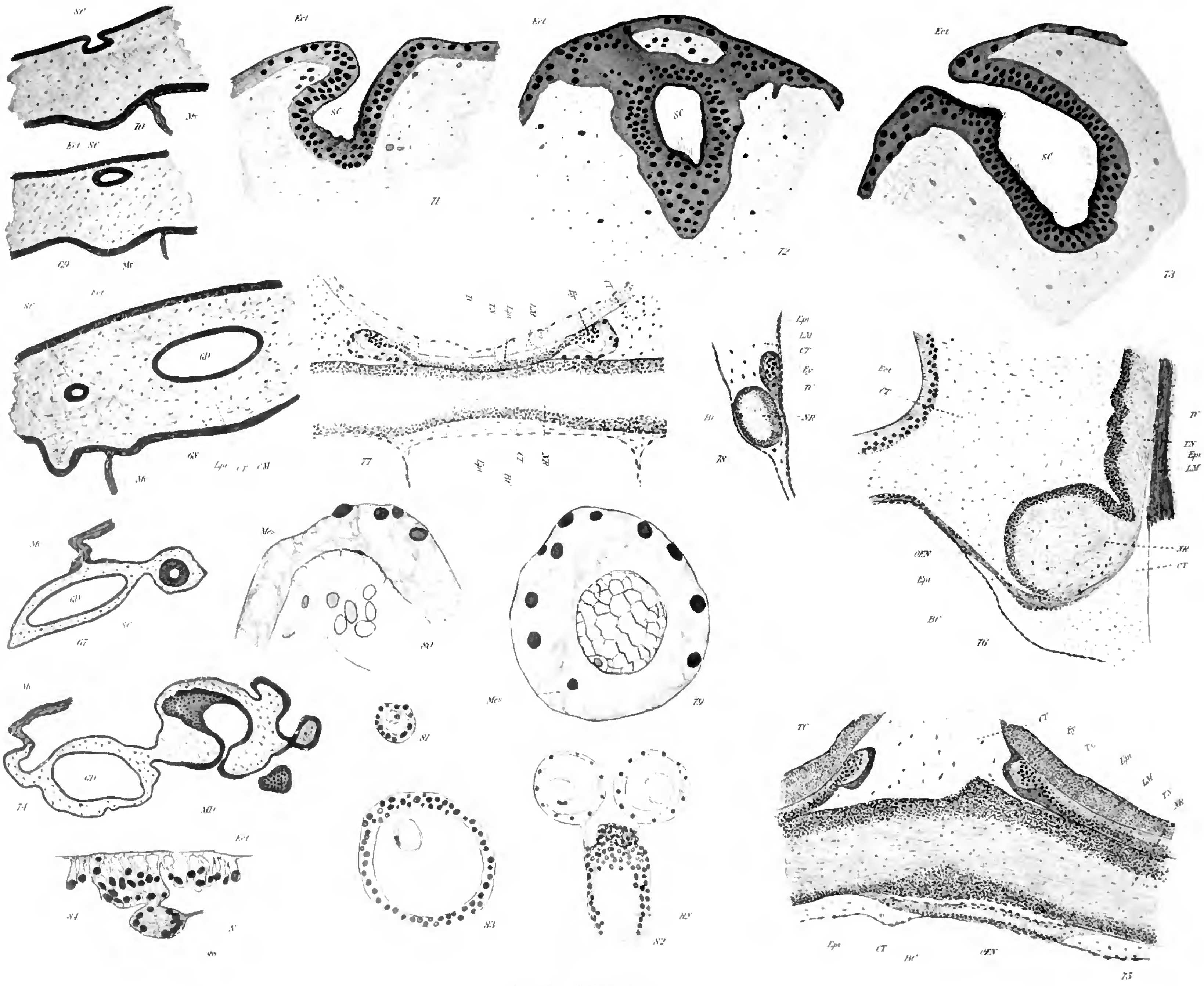
PLATE 14.



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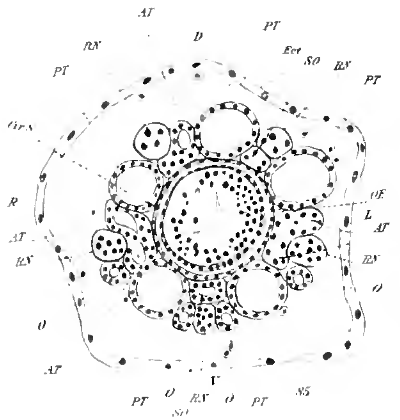

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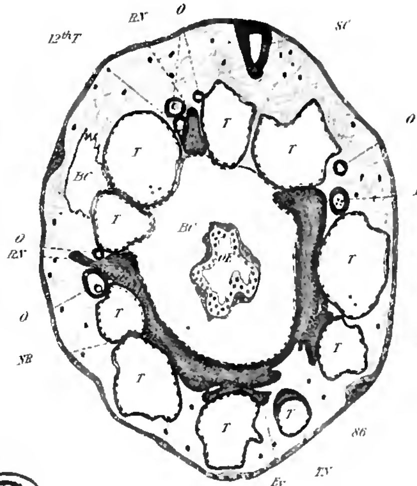

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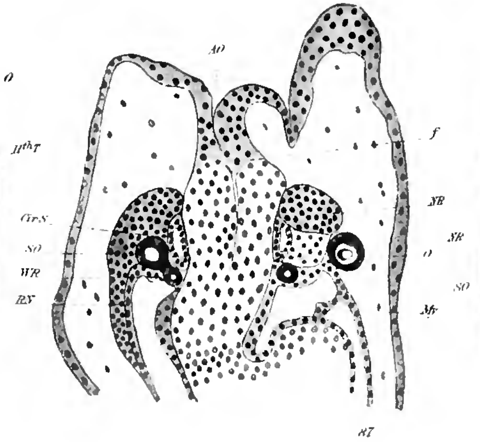

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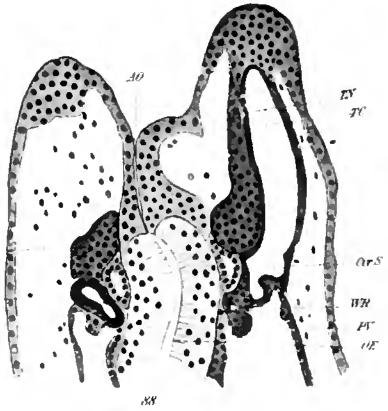

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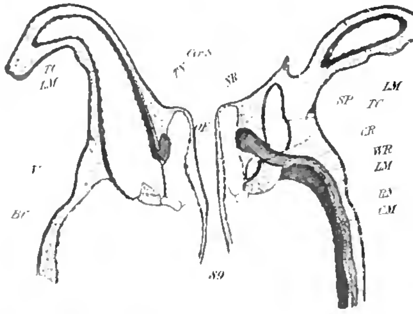

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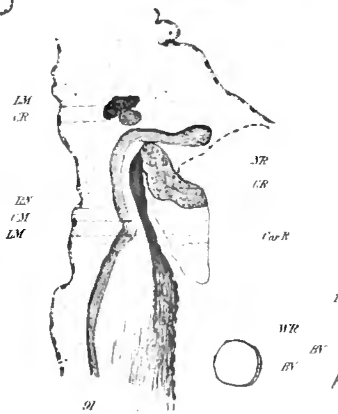

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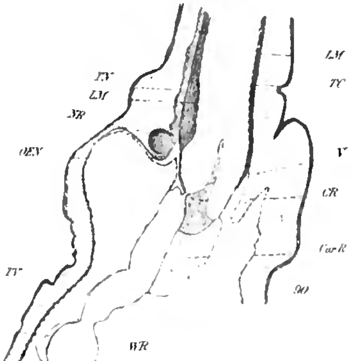

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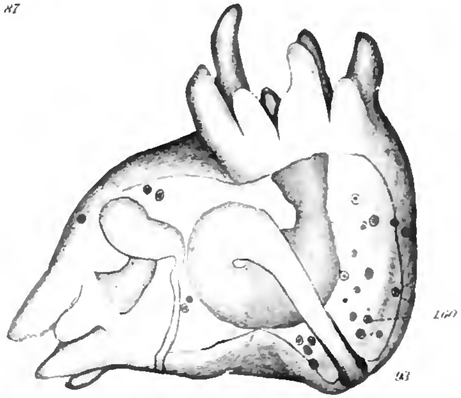

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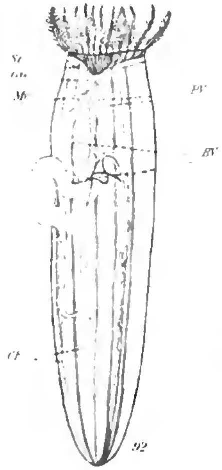

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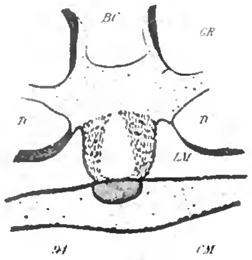

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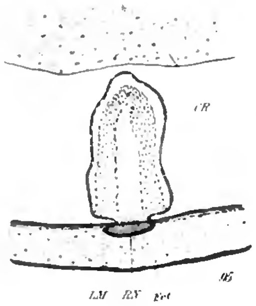

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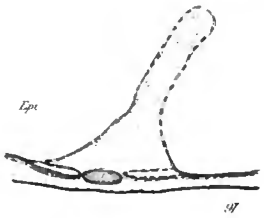

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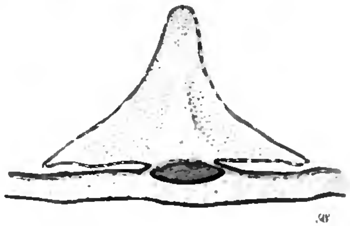

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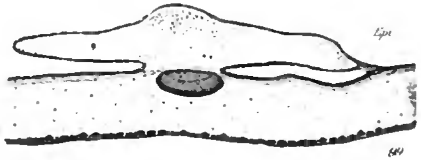

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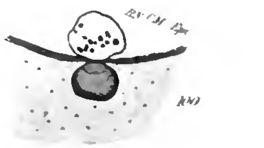

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THE ANATOMY, HABITS, AND EMBRYOLOGY OF YOLDIA LIMATULA

A DISSERTATION PRESENTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN THE
JOHNS HOPKINS UNIVERSITY, JUNE, 1898

BY

GILMAN A. DREW

[From the Memoirs from the Biological Laboratory of the Johns Hopkins University, 1899]

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THE ANATOMY, HABITS, AND EMBRYOLOGY OF YOLDIA LIMATULA, SAY.

Yoldia limatula is widely distributed along the coast of Maine, and large specimens are abundant. Their principal habitat, however, is in the shallow coves and inlets, where the tidal currents sweep by without entering. Here, soft mud has accumulated, and is constantly being added to by sediment, and by the decay of the plants and animals that are swept in from the surrounding sea and land. Specimens are most abundant in water from one to five fathoms deep, and probably never occur above low tide mark.

During the two seasons of my stay at Casco Bay, Maine, Mr. C. B. Wilson generously allowed me the free use of his equipment, which was of great value to me. Previous to this, specimens from Woods Holl, Mass., were furnished me through the kindness of Professor W. K. Brooks, Mr. Richard Rathbun and Dr. James L. Kellogg. Most of these specimens were collected by Mr. Vinal Edwards.

My own work, like the work of Drs. Mitsukuri[8] and Kellogg[5] upon this animal, has been carried on under the direction of Professor Brooks, who has for many years manifested a great interest in this rather peculiar lamellibranch. It is a pleasure to acknowledge my indebtedness to him. I wish publicly to acknowledge my indebtedness to my wife, who has materially aided me in securing, tending and preserving specimens.

ANATOMY AND HABITS.

The distinctive characters for the genus Yoldia as given by Verrill and Bush[17] are: "shell nearly smooth, compressed, lanceolate, gaping, more or less prolonged and tapering posteriorly, with a poorly defined wide rostrum, generally without carinations. The external ligament is marginal, feebly developed, continuous under the beaks and not much differentiated from the general epidermis. The chondrophore is large, concave, and projects within the margin. The pallial sinus is large and deep. The siphon-tubes and posterior pallial tentacle are long. The palpal tentacles are long and tapered; in life they may extend nearly to the end of the expanded siphon."

SHELL.

Figures 1 and 2.

To the above characters of the shell may be added a few others, part of which, no doubt, are common to all the species of the genus, while others are specific.

When the animal is taken from the mud in which it lives, the anterior portion of the shell is jet black. Posteriorly it gradually assumes olive green. The black is no doubt a stain, as it bleaches out in animals kept in aquaria, and the shell assumes a rather uniform olivaceous tint, somewhat streaked along some of the more prominent lines of growth with yellow or brown.

On each valve, two more or less pronounced radial stripes extend from the beak to the ventral margin, one anterior, the other posterior, Fig. 1. The margin of the mantle opposite the extremity of each of these stripes is specially modified and sensitive. Internally, near the dorsal margin of each valve, are two rows of toxodont teeth, one extending anteriorly and the other posteriorly from the cartilage pit, Fig. 2. Near the cartilage pit these teeth are very small and closely placed. They attain their greatest length about midway along each row, and become short and rather widely separated at the ends furthest from the cartilage pit.

Internal markings are rather obscure. Besides the scars of the foot and adductor muscles, and the pallial line with its deep and broad sinus, there is on each valve a rather distinct, curved line, extending from the ventral margin of the scar of the anterior adductor muscle, nearly to the cartilage pit. Dissection shows that this line marks the limit of the genital mass and digestive gland.

Tryon* refers to this mark on the right valve, and thinks it is caused by the loop of the intestine that extends forward, on the right side, very near the shell. That this view is wrong is shown by the presence of similar markings on both valves.

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* Structural and Systematic Conchology.

MANTLE.

FIGURES 1 AND 3.

The lobes of the mantle are free along their ventral borders, and are ciliated in patches on their inner surfaces. They are modified to form the siphons, the marginal tentacles, an unpaired, very much elongated, tentacle situated near the base of the siphons, a flattened expansion opposite the extremity of each radiating stripe on the posterior end of the shell, and a rounded projection opposite the extremity of each radiating stripe on the anterior end of the shell. These will be treated in turn. There are also two pairs of patches that are apparently glandular. One pair is situated ventral to the anterior adductor muscle, and the other ventral to the base of the siphons.

Siphons.—The oldest specimens reared from eggs did not begin to develop siphons. The youngest specimen collected with a dredge (about .5 mm. long) had already formed the exhalent siphon.

This siphon, Fig. 11, seems to have been formed by the union of the margins of the lobes of the mantle, followed by their growth into a tube, and the withdrawal of the tube between the lobes of the mantle. In withdrawing the tube, its dorsal surface, corresponding to the dorsal surface of the united lobes of the mantle, is drawn in, forming a complete septum. A ridge on each lobe of the mantle indicates where the point of union of the margins of the mantle has been drawn along its inner surface.

The ventral surface of the base of this siphon arches dorsally, Fig. 12, the ridges on the lobes of the mantle near its base thicken, and finally fuse. Thus a second tube is formed lying ventral to the exhalent siphon, Fig. 13. The wall separating the two siphons remains arched upward for some time, but subsequent growth straightens it. Even in the adult the line of fusion along the ventral side of the inhalent siphon remains distinct, Fig. 14, and offers little resistance to splitting. Although the inhalent siphon is formed between the lobes of the mantle, at the base of the exhalent siphon, it may morphologically be considered marginal in formation, as it is formed by thickenings of, and growth from, ridges that seem to have been carried back from the margin. The adult siphons are united along their whole length, Figs. 1 and 3, and may be extended beyond the shell to a distance considerably exceeding the length of the shell. Normally the inhalent siphon is shorter, broader, and has thicker walls than the exhalent siphon, but they are frequently rendered of equal length by injury. Both siphons, Fig. 14, have, between their outer and inner layers of epithelium, large bundles of longitudinal muscle fibres, separated by sheets of radial muscles. A few circular fibres lie near the epithelium, but they are not numerous. The siphons are extended by forcing blood into the spaces hollowed out in the connective tissue. If the siphon of a young specimen is examined with a moderately high power of the microscope, small, conical papillæ will be seen projecting from its surface, Fig. 15. Each papilla bears at its tip a long, rigid filament. Older specimens show similar papillæ, but instead of bearing a single elongated filament, several shorter filaments are borne on the tip of each. Similar papillæ are found in various places on the mantle and its modifications. They probably correspond to the "Pinselzellen" of Fleming,[3] later described by Dorst[2] and Rawitz.[13]

Siphonal tentacle and marginal tentacles.—The youngest specimen collected with a dredge shows a little rounded knob, Fig. 11, st., lying on one side, between the mantle and the siphon. This knob, the rudiment of the siphonal tentacle, is an outgrowth from the line of union of the mantle with the base of the siphon, which line, as has been shown, seems morphologically to be a portion of the margin of the mantle.

During the development of the siphons the tentacle is carried ventrally and, in the adult, comes to lie nearly opposite the ventral border of the inhalent siphon. This unpaired tentacle was first described by Brooks[1] and has frequently been referred to since. Pelseneer[10] found that it occurred on either the right or left side of Yoldia isonota, an observation that also holds true for Y. limatula. From its position and innervation Pelseneer[10] was led to conclude that it might be compared to the osphradium of gastropods, a conclusion that he later modified.[11] Another organ corresponding in innervation and position to the osphradium of other lamellibranchs is present and will be described later.

When extended, Figs. 1, 3 and 10, st., the siphonal tentacle is a long and slender filament, gradually tapering to its free extremity, and generally lying loosely coiled on the bottom of the aquarium, or on the surface of the mud in which the animal lives. Throughout its length it is set with small, conical papillæ, Figs. 6 and 7, such as have already been described for the siphons. Each papilla, like the papillæ on the adult siphon, bears a cluster of filaments at its tip.

When retracted the tentacle presents a series of transverse wrinkles, Fig. 6. Beneath the layer of epithelium, Fig. 8, ep., run strands of longitudinal muscle fibres, lm., imbedded in connective tissue. On the side of the tentacle nearest the lobe of the mantle to which it is attached, inside the layer of muscles, is a large nerve, tn., which can be easily traced to the tip of the tentacle. This nerve is a branch of the posterior pallial nerve. It is not given off directly opposite the base of the tentacle, but some distance above it, and the two nerves continue along, side by side, until the tentacle is reached. The appearance of the two nerves lying side by side is quite like that of a ganglion, and has, no doubt, been mistaken for one. On the side of the tentacle opposite the nerve, also within the layer of muscles, is a more or less definite blood-space, bs.

Extension of the tentacle seems to be accomplished by forcing blood into this space. In favorable cases blood corpuscles can be seen moving along it when the tentacle is being extended. If considerable force is exerted in extending the tentacle, swellings, Fig. 7, may occur in it. Such swellings are filled with blood and disappear when the pressure is removed. When the muscles of the tentacle contract, the blood is forced back and the blood-space may be completely obliterated.

The tentacles that fringe the postero-ventral margins of the mantle, have, beneath their epithelium, both longitudinal and transverse strands of muscle fibres, and generally several blood-spaces. While branches of the pallial nerves have not been traced into these tentacles, such branches can be traced to their bases, and there can be no doubt that the tentacles are supplied by fibres from these nerves.

Each tentacle has at least one papilla and frequently there are several papillæ upon its surface. In development the tentacle is preceded by a single sense papilla which is carried out by the growth of the mantle near its base into a conspicuous projection. As this projection grows, other sense papillæ make their appearance on its sides, and the papilla at its tip may or may not retain its position. In a few cases the tentacles divide or branch. This is most common with the tentacles fringing the posterior expansions of the mantle, soon to be described.

Considering the origin, structure, and innervation of the siphonal tentacle and the marginal tentacles, there can be but little doubt that the siphonal tentacle is a greatly enlarged and specialized marginal tentacle.*

Both structure and experiment agree in assigning to these tentacles a tactile function. The siphonal tentacle is not, as might be supposed, the most sensitive to touch of any of the organs. It seems to be rather more sensitive than the marginal tentacles, about as sensitive as the expansions of the mantle opposite the extremities of the stripes on the posterior end of the shell, and rather less sensitive than the projections opposite the extremities of the stripes on the anterior end of the shell, the foot, and the siphons. It may be moved about with the point of a pencil without causing much disturbance, but if it be pressed slightly, moved quickly, or jarred, it is quickly withdrawn, and the withdrawal may be accompanied by the partial or complete retraction of siphons, the closing of the shell, and, in some cases, by the activity of the foot. It seems especially sensitive to sudden movements or jars, and its special function may lie in this direction, in enabling the creature to detect the approach of enemies, of which flounders seem to be among the most dangerous.

If a vessel, containing several specimens partially buried in the mud, is not disturbed for some hours and is then jarred, all will generally disappear with astonishing rapidity. All of the experiments that were tried to determine the function of the tentacle resulted in failure, inasmuch as specimens in which the tentacle had been removed seemed to be as sensitive to jars as uninjured specimens. It may be remarked, however, that the jars of a small vessel can at best bear only a slight resemblance to jars affecting the surface of the mud on the bottom of the ocean, such as would be caused, for instance, by the swimming of a flounder.

Posterior expansions of the mantle.—These expansions, Figs. 1, 3 and 10, pe., lie opposite the extremities of the stripes on the posterior end of the shell. They consist of flat, somewhat triangular extensions of the edges of the mantle. The anterior border of each is fringed with tentacles, resembling the ordinary marginal tentacles, but more frequently branched, and usually with a rather larger proportion of sense-papillæ. The inner surfaces of the expansions are very densely ciliated. Near the base of each is a fold or ridge, along the side of which such dirt as gains access to the mantle chamber is swept.

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* See note at the end of the paper.

This dirt is swept back over the expansions and so out of the cavity. The rich nervous supply comes as branches of the posterior pallial nerves.

Anterior projections of the mantle.—The antero-ventral margins of the mantle may be protruded a short distance beyond the margin of the shell, Fig. 1, and seem to aid in cleaning the foot when it is being withdrawn from the mud. These margins are destitute of tentacles, but they are well supplied with sense-papillæ.

Arising from each margin, opposite the extremity of the stripe on the anterior end of the shell, is an oblong projection, Fig. 1, ae. This projection carries a row of sense-papillæ, and is ciliated on either side, Figs. 16 and 17. Branches of the anterior pallial nerve undoubtedly enter it, and enlarged pallial muscles act as its retractor.

These organs are very sensitive to mechanical stimulation, and probably serve as tactile organs, but their function is not known. They are placed so near the edges of the retracted foot that it seems possible that they may serve some function in connection with it, but no observations were made that support this surmise or that give a clue to any other function.

FOOT.

FIGURES 3, 5 AND 9, f.

The foot, Fig. 3, f., is very large and powerful. Its sides form two muscular flaps, that lie side by side, and are capable of being extended laterally, Fig. 9, in which position they form an almost flat or arched surface. It is this part of the foot that is called the sole.

Notwithstanding its being a rigid muscular organ, known to be adapted for burrowing[5 and 16] and executing movements with remarkable rapidity,[1 and 17] this part of the foot is still referred to as a "creeping sole."*

The free margins of the flaps are thin, and are fringed with flattened papillæ that are very sensitive to touch. There are four pairs of foot-muscles, one posterior and three anterior. The posterior foot-muscles, Fig. 3, pfm., are inserted on the shell, just in front of the posterior adductor muscle and very near the bases of the teeth. They are very large and send all of their fibres forward, along the

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*See note on page 9 of the paper.

sides of the foot, to be distributed to its anterior and ventral portions. Their function is to retract the foot.

The anterior foot-muscles, afm., are inserted on the shell just behind the anterior adductor muscle and very near the bases of the teeth. Of these muscles there are three pairs. The anterior pair pass ventrally and posteriorly along the sides of the foot, and are distributed to its posterior portion. The middle pair pass ventrally, between the pair just mentioned, and are distributed to an intermediate portion. The posterior pair pass ventrally and anteriorly, between both of the preceding pairs and are distributed to the anterior and ventral portion of the foot, including the muscular flaps. These three pairs of muscles are undoubtedly used in producing the varied and energetic movements of the foot.

Besides these special foot-muscles, which together form a large part of the outer walls of the foot, there are transverse strands of muscle fibres extending from one wall to the other. Large blood-spaces are hollowed out between these strands.

Movements of the foot are always very rapid and are remarkably diversified. The movements of burrowing consist of thrusting the closed foot, which is wedge-shaped, deep into the mud, reflecting its margins to form an anchor, and then withdrawing it. These movements follow each other in quick succession and enable an animal to bury itself with great rapidity. When a specimen is placed upon its side, the closed foot is bent back under the shell, its margins are reflected, and it is then withdrawn. If these movements are executed on mud, the lower reflected margin of the foot buries itself, and gives the necessary purchase for the animal to right itself. If instead, they are executed on a smooth, hard surface, where no purchase can be obtained, these movements are likely to be replaced by leaping movements.

One leaping movement consists of bending the foot back under the shell, turning the shell nearly on its dorsal margin, planting the surface of the expanded "sole" on the bottom, and giving a quick downward movement. If the foot does not slip, the shell is generally turned end for end and thrown some inches. If the foot slips, as more frequently happens in smooth-bottomed aquaria, it shoots forward with wonderful rapidity and causes a posterior movement. Other movements are common but will not be described. It seems very hard to imagine that the foot could possibly be used as a creeping organ, and its present function, for which its structure so admirably fits it, is to burrow in soft mud.*

BYSSAL GLAND.

FIGURES 4 AND 5, bg.

In none of the specimens that came under my observation, did this organ seem to be functional. The youngest specimen collected with a dredge shows a small pouch, lined with epithelium, which opens into the posterior end of the groove that separates the muscular flaps of the foot. The gland receives a rather large nerve from each pedal ganglion, and it often contains a few fine threads. These threads have never been seen protruding from the duct of the gland.

ALIMENTARY CANAL.

FIGURES 4 AND 5.

The rather broad and long œsophagus opens into the dorsal end of a capacious stomach, Fig. 4, sto., which extends from near the dorsal margin of the animal, well into the foot. The stomach is divided transversely by a well-marked constriction, and internally by a prominent ridge, formed by elongated epithelial cells. Above this ridge the epithelial cells are rather slender, and stain deeply. Below the ridge the epithelial cells are broader and stain less deeply.

From the ventral end of this portion of the stomach, the intestine bends back along its posterior side, ascends to a point just beneath the pericardium, makes a forward turn, comes very near the surface on the right side, follows the edge of the genital mass and digestive gland

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*Specimens of Yoldia limatula, Say, Nucula proxima, Say, and Nucula delphinodonta, Mighels, have been observed for hours together, in smooth and rough-bottomed dishes, in dishes containing sand, and in dishes containing the soft mud in which the animals normally live. They all burrow with rapidity and in the same manner, but in no case was a specimen observed to creep, even for the shortest distance. The expanded foot of N. delphinodonta is very large in proportion to the size of the animal; the movements are comparatively sluggish, and the almost spherical shell is raised or turned over with but little difficulty, but the movements of the foot are always such as are used in burrowing. Furthermore, in none of these forms does the foot correspond in structure with that of known creeping organs.

nearly to the anterior adductor muscle, then turns dorsally and posteriorly, gradually assumes a medium position again, passes through the ventricle, and opens into the mantle chamber at the base of the exhalent siphon, just behind the posterior adductor muscle. The intestinal epithelium is composed of short, deeply staining cells, which are frequently arranged in longitudinal ridges.

DIGESTIVE GLANDS.

The racemose digestive glands open into the stomach near its dorsal end by short broad ducts. The lobes are very numerous and form a rather compact mass in the dorsal region of the body, which latterly overhangs the dorsal part of the foot. The left gland is larger than the right.

LABIAL PALPS.

Figures 3 and 5, lp.

The palps of the adult animal are very large, Fig. 3, lp. Each united pair is suspended from the body wall by a thin membrane, which contains a few muscle fibres. This membrane is attached to the body wall beneath the overhanging digestive gland. The palps are triangular in shape and have their inner surfaces ciliated and thrown into series of ridges and grooves that do not extend quite to their free margins. Large blood-spaces follow along the bases of many of these ridges. The supposition that the large expanded palps serve in respiration seems probable.

Each outer palp is supplied with a long appendage, Fig. 3, pap., which originates from its posterior end, near its dorsal margin, and can be extended far beyond the posterior margin of the shell.

In young specimens, this appendage is flat and is entirely confined to the external palp, Fig. 5, pap. As it grows it folds longitudinally, so as to form a groove on its inner side, and, at the time, twists so that it may appear like a continuation of the united dorsal margins of the outer and inner palps.

Each palp-appendage is supplied with longitudinal muscles, Fig. 18, lm., a large nerve, pn., that is continued into it from the dorsal margins of the palps, and a continuous blood-space, bs., lying beside, and morphologically ventral to it. Under favorable conditions, blood corpuscles may be seen moving along this space when the appendage is being extended. Other blood-spaces occur in the connective tissue of the appendage, but they are much smaller and anastomose freely.

The epithelium lining the groove formed by the longitudinal folding of the appendage is densely covered with cilia.

The animal while feeding, Fig. 10, is usually slightly tipped ventrally from the perpendicular, and frequently has about one-third of its posterior end above the mud. While in this position, the palp-appendages are thrust out of the shell and one, at least, bends over and inserts its tip in the mud. The cilia lining its longitudinal groove immediately begin to elevate the mud, which is rich in living organisms. The stream of particles passing along the groove is large enough to be distinguished at a distance of some feet. In this way foraminifers, ostracods, and even small lamellibranchs, and gastropods, together with the smaller forms and mud, are passed along the groove, finally between the palps, and so on into the mouth. Thus we find that Mitsukuri's surmise,[8] based on finding sand in the grooves of the palp-appendages of preserved specimens, was right. The palp-appendages are food collectors.

GILLS.

FIGURES 3, 19 AND 20.

Although the gills have been well treated by Mitsukuri,[8] Kellogg[5] and others, some additional facts, both on the structure and function of these organs, seem to make it allowable to go over the already rather familiar ground.

Each gill, Fig. 3, g., consists of a double series of rather broad, flat plates, placed laterally edge to edge, and antero-posteriorly with their flat surfaces opposed.

This double series of plates is suspended from the body wall by a thin muscular membrane. Anteriorly the gills pass beneath the overhanging digestive glands, on the under sides of which the plates gradually become smaller and smaller, and finally fade away. The extreme anterior ends are continued as ridges which seem to represent continuations of the suspensory membranes rather than gill plates, and point to the probable origin of the membranes as folds from the body wall. Posteriorly the gills likewise become smaller, and are finally attached to the wall that separates the inhalent from the exhalent siphon. The suspensory membranes are continued posteriorly as ridges, beneath the posterior adductor muscle, and finally disappear.

With the exception of a few of the plates at the extreme anterior ends of the gills, which are sometimes much distorted and swollen, all of the plates are alike in shape and structure. Laterally the plates of each gill lie opposite each other. Generally in the length of each gill one or more plates are interpolated on one side or the other, Fig. 20, and thus the plates are made to alternate for a short distance, but they soon become opposite again. Kellogg's[5] opinion that the plates of each gill are alternate and not opposite, is based on horizontal sections taken below the upper longitudinal muscle, in which position the inner edges of the plates are alternate. This seems to be due to bending, caused, perhaps, by the pressure of blood in them. Horizontal sections through the bases of the gills, as well as whole specimens, show the plates to be opposite as a rule.

The plates on the two sides of each gill are separated from each other except below, where they are fused, either leaving a connecting ridge, as frequently happens anteriorly, or a smooth intermediate portion, as is generally the case further back. Each plate is also joined to the suspensory membrane, Fig. 19, gs., above, and to two longitudinal muscles, llm. and ulm., that are continuous the length of the gill. Each plate is hollow and may be likened to a loosely folded sheet of paper, leaving a space between, which space is traversed by a few fibres of connective tissue. The unshaded line, Fig. 19, represents the wall that has been cut in separating the plate from the plate lying in front of it. The opposite wall of the plate is continuous with the wall of the plate lying behind it. Along each side of the ventral portion of each plate, lying just inside and closely applied to the wall, is a chitinous rod or plate Fig. 19, cr. These rods are quite heavy near the median line of the gill, become thinner laterally, and finally disappear. Furthermore the chitinous rod on each side of each plate is continuous with the chitinous rod of the opposing side of the plate adjoining. Each rod might then be described as hairpin-shaped, with two prongs, each of which extends along the inner side of the wall of one side of one plate. Each plate receives one prong from each of two hairpin-shaped rods, Fig. 20, cr.

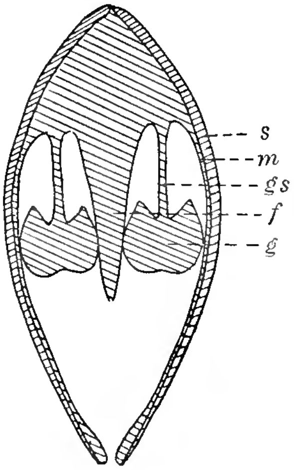
Many of the muscle fibres of the suspensory membrane are continued down along the inner surface of the anterior wall of each plate, Fig. 19, mp. These were supposed by Mitsukuri[8] to be chitinous, but they were later shown by Kellogg[5] to be muscles. They start from the suspensory membrane as bundles of fibres, which branch and spread out laterally as they descend. Many of the fibres apparently find insertion in the wall of the plate itself, but not a few are extended to the chitinous rods and are inserted over their surfaces. Kellogg,[5] no doubt rightly referred movements of the plates, which are common in the gills of mutilated specimens, and in the excised gills themselves, to these muscles. The normal function of these muscles will be made apparent later, in connection with the special function of the gills.

Each plate bears cilia along its ventral margin, and for a short distance along each side, but not over its general surface.

The cilia between the plates are arranged in rows that run parallel with the margins of the plates, there being one or two rows on each side of each plate. Near the ends of the chitinous rods, the cilia on the edges of the plates disappear, and those between the plates become modified, as described by Kellogg,[5] for holding the plates together. They do not seem to be hooked, but are very numerous, rather stout, and freely intermingle with the cluster on the adjoining plate. The area covered by these cilia is rather limited, and above them the plates are not ciliated. The cilia of the gills seem to drive water between the plates and aid in lowering the gills.

Each gill has two rather large bundles of muscles running its entire length, one above, Fig. 19, ulm., and one below, llm. The lower bundle is somewhat crescent shaped in cross-section, the concave surface being directed upward and forming part of the ventral wall of a large blood-space, bs., that is also continuous the length of the gill. These longitudinal muscles were supposed by Mitsukuri,[8] whose material was poorly preserved, to be fibrous tissue, but there seems to be no doubt that they are muscles. Their contraction causes the gills to shorten, a movement already described by Kellogg,[5] and a movement necessarily of service in their special function.

The cavities of the plates on the two sides of each gill open freely into each other, and the cavities of all of the plates are put into communication through the blood-space, bs., which is continued upward between the plates as a narrow slit reaching to the upper longitudinal muscle. Above this muscle, at the base of the suspensory membrane, is another blood-space, also running the length of the gill, separated from the blood-spaces between the muscular walls of the suspensory membrane only by occasional strands of connective tissue. This space communicates laterally with the cavity of each gill plate. Mitsukuri[8] supposed that these blood channels in Nucula were connected with some definite blood circulation. In Yoldia there seems to be no evidence that the blood follows a very definite course. The blood from the gills passes into the auricles, which are situated near the anterior extremities of the gills. It seems probable that the movements of the blood in all of the blood-spaces of the gills tend toward the auricles. The continuous longitudinal spaces are probably the means of equalizing pressure throughout the gills, by allowing a free movement of the blood to different parts as circumstances demand.



Diagrammatic transverse section of Yoldia, showing the position and attachment of the gills. f, foot; g, gill; gs, gill suspensory membrane; m, mantle; s, shell.

It will be remembered that the gills are suspended by muscular membranes (gs, in the accompanying diagram), which probably represent folds of the body wall. The gills, g, are composed of wide plates that are sufficiently wide to span the space between the foot, f, and the mantle, m, and, behind the foot, unitedly to span the mantle-chamber itself. Anteriorly they gradually diminish in size and finally disappear. Posteriorly they are attached to the wall that separates the inhalent from the exhalent siphon. The mantle-chamber is thus divided by a movable partition, into a ventral chamber, opening through the inhalent siphon and a dorsal chamber, opening through the exhalent siphon.

In young specimens the movements of the brown gills are visible through the shell. They are gradually pressed ventrally, probably by the blood forced into them, possibly aided by the cilia, which, as Kellogg[5] has pointed out, are so powerful in their action as frequently to cause excised gills to move about in the water. As the gills descend, the water passes between the plates. After reaching their greatest ventral depression the gills may remain quiet for a longer or shorter time. The period of rest is followed by energetic contractions of the suspensory membranes, resulting in a vigorous discharge of water through the exhalent siphon, as the chamber dorsal to the gills diminishes, and a corresponding influx of water through the inhalent siphon, as the chamber ventral to the gills enlarges. During this exchange, the siphons are made quite rigid, probably by having blood forced into them. The movements of the siphons accompanying the movements of the gills are very conspicuous and have been mentioned by Brooks[1].

The movements of the gills are more or less rhythmic, the time varying with the needs of the animal. Thus the rhythm is much faster after a disturbance that has caused all movements to be suspended for some time, than when no such disturbance has occurred.

The currents of water are probably for respiratory purposes, and to keep the mantle-chamber clear of the dirt that is constantly finding its way in, more especially the fæces, which, being so largely composed of sand and other heavy particles, would otherwise drop into, and soon clog, this chamber.

It seems to be a justifiable suggestion that the contraction of the gills may aid in the movements of blood as well as the movements of water. The blood-spaces of the plates, and especially of the suspensory membranes are considerably diminished in size during each contraction, and, as the openings where the spaces of the suspensory membranes communicate with the auricles are guarded by ridges that probably act as valves, each contraction must modify the blood-supply.

A little study will show how admirably the gills are fitted for the function of pumping water.

In shape they exactly fit the mantle-chamber, in which they form a movable partition. Contact is insured by the pressure of the blood inside the plates, and by the soft dorsal projections of the plates. These projections must act much like the leather on the plunger of a suction pump, making good contact when there is pressure from above but not hindering its descent.

When the gills are depressed, the plates are loosely opposed and allow water to pass freely between them. In this position the gills are much longer than during contraction, and lie in curves, Fig. 3, g. When the suspensory membranes contract, the longitudinal muscles, Fig. 19, ulm., and llm., also contract, the gills are shortened, and the plates are more closely opposed.

Each plate is rendered rather rigid ventrally by chitinous rods that are so disposed as to allow flexibility. Many of the muscle fibres of the plate are attached to these rods in such a way as to insure an even strain, and keep the plate from bending ventrally when pressure is applied.

Experiments were tried to determine, if possible, the part taken by the gills in the collection of food. For this purpose both mutilated and uninjured specimens were used. No definite results were reached, but they were not observed actively engaged in collecting food. Considering the remarkable activity of the palps as collectors of food, such activity for the gills seems rather unnecessary, and it would also seem that the pumping action of the gills would seriously interfere with their normally performing such a function.

As an experiment, specimens were placed in shallow dishes and supplied with water in which living organisms were very abundant. Under these conditions many specimens died with all the symptoms of starvation, and those that still survived after several weeks of this treatment were very weak and without the usual color. These weak specimens, when placed in their native mud, where the palp-appendages could be used, regained their strength and color very rapidly.

EXCRETORY ORGANS.

FIGURE 23.

The excretory organs of the adult animal are very extensive. They consist of many loops, the walls of which are much sacculated. They lie ventral to the pericardium, and are continued into the foot along the posterior side of the stomach. The inner, pericardial, opening of each excretory organ is separated from the outer, mantle-chamber, opening by a very short space.

Fig. 23 is a drawing of a wax model of the ends of the left excretory organ and genital duct, seen from the ventral side. The inner end, ie., opens into the pericardium, pc., by a rather large opening, turns abruptly towards the middle line of the body, crosses the outer end, oe., and is continued anteriorly close to the pericardium. After passing through the many sacculated loops already mentioned, the tube again comes near the pericardial wall, enlarges, runs alongside the anterior turn of the inner end, narrows down again and opens into the mantle-chamber through an antero-posteriorly elongated opening, mco., just posterior to the point where the outer and inner ends of the tube cross.

The genital duct, gd, following the course of the cerebro-visceral commissure, turns ventrally when almost in contact with the inner end of the excretory organ, meets the outer end, and opens with it. The common opening of the excretory organ and genital duct is, as has been noticed, elongated in an antero-posterior direction, Fig. 23, mco., and may represent a fusion of the two rather than an opening of one into the other.

As has been seen, the condition described by Pelseneer,[11] viz: the genital duct opening into the excretory organ near its pericardial opening, is not borne out by these observations.

In material that is not well preserved it not unfrequently happens that the walls of the genital duct and the inner end of the excretory organ are ruptured in sectioning, at the point where they come in contact, thus placing their cavities in communication.

It may be well to state in passing that the genital ducts of Nucula proxima open into, or with, the outer end of the excretory organs, in a manner similar to that just described for Yoldia limatula.

GENITAL GLANDS.

These, when distended with their products, are very extensive. They push in between the excretory organs, below the pericardium, between the stomach and intestine nearly to the pedal ganglia, and cover and dip in between the lobes of the digestive glands. The opening of the genital duct, Fig. 23, gd, has already been described in connection with the excretory organ.

The sexes are separate and, when the genital products are abundant, they may easily be distinguished by the color of the genital mass surrounding the digestive glands. This portion is chocolate brown in females and yellow in males.

NERVOUS SYSTEM.

Figures 4 and 5.

The cerebral ganglia, Fig. 4, cg, united in front of the œsophagus by a very broad commissure, which differs very little in structure from the ganglia themselves, lie just posterior to the ventral side of the anterior adductor muscle. Each ganglion is almost circular in transverse section and gradually tapers posteriorly into the cerebro-visceral commissure. So gradually does this tapering take place, that it is impossible to determine where the ganglion ends and commissure begins. Even in structure there is only a difference in degree, there being proportionally more nuclei in the ganglion than in the commissure. Posteriorly each commissure gives place, in the same gradual way, to a visceral ganglion. The visceral ganglia, vg., lie anterior to the ventral side of the posterior adductor muscle, and almost equal the cerebral ganglia in size. The commissure connecting these ganglia is also very broad and, like the cerebral commissure, tends to share the structure of ganglia.

The pedal ganglia, pg., are rounded and fully as large as the cerebral ganglia. They lie very close together and are connected by a very broad commissure.

The cerebro-pedal, unlike the cerebro-visceral commissures are not surrounded by nuclei and show ordinary commissural structure.

Although a great many specimens of widely differing ages have been examined, the double origin of each cerebro-pedal commissure from the cerebral ganglia has not been observed in Yoldia.* Neither is a separation into cerebral and pleural ganglia evident. It is true that the cerebral ganglia are not quite smooth and, in some places, the outer layer of nuclei dips into the fibrous layer, but it seems possible that this may be accounted for by the origin of nerves in the immediate vicinity.

Each cerebral ganglion gives rise to several nerves. A large nerve passes forward, under the anterior adductor muscle, branches, and supplies the anterior portion of the corresponding lobe of the mantle. Another large nerve passes down to the dorsal margins of the palps, follows them posteriorly and is finally continued the whole length of the palp-appendage. Of the smaller nerves one supplies the anterior adductor muscle and another passes to the body wall.

Each visceral ganglion gives rise anteriorly to a small osphradial nerve, and posteriorly to a nerve that branches almost immediately. Sometimes these branches originate as separate nerves. One of the

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* There seems to be no doubt that this commissure does have a double origin in Nucula proxima, Say, and N. delphinodonta, Mighels.

branches sends a small nerve to the posterior adductor muscle and another below the adductor muscle, to the postero-dorsal portion of the mantle. The main nerve bends ventrally and is distributed to the siphons. The other branch passes ventrally, beside the nerve just described, sends a large nerve to the siphonal tentacle, on the side where this tentacle is present, and is continued to supply the postero-ventral margin of the mantle. Several branches are given to the posterior expansion of the mantle.

Each pedal ganglion gives rise to a nerve that runs directly to the byssal gland, and to six or more nerves that supply the muscles of the foot. Frequently one nerve, and sometimes several nerves, may run up the cerebro-pedal commissure for some distance before issuing to be distributed to the muscles of the foot.

The nerve that supplies the otocyst issues from the cerebro-pedal commissure but, judging from the direction of the fibres in the commissure, probably has its origin in the cerebral ganglion.

OTOCYSTS.

Figures 4, 21 and 22.

The otocysts are rather large and, as Kellogg[5] has pointed out, each contains a single large otolith, which plainly shows concentric structure. The epithelial cells of the otocysts carry rather long and slender cilia. In adult specimens there is a well-defined canal connected with each otocyst. Pelseneer[11] describes this canal as opening at the surface of the foot and gives a figure indicating the position of its opening.

I have found that, by the careful dissection of specimens preserved in formaline, the cerebro-pedal commissures, with the otocysts, otocystic nerves, and otocystic canals, all held together by connective tissue, can be removed. Study of these preparations, of which I have made about thirty, shows the otocystic canals to be cylindrical and of uniform size for about three-fourths of the length of the otocystic nerves, Fig. 21, ot., at which point there is nearly always a swelling. A thin strand of fibrous tissue, probably connective tissue, is continued beyond the swelling. At the distal end of the swollen portion of each canal there is generally, probably always, a wall that can easily be seen in dissected preparations, and verified in sections. This wall is the rounded end of the otocystic canal.

Sometimes one or more little closed pouches are found, lying in the strand of tissue that is continued on past the swollen portion of the canal. Two such pouches are shown in Fig. 22, which represents the distal swollen portion of a canal and part of the continuing strand of tissue. These pouches, when found, show the same structure that is shown by the canals, and like them contain numerous, very long cilia.

It seems to me that these walls and pouches show conclusively that in each of the several cases the whole canal was removed and, that in this species, the canals do not reach the surface of the foot.*

In both Nucula proxima and Nucula delphinodonta there is a strand of tissue passing from each otocyst to the surface of the foot. This corresponds in position to the canal described by Pelseneer[11] for Nucula nucleus, and is probably an open canal, but I have not had time to demonstrate this point.

In Yoldia limatula, the strand of tissue, with the series of pouches which it sometimes incloses, seems to indicate that these canals have undergone degeneration.

The otocystic nerves lie alongside the canals and seem to send fibres to their walls. In fact it is difficult to demonstrate that the nerves reach the otocysts other than through the walls of the canals.

OSPHRADIUM.

On the inner side of each suspensory membrane of the gills, lying just beneath the visceral ganglion of the corresponding side, is a rather large patch of modified epithelium, which probably represents an osphradium.

This epithelium is supplied by a rather large nerve that leaves the corresponding visceral ganglion near its anterior end.

CIRCULATORY SYSTEM.

The heart, Fig. 4, is situated just posterior to the beaks of the shell, and very near the dorsal margin. The cavity of each auricle is connected with the blood-spaces of the corresponding gill, through a

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* Perhaps individuals living in widely separated localities may differ in this regard.

slit in a muscular partition that projects dorsally into the cavity of the auricle. The arrangement of this partition is such as to tend to stop the backward flow of blood into the gills. The ventricle is perforated by the intestine. Where each auricle joins the ventricle, there is a marked constriction and, internally, a muscular septum perforated by a single opening. When the ventricle contracts, this septum probably contracts and more or less completely closes the opening in it.

Two blood-vessels leave the ventricle, one anteriorly on the left side of the intestine, the other posteriorly, beneath the intestine.

EMBRYOLOGY.

The eggs of Yoldia limatula, are about .15 mm. in diameter, of a chocolate brown color, and very opaque. They are not encumbered by any kind of envelope. The polar bodies are lost soon after they are formed. The first cleavage, which takes place about two hours after the eggs are fertilized, results in the formation of sub-equal blastomeres, Fig. 24.

In the next cleavage, Fig. 25, the smaller blastomere divides equally and the larger unequally. The eight-celled stage is formed by a cleavage at right angles to the two preceding planes of cleavage, and the two sets of four cells each come to lie in the position indicated by Fig. 26, the last division being in the plane of the paper.

One of these cells is considerably larger than the other seven and, with the beginning of the next cleavage, begins to be inclosed by the other cells, Fig. 27. The small cell formed by the unequal division of this large cell, Fig. 28, becomes a surface cell. What becomes of similar cells in later divisions has not been determined, but, from sections, it appears probable that the next small cell, cut from the large cell, Fig. 29, crowds in over the tip of the large cell and divides into two, Fig. 37.

About this time the outer cells, or at least part of them, acquire cilia, Fig. 30, and the embryo begins to roll around on the bottom of the dish. It finally rises to the surface of the water and swims freely.

Just what internal changes take place during this interval is rather hard to determine. Surface cells in the region of the blastopore became especially active, dividing and crowding in around the large internal cell, which now divides into nearly equal cells, Fig. 39.

Most of the outer cells now take on a decidedly different appearance from the internal cells. There is a layer of protoplasm against the outer wall of each cell that stains rather deeply, but the remainder of the cell is occupied by vacuolated protoplasm. These vacuoles become larger with age.

Beside the vacuolated cells, there is a group of cells, Figs. 38 and 39 cg., and Fig. 40, ap., which are largely surface cells and later give rise to the cerebral ganglia and the apical plate. The apical plate, Fig. 40, ap., is already distinguishable.

Whether there is a general migration of surface cells into the interior is doubtful, but it is certain that their number is reduced. The reduction is probably not more than is accounted for by the pushing in of those around the blastopore, and the setting aside of the group from which the cerebral ganglia and apical plate arise.

The embryo now elongates, Fig. 31, the apical plate acquires a tuft of apical cilia, ac., and the outer, vacuolated cells, which will hereafter be referred to as test-cells, arrange themselves in five rows that surround the embryo. Frequently the fifth, last, row of test-cells, counting from the anterior end, is not complete on the dorsal side at this stage, but this does not long remain so. Occasionally a sixth more or less complete row is present. The blastopore and the apical plate occupy nearly opposite ends of the embryo, but for some time the blastopore may be twisted around somewhat to one side. The position of the group of cells from which the cerebral ganglia are formed is indicated in the external view of the embryo by a depression, x, where the cells of the first, or anterior, row of test-cells are pushed away from the second row. As later stages show this to be the ventral side of the embryo, it is easy to determine that the blastopore is always twisted toward the same, that is, toward the dorsal, side.

The test-cells are distinctly rounded and the cilia on each of the three intermediate rows are collected into a band. The embryo now swims in more or less definite lines, rotating the while upon its longitudinal axis. The rotation is quite rapid, but is not always in the same direction, there being frequent changes. During activity the apical cilia are bunched together into a sort of whip, which lashes vigorously from side to side, and always precedes the embryo in its movements.

Inside the test the cells in the region of the blastopore are still actively undergoing division and are quite small, Fig. 41.

The cells of the apical plate, ap, and those from which the cerebral ganglia cg, arise, are separated externally by test-cells, but internally they are, and continue to be, connected by cells that do not take part in the formation of other organs.

The other internal cells have increased in number, and their origin can no longer be determined. At a little later stage, Fig. 42, the dorsal internal cells are found to be arranged in a layer, sg, that represents the beginning of the formation of the shell-gland. Other cells soon arrange themselves over the remainder of the surface inside the test and, together with the shell-gland, form a new ectoderm. This ectoderm probably is formed from cells that were originally surface cells. If this view is true, the original surface cells give rise to at least three groups: those that remain at the surface, acquire cilia, and become differentiated as test-cells; those that form the cerebral ganglia and the apical plate; and those that form the new ectoderm inside the test.

In the stage of which Fig, 42 represents a section, a space seems always to be present in about the same position. This space probably represents the beginning of the lumen of the mid-gut.

The embryo continues to elongate, Fig. 32, becomes cylindrical, and the test-cells flatten and become less distinct from one another. Between about the 32nd hour and about the 70th hour, there is no appreciable change in the external appearance of the embryo and, as the test-cells are quite opaque, few internal changes can be followed in living specimens.

The test, which is now fully formed, is composed of large vacuolated cells, Fig. 44, t, the nuclei of which are almost, if not quite, in contact with their inner walls. Just beneath each band of cilia the protoplasm stains very deeply. Just inside the test, between it and the new ectoderm, there are, frequently, a few scattered nuclei lying in a very thin film of protoplasm. Their significance is not known.

The shell-gland becomes more definite, the lumen of the mid-gut, Fig. 43, becomes surrounded by a definite wall of rather large cells, and an invagination, std, extends into the mass of cells from the ventral side of the blastopore. This invagination is the beginning of what I have called the ventral tube,* but, as it has since been found that it is formed as an ectodermal invagination that does not at first communicate with the mid-gut, a special name is unnecessary, and it will hereafter be referred to as the stomodæum.

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* Johns Hopkins University Circulars, No. 132, 1897.

The stomodæum elongates and soon establishes communication with the mid-gut, Figs. 44 and 48. It lies along the ventral side of the embryo, just inside the test, and is joined, but is not inclosed, by the layer of ectoderm, Fig. 49, std. The shell-gland becomes slightly invaginated, Figs. 44 and 45, sg, but it very soon arches upward preparatory to protruding laterally to form the mantle, Fig. 49. The mid-gut becomes prolonged posteriorly, and the mass of cells from which the cerebral ganglia are formed arch inward and form two pouches that open at the surface. The pouches lie side by side, Fig. 46, and generally open to the exterior together. Sometimes, however, they open between different test-cells, Fig. 47, and seem to be only slightly connected with each other. In other cases only one of the pouches opens to the exterior and this opening may be small. In some cases there may be no opening. The walls of the pouches are rather thick but each is composed of a single layer of cells.

The shell-gland folds out at the edges and most of the dorsal cells assume the character of mantle cells. Only those near the edges remain especially large and glandular. The formation of the mantle is accompanied by the formation of the pedal ganglia, Fig. 57, pg, as ectodermal thickenings, and the formation of the otocysts, Fig. 56, as ectodermal invaginations. The next stage shows the otocysts *apparently* completely closed off, lying very close to the clefts that separate the mantle from the body wall.

The formation of the mantle and shell is accompanied by a slight lateral compression and a corresponding dorso-ventral widening of the embryo. The test-cells become very much thinner and the vacuoles nearly or quite disappear, but the cilia remain as described and the movements of swimming are not altered. Several new organs make their appearance.

Cleared whole mounts show some of the internal organs, but throughout it is necessary to resort to reconstructions from the study of serial sections to get the relationship of the different parts.

The body of the embryo now lies between the valves of the shell and these are inclosed in the test. The foot, Figs. 33 and 55, f, is formed by a rapid increase of cells between the mid-gut and the stomodæum. The anterior adductor muscle, Figs. 33, 55 and 58, aa, is formed at a corresponding time (about 85 hours) and consists of a few muscle fibres which stretch from one shell-valve to the other. It is left, by the growth of the embryo, separated from the rest of the body, except at its ends, which penetrate the mantle, and are attached to the shell. The posterior adductor muscle, Figs. 33 and 55, pa, does not appear until some hours later. It is always surrounded by other tissue. The digestive glands, Figs. 33, 62 and 63, are formed as evaginations from the anterior end of the mid-gut, which now extends posteriorly nearly to the blastopore. The visceral ganglia appear as groups of nuclei, whose position suggests ectodermal origin. The cerebral pouches have moved some distance dorsally and posteriorly into the interior of the embryo, and are situated at the end of a single pouch, Figs. 33, r, which opens to the exterior between the test-cells at the point where the pouches were originally formed. The paired pouches thus appear as diverticula of a single elongated pouch. As the pouches are carried into the interior, the cells forming their walls push in and fill up their cavities, and a commissure is formed connecting the two masses of cells. The relation of the unpaired pouch to the cerebral ganglia has been shown by three succeeding transverse sections of the same embryo. Fig. 58 shows the external opening of the unpaired pouch, Fig. 59 shows the anterior portion of the cerebral ganglia, cg, with the laterally compressed unpaired pouch, r, lying beneath them, and Fig. 60 shows the commissure connecting the ganglia.

Having described the formation of the various organs attention will be given to the embryo's appearance.

Further than the lateral compression and the corresponding dorso-ventral widening, there has been little change in the embryo's external appearance, but the internal appearance is greatly altered.

Inside the test a shell has been formed, the two valves of which gape ventrally. The anterior adductor muscle, Fig. 33, aa, is quite large and, being isolated from the general mass of the body, is very conspicuous. The posterior adductor muscle, pa, as yet consists of very few fibres and is inclosed in other tissue. It is not easily seen in whole mounts. The apical plate, ap, is connected with the ventral end of the group of cells that form the wall of the unpaired pouch, r. This group of cells forms a distinct stalk which runs dorsally and posteriorly to connect with the anterior part of the body. The mid-gut, mg, and the stomodæum, std, are widely separated by the foot, f. The stomodæum opens to the exterior through the blastopore, bl, and the posterior end of the mid-gut almost reaches, and finally breaks through into, it.

The stomodæum is often attached to the anterior, and to part of the ventral margins of the foot, but its posterior end, Fig. 61, std, lies free between the lobes of the mantle, sometimes almost, if not quite, in contact with the test, sometimes raised well above it. The anterior end of the mid-gut is enlarged to form the stomach, which communicates with the pouches of the digestive glands. Most of the tissue dorsal to the intestine has been used in forming the mantle, which is now separated from it by a large space. This space extends to and around the anterior adductor muscle anteriorly, and nearly to the margin of the shell posteriorly. The cerebral, pedal, and visceral ganglia, with their commissures, have been formed. The otocysts, Fig. 61, ot, have *apparently* been entirely closed off, and each contains an otolith, which stains deeply with hæmatoxylin, and, a little later, plainly shows concentric structure. As the otocysts have never been open to the exterior, development having taken place inside a closed test, the otoliths cannot be foreign particles.

The only places where the test is attached to the body of the embryo, lying inside it, are around the blastopore, along the sides of the apical plate, and around the opening of the unpaired pouch, Fig. 33, r. The embryo still swims rapidly, but has periods of rest.

This condition of the embryo is reached in from 90 to 120 hours. It now stops swimming, settles to the bottom, the apical cilia shrivel, and the test-cells break apart and frequently go to pieces at once. The process of casting the test generally begins with the posterior row of cells and works forward. It generally takes but a very few minutes. Casting includes, besides the test, the stalk which extends from it to the cerebral ganglia, the apical plate and its connection, and the stomodæum from the blastopore to the position of the definitive mouth. These parts, together with a few adhering test-cells that are no longer stretched flat, but have rounded up, may not sever their connection for a half hour or more, Fig. 34, but they finally break off just below the cerebral ganglia, and casting is complete.

Until about the time that the test is cast, the valves of the shell gape ventrally, and the tissues of the body extend completely across from valve to valve. When the shell is finally closed, by the contraction of the adductor muscles, there is no longer sufficient space for the organs in their original position. The principal change of importance due to this crowding takes place in the pouches of the digestive glands, which are forced into the space dorsal to the alimentary canal, and, in all of the specimens examined, seem to give rise to a mass of large cells, Figs. 35, 64 and 65, z, that are not arranged in any definite manner. It was at first thought that this appearance was due to poor preservation, an explanation that very naturally suggested itself, but later the large cells were found in the living as well as in the preserved specimens. Reformation of the digestive glands is accompanied by the disappearance of these cells.

The anterior adductor muscle soon becomes inclosed by the forward growth of the body. For a few hours a space may remain between it and the cerebral ganglia, but this soon disappears.

The foot, which at first is capable of only feeble movements, grows quite rapidly, and is soon very active. Locomotion is chiefly effected by the means of long and powerful cilia arranged along the sides of the foot, Figs. 35 and 36, which are very active whenever the foot is thrust out of the shell. These enable the animal to glide over the surface on which it lies, but they do not enable it to rise. For some hours after the test is cast, the foot shows no indication of the modification which is later generally known as the sole, Fig. 52. The first indication of this modification is a groove which appears along the middle line of the ventral surface of the foot, Fig. 53. This groove deepens, apparently by the growth of the parts on each side, Fig. 54, and gives rise to a "sole" resembling that of the adult, Figs. 3 and 9. The movements of the foot now closely resemble those of the adult, but locomotion on smooth surfaces is still chiefly by means of the powerful cilia along its sides.

The formation of the "sole" is accompanied by the growth of the postero-ventral portion of the foot into a more and more prominent portion resembling a heel. The use of this outgrowth is not evident. It remains in the adult as a small projection, just behind the opening of the byssal gland; an organ that makes its appearance about a day after the test is cast, but does not seem to secrete threads.

About the time that the test is cast away, a thickening makes its appearance on the inside of each lobe of the mantle, near its posterior border, Figs. 34 and 35 g. This thickening, the rudiment of the gill, acquires cilia and grows anteriorly so as to project over the surface of the mantle. A constriction appears near the middle of each gill, Fig. 36, g, the lobes become more prominent, and it is thus divided into almost equal parts. Beneath its epithelium, following the curve of its anterior margin, is a chitinous rod, the two ends of which lie near the ends of the lobes, Fig. 36.

Figs. 50 and 51 represent sections of a gill, taken in the planes indicated in Fig. 36. The chitinous rod is cut in one, but the plane of the other lies below it. These sections show the gill to be rather evenly ciliated. Later stages, after the lobes have elongated, show the cilia to be confined to the side next to the mantle. The third lobe is formed from the ventral lobe, which broadens and constricts in the manner detailed above. Other lobes are formed in a similar manner.

The alimentary canal elongates, bends ventrally, and the stomach enlarges. In from two to four days after the test is cast, the digestive glands reappear. At first they do not have very definite walls, but they gradually become well defined, and it is noticeable that the large scattered cells disappear at a corresponding time. The two pouches are no longer symmetrical, the left being prolonged posteriorly fills up the space between the dorsal end of the stomach and the intestine, Figs. 36 and 66. The greater development of the left digestive gland, at this early date, possibly affects the future position of the intestine, a loop of which comes to lie on the right side of the animal, very near the shell.

About the 25th day, a ridge, corresponding in position to the outer labial palps, appears as an outgrowth from the body wall. The palps did not attain any considerable development in any of the embryos reared from eggs.

The ganglia are all distinct in whole mounts as well as in sections. At first the cerebral ganglia are much larger than either of the others, Fig. 33, but the pedal ganglia grow rapidly, and soon come to equal if not to exceed them in size, Fig. 36. No division into cerebral and pleural ganglia has been observed.

GENERAL REMARKS.

ANATOMY.

Since Mitsukuri's[8] paper appeared in October, 1881, much has been written on the anatomy of members of this group. Pelseneer[11] and others have called attention to certain characters in support of the supposition that the group is primitive.

Some of these characters do not seem to hold good with Yoldia. Thus on page 274 in speaking of the primitive characters of the group Pelseneer[11] includes among others the following:

"2°. Foot has a ventral 'creeping' disc (not existing in others except *Pectunculus*)."

"5°. Absence of a posterior aorta."

"7°. Genital glands opening into the pericardial extremities of the kidneys."

"8°. Pleural ganglia still distinct from the cerebral, and pleuro-pedal connectives arising by distinct origins from the cerebro-pedal."

Again on the same and succeeding pages:

"2°. With the Nuculidæ (Leda, Yoldia, etc.), one sees again that the retractors of the foot (columellaires) form an almost continuous series (without specialization) between the two adductors."

"6°. With the Nuculidæ the otocysts open freely to the outside."

I can do no better than to refer the reader to what has already been said on these subjects (see pages 8, 16, 18 19, and 21). The foot muscles of Yoldia are surely among the most highly developed of any to be found in the Lamellibranchia, and the only reason they occupy so much of the dorsal margin is because of their enormous size.

EMBRYOLOGY.

The most striking peculiarities in the development of Yoldia are connected with the formation and disappearance of the test.

I find similar tests in the embryos of two species of Nucula (N. proxima and N. delphinodonta), in both of which cases the tests are cast. In the former, the eggs are thrown free in the water, and the embryos closely resemble those of Yoldia, but are considerably smaller. In the latter species, the embryos are much larger, and are somewhat modified by being carried in a mucous case, which is attached to the posterior end of the shell.

Outside of the group, so far as I have been able to learn, Dondersia is the only other Mollusk whose embryo is known to be provided with a similar test.

Comparing the embryo of Yoldia with Pruvot's[12] account of the embryo of Dondersia, we find that the fully formed tests of both are composed of five rows of cells, all of which bear cilia. Counting from the anterior, the cilia on the third row of cells in the test of Dondersia, and the second, third and fourth rows of cells in the test of Yoldia, are long and collected into bands which surround the embryos. The body of the embryo of Dondersia protrudes posteriorly during development. No such protrusion takes place with Yoldia. Each is provided with an apical plate, and, in either case, the test is finally cast off. Internal changes in the embryos of Dondersia not being known, further comparisons are denied us.

The young embryos of Dentalium as described and figured by Lacaze-Duthiers[7] and Kowalevsky[6] bear a certain resemblance to those of Dondersia and Yoldia. This is largely due to three or more rows of cells, each bearing a band of cilia. At this stage these ciliated cells form the greater portion of the surface of the embryo. As the body elongates posteriorly, these cells are crowded forward to form the velum, but this does not seem to be cast off.

A somewhat similar resemblance is noticeable in the case of the embryos of Patella as figured and described by Patten.[9] In either Dentalium or Patella, if we imagine the velum to be stretched posteriorly over the shell-gland dorsally, and the foot ventrally, so as to inclose the body, the œsophagus will be pulled out into a long narrow tube ventral to the foot, and the position of the blastopore will correspond to its position in Yoldia. Furthermore, the position of the foot and shell-gland will correspond, and the alimentary canal will necessarily be bent in the same way.

In a similar manner, if we imagine the cells of the velum of a typical lamellibranch larva to be drawn posteriorly over the shell, there will be the same relation of parts. The same seems to be true of the typical larvæ of gastropods if we take into account the twisting that accompanies development in these forms.

Thus we may perhaps trace an homology between the test of Yoldia and the velum of other forms. In this connection it is of interest to notice that in a few forms the velum is known to be cast away. This has been observed by Heath* for Chiton, Sigerfoos[15] for Teredo, and Mrs. Drew†, for Cardium. Wilson[18] has described a similar casting of the cells of the velum for Polygordius.

It seems quite possible that the embryo of Yoldia represents a rather primitive form, and that the typical molluscan larvæ may have been developed from an ancestor approaching it in form and structure. If this is true, the probability is that organs of Yoldia and its relatives, which now show high specialization, have been developed from the more primitive rather than from the highly complex.

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* Dr. Heath has kindly allowed me to notice this point, although his observations are not yet published.

† This work has not been published. The species upon which the observations were made seems to be C. pinnulatum, Con.

SUMMARY.

A brief statement of the chief points is as follows:

ANATOMY AND HABITS.

1. The mantle has two pairs of sense organs, Fig. 1, ae, and pe, one long unpaired tentacle, st, and a fringe of marginal tentacles. All of these organs are sensitive to mechanical stimulation. The unpaired tentacle seems to be homologous to one of the ordinary marginal tentacles.
2. The foot, Figs. 3 and 9, f, is a highly specialized burrowing organ.
3. The palp-appendages, Figs. 3, 10 and 18, pap, are food-collectors.
4. The gills, Figs. 3, 19 and 20, are used in pumping water, for which function they are well fitted by their structure.
5. Each genital duct, Fig. 23, gd, joins the outer, not the inner, end of the corresponding excretory organ, very near its opening into the branchial chamber.
6. No division into cerebral and pleural ganglia has been observed. Neither do the cerebro-pedal commissures seem to have a double origin.
7. The otocysts are not connected with the surface by canals. Canals, apparently in process of degeneration, Figs. 21 and 22, oc, are present in adults.
8. Both an anterior and a posterior aorta are present.

EMBRYOLOGY.

1. The original surface cells seem to give rise to the test, the cerebral ganglia, the apical plate, and a new ectoderm inside the test.
2. The cerebral ganglia, Figs. 46 and 47, are formed as invaginations from the surface.
3. The otocysts contain otoliths before the test is cast. Fig. 61.
4. The test, the apical plate, the stalk connecting the test with the anterior portion of the body, and the stomodæum from the blastopore to the position of the definitive mouth, are all cast away.
5. It seems that typical molluscan larvæ may have been developed from embryos resembling those of Yoldia, and that the test of Yoldia and the velum of other forms are homologous.

NOTE.

Since the preparation of this paper, Dr. Walter Stempell's paper, entitled Beiträge zur Kenntniss der Nuculiden (Fauna Chilensis, Heft 2. Zool. Jahrbucher Supplement IV, 1898), has appeared. While it seems that Dr. Stempell has not worked directly upon Yoldia, his paper treats in detail on the anatomy of related forms, and can easily be made the basis of interesting comparisons. It is a point of much interest that closely related forms of this group, even two species of the same genus, may differ markedly in some not unessential details. This probably accounts for most of the differences recorded in these papers.

In only two points do our papers seem to conflict. On page 355 Dr. Stempell, in speaking of the hypothesis* that the unpaired tentacle is homologous with the tentacles fringing the postero-ventral margins of the mantle, objects on the ground that Leda sulcata, while possessing the unpaired tentacle, has no marginal tentacles along the posterior portion of the mantle. It seems to me that the evidence cited, beginning with page 6 of the present paper, will outweigh this objection.

The other point of difference lies in the probability of the modified foot of these forms acting as a creeping organ. Dr. Stempell has not studied the animals alive and relies on published evidence that I cannot fully accept. (See Stempell's paper, page 374, and the present paper, foot-note, page 9.)

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* Brooks and Drew. Notes on the anatomy of Yoldia I. Johns Hopkins Univ. Circulars, No. 126, 1896.

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KEY TO LETTERS.

aa.	Anterior adductor muscle.
ac.	Apical cilia.
ae.	Anterior projection of the margin of the mantle.
afm.	Anterior foot-muscle.
ap.	Apical plate.
bg.	Byssal gland.
bl.	Blastopore.
bs.	Blood-space.
cg.	Cerebral ganglia.
cr.	Chitinous rods.
ec.	Ectoderm.
ep.	Epithelium.
es.	Exhalent siphon.
f.	Foot.
g.	Gill.
gd.	Genital duct.
gs.	Gill suspensory membrane.
h.	Heart.
ie.	Inner end of excretory organ.
int.	Intestine.
is.	Inhalent siphon.
lbs.	Lower blood-space.
ll.	Left lobe of liver.
llm.	Lower longitudinal muscle.
lm.	Longitudinal muscle.
lp.	Labial palp.
m.	Mantle.
mco.	Common opening of the excretory organ and genital duct into the mantel chamber.
mg.	Mid-gut.
mp.	Muscles of the gill plates.
oc.	Otocystic canal.
oe.	Outer end of the excretory organ.
on.	Otocystic nerve.
ot.	Otocyst.
pa.	Posterior adductor muscle.
pap.	Palp-appendage.
pc.	Pericardial wall.
pe.	Posterior expansion of the margin of the mantle.
pfm.	Posterior foot-muscle.
pg.	Pedal ganglia.
pn.	Palp nerve.
r.	Pouch leading to the cerebral ganglia.
rl.	Right lobe of liver.
s.	Shell.
sg.	Shell-gland.
st.	Siphonal tentacle.
std.	Stomodæum.
sto.	Stomach.
t.	Test.
tn.	Tentacle nerve.
ulm.	Upper longitudinal muscle.
vg.	Visceral ganglia.
x.	Depression at the point where the cerebral ganglia are formed.
y.	Cut wall of gill plate.
z.	Large cells that appear when the liver is forced into the space dorsal to the intestine.

EXPLANATION OF FIGURES.

Fig. 1. Expanded adult specimen, seen from the right side.

Fig. 2. Left shell-valve, seen obliquely from the dorsal margin.

Fig. 3. Adult specimen represented as seen from the right side, with the right shell-valve and mantle-lobe removed. The siphons are shown cut longitudinally.

Fig. 4. Same as the above with the right palp and gill removed, figured to show the relations of internal organs. The nerves leaving the ganglia are shown only on the left side. (Partially reconstructed.)

Fig. 5. Specimen about 1 mm. long. Represented as a partially transparent object, seen from the right side, after the right shell-valve and mantle-lobe have been removed. (Partially reconstructed.)

Fig. 6. Tip of a retracted siphonal tentacle.

Fig. 7. Portion of an extended siphonal tentacle, with a swelling caused by the pressure of the blood, seen as a transparent object.

Fig. 8. Transverse section of a siphonal tentacle.

Fig. 9. Anterior portion of the shell, and the reflected margins of the foot, just before they are brought together and withdrawn into the shell.

Fig. 10. An animal as it appears while feeding.

Fig. 11. Posterior portion of a specimen about .5 mm. long.

Fig. 12. Transverse section of a specimen about 1 mm. long, showing the thickening of the ridges leading to the base of the siphons, and the pushing in of the ventral wall of the exhalent siphon. Taken near the base of the siphons.

Fig. 13. Posterior portion of a specimen about 2 mm. long.

Fig. 14. Transverse section of a specimen about 1 cm. long, taken through the bases of the siphons. One of the ridges is shown joining the inhalent siphon. The section also includes a portion of the wall attaching the exhalent siphon to the dorsal portion of the mantle.

Fig. 15. End of the exhalent siphon of a specimen .7 mm. in length.

Fig. 16. Projection of the margin of the mantle opposite the extremity of stripe on the anterior end of the shell.

Fig. 17. Section of the anterior projection of the margin of the mantle.

Fig. 18. Transverse section of a palp-appendage.

Fig. 19. A pair of gill plates seen from their anterior surfaces. The suspensory membrane, the walls of the plates joining the plates next in succession, the longitudinal muscles, and the bases of the chitinous rods are shown in section. These are all cut across in separating the pair of plates from the pair lying in front. (Drawn from a study of sections.)

Fig. 20. Portion of a gill, seen from the ventral side.

Fig. 21. Otocyst with its canal and nerve, and a portion of the cerebro-peda commissure. A nerve frequently leaves the commissure near the otocystic nerve and is distributed to the muscles of the foot.

Fig. 22. Portion of the extremity of an otocystic canal, showing two closed pouches.

Fig. 23. Inner and outer ends of the left excretory organ and genital duct, seen from the ventral side.

Fig. 24. Two celled stage.

Fig. 25. Four celled stage.

Fig. 26. Eight celled stage seen from the animal pole.

Fig. 27. Eight celled stage. The cells preparing for the next cleavage.

Figs. 28 and 29. Later cleavage stages.

Fig. 30. Ciliated embryo about 14 hours old.

Fig. 31. External appearance of an embryo about 22 hours old.

Fig. 32. External appearance of an embryo about 70 hours old.

Fig. 33. Reconstruction of an embryo about 90 hours old. The outline and test-cells were obtained from a whole mount. The cilia are indicated only at the margins. The anus breaks through later.

Fig. 34. Reconstruction of an embryo that has just cast the test, represented with the right shell-valve and mantle-lobe removed. The stomodæum and the stalk extending from the cerebral ganglia, together with adhering test-cells, are still attached.

Fig. 35. Reconstruction of an embryo about 10 hours after casting. Represented with the left shell-valve and mantle-lobe removed.

Fig. 36. Reconstruction of an embryo about 12 days old. Represented with the right shell-valve and mantle-lobe removed.

Fig. 37. Section of an embryo about 10 hours old. The plane of the section lies through the blastopore.

Figs. 38, 39 and 40. Successive sections of an embryo about 13 hours old. Some of the surface cells are beginning to assume the character of test-cells. The group of cells cg., figures 38 and 39, are connected with the cells ap., figure 40, by cells of the same character.

Fig. 41. Median vertical section of an embryo about 17 hours old.

Fig. 42. Median vertical section of an embryo about 22 hours old.

Fig. 43. Median vertical section of an embryo about 30 hours old.

Fig. 44. Median vertical section of an embryo about 36 hours old.

Fig. 45. Transverse section of an embryo about 35 hours old, taken near the third band of cilia.

Fig. 46. Transverse section of an embryo about 45 hours old, taken through the cerebral pouches.

Fig. 47. A section similar to the preceding showing the pouches separate.

Fig. 48. Transverse section of an embryo about 45 hours old, taken where the stomodæum joins the mid-gut.

Fig. 49. Transverse section of the same embryo as the preceding, a little further posterior.

Fig. 50. Section of the gill rudiment in the plane indicated by the line 50, Fig. 36.

Fig. 51. Section of the same gill rudiment as the preceding in the plane indicated by the line 51, Fig. 36.

Figs. 52, 53 and 54. Transverse sections showing the formation of the "sole" of the foot.

Fig. 55. Median vertical section of an embryo about 90 hours old. (A portion of the stomodæum was drawn from the next section.)

Fig. 56. Transverse section of an embryo about 75 hours old, showing the invaginations that form the otocysts.

Fig. 57. Transverse section of an embryo about 70 hours old showing the forming pedal ganglia.

Figs. 58, 59 and 60. Successive transverse sections through the anterior portion of an embryo about 95 hours old.

Fig. 61. Transverse section of an embryo about 95 hours old, taken through the otocysts.

Fig. 62. Transverse section through the liver pouches of an embryo about 95 hours old.

Fig. 63. Horizontal section through the liver pouches of an embryo about 95 hours old.

Fig. 64. Median vertical section of an embryo about 10 hours after casting.

Fig. 65. Transverse section of an embryo of the same age as the preceding.

Fig. 66. Horizontal section through the dorsal portion of an embryo about 12 days old.

LIFE.

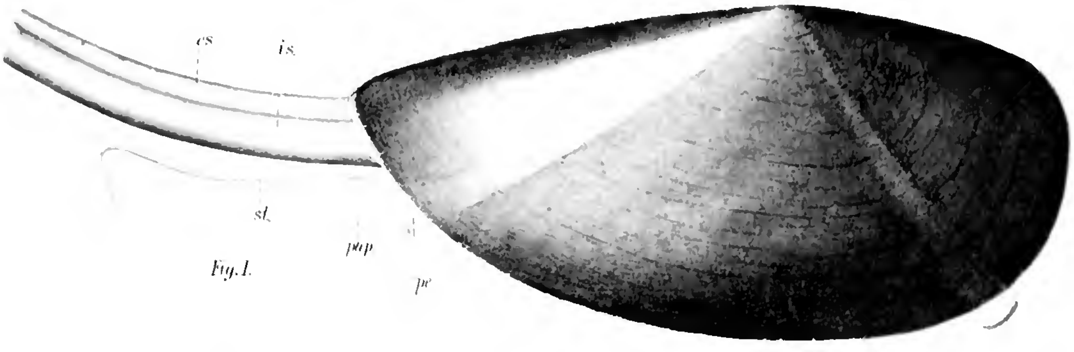
The writer of this dissertation was born in Jasper County, Iowa, November 15, 1868. He received his early educational training in the public schools of that State, and in the year 1890 was granted the degree of Bachelor of Science at the State University of Iowa.

Three years have since been spent in teaching, and five years have been devoted to study in this University.

In the year 1897 he was awarded a University scholarship, and he has since held a fellowship.

YOLDIA LIMATULA. SAY.

PLATE I.



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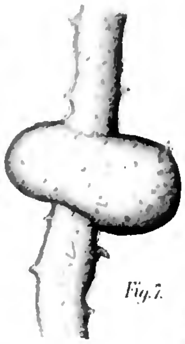
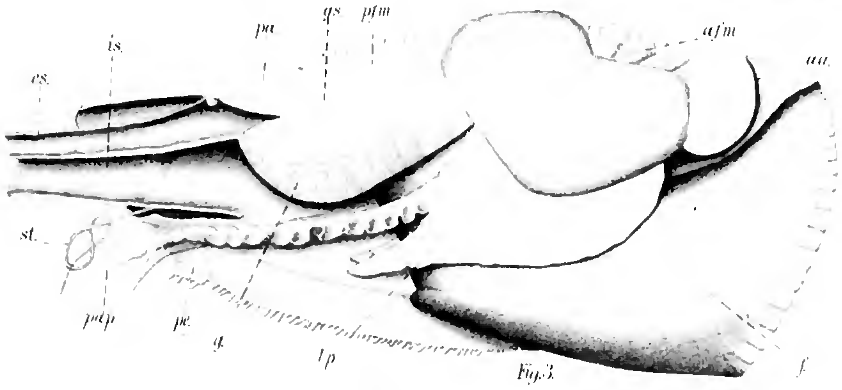


Fig. 7.

Fig. 6.



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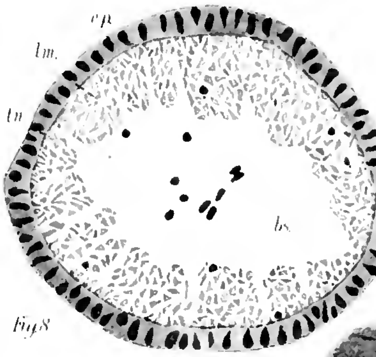
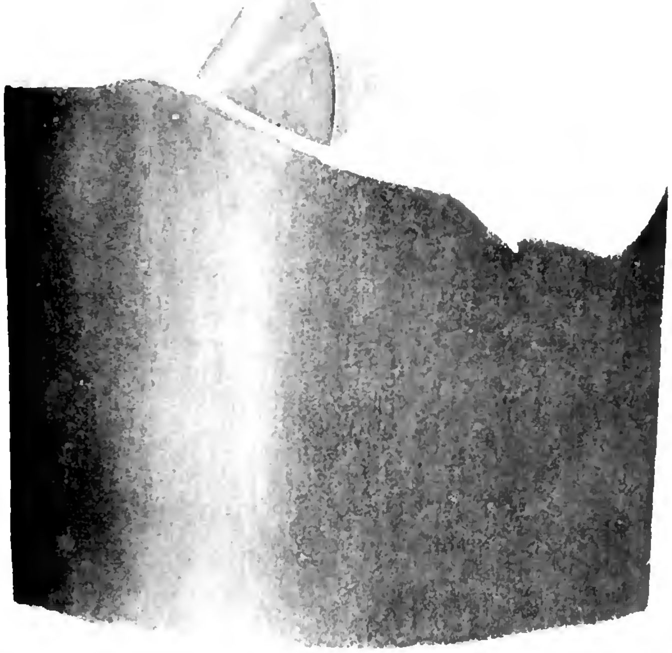


Fig. 8.

Fig. 9.

Fig. 2.

Fig. 5.



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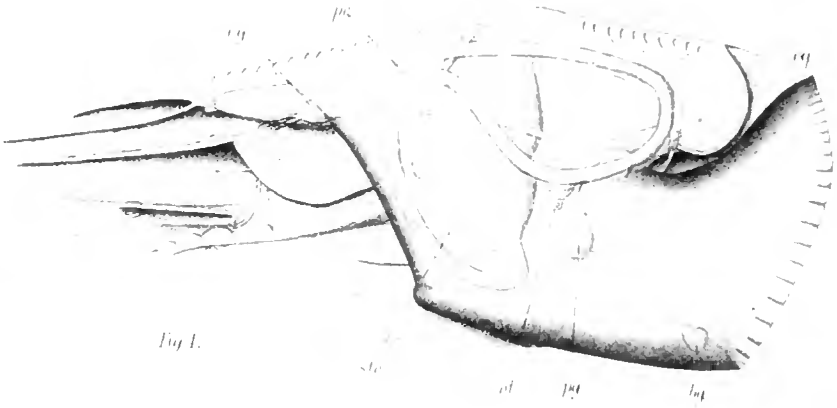


Fig. 4.

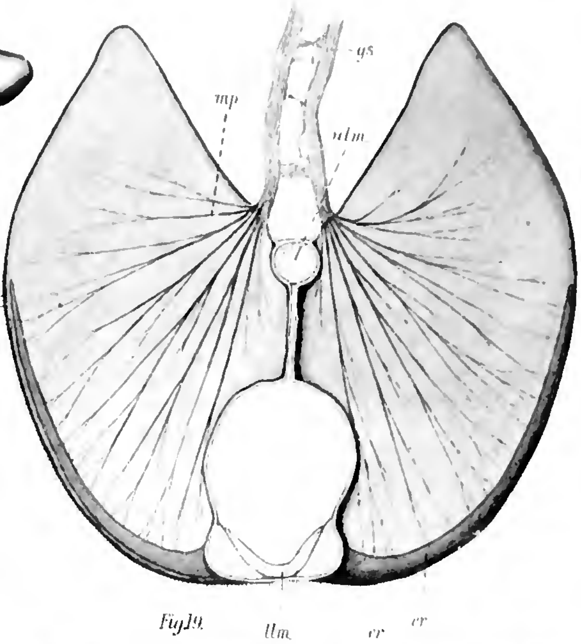
YOLDIA LIMATULA, SAY.

PLATE II

Fig.11.

Fig.12.

Fig.13.



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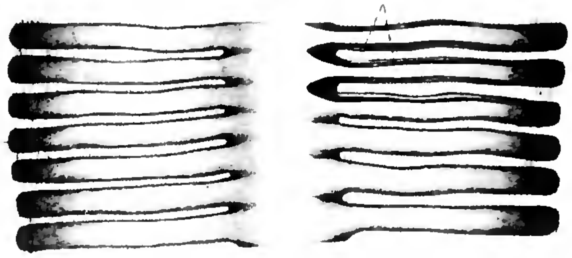

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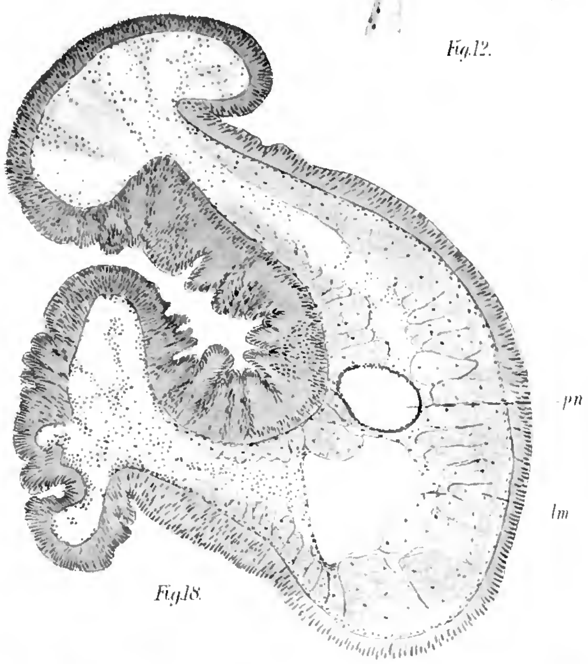

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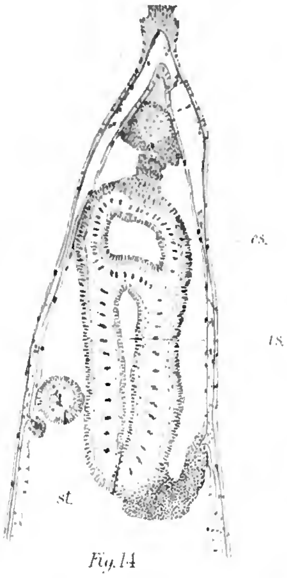

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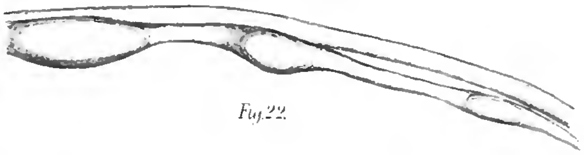
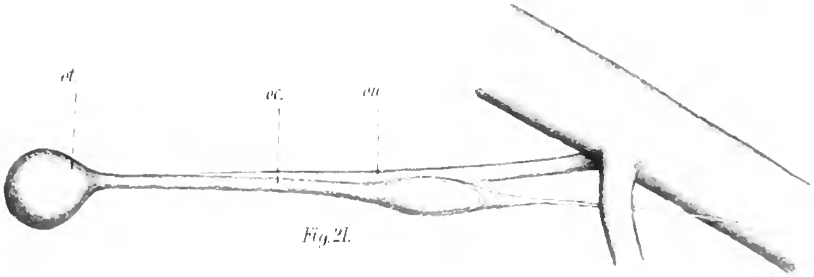


Fig.22.

Fig.16.



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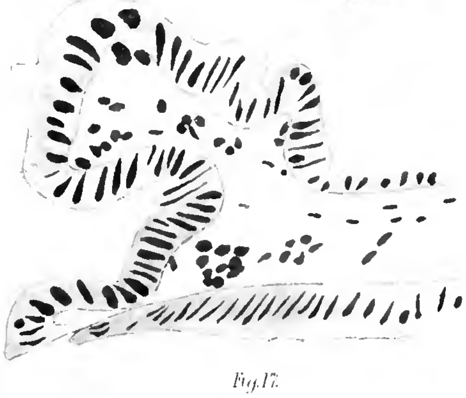

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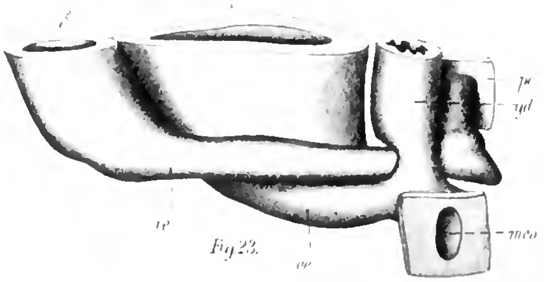

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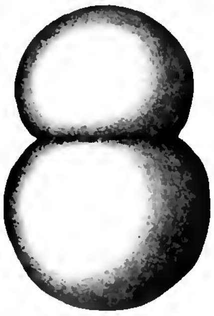
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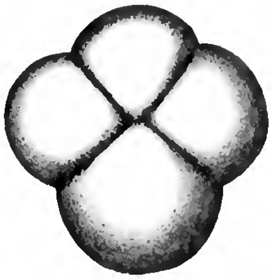
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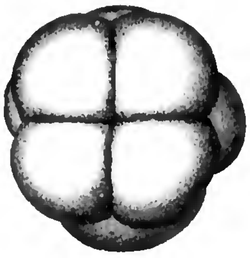
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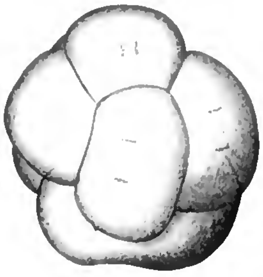
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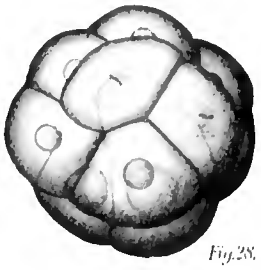
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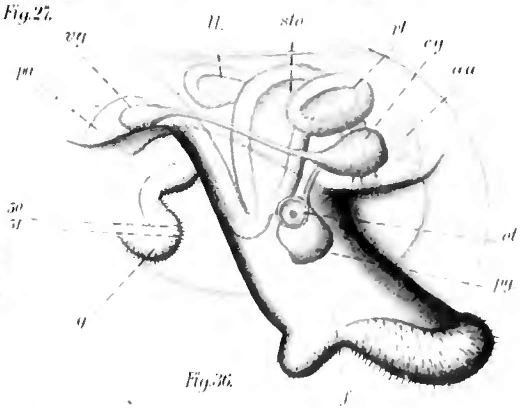

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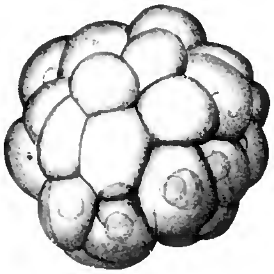
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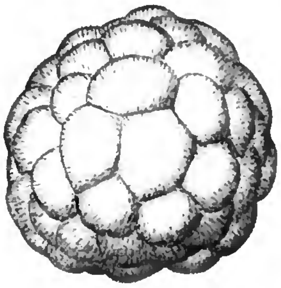
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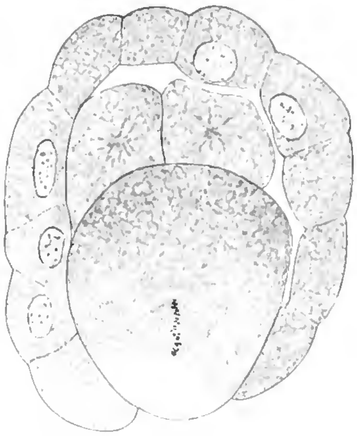
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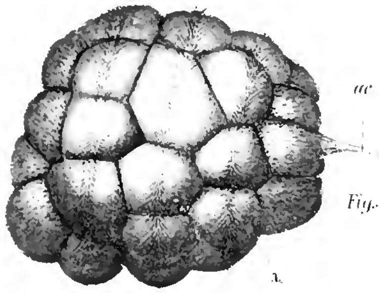

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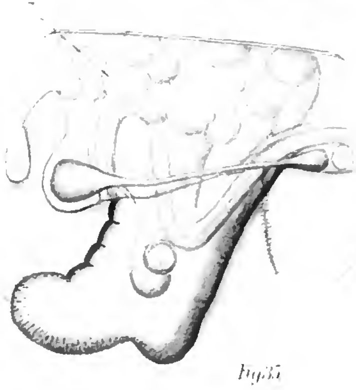

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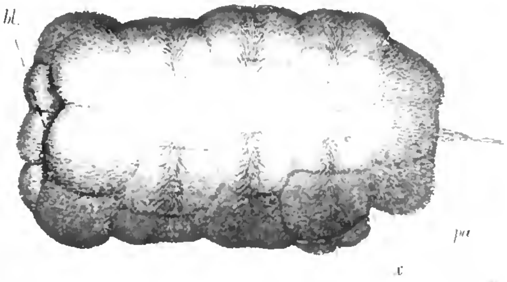

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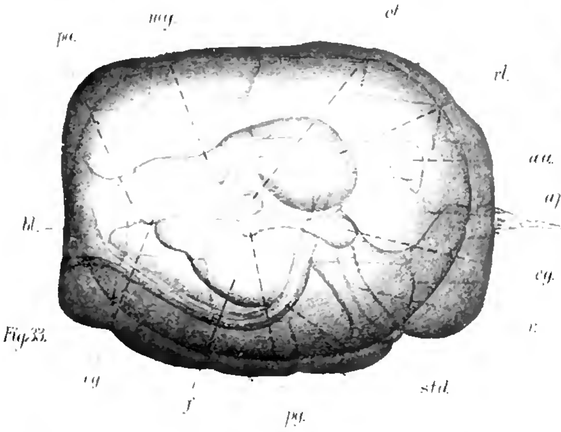

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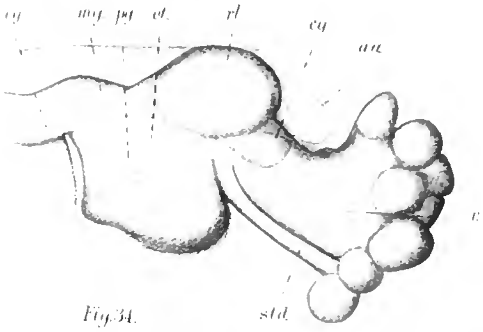

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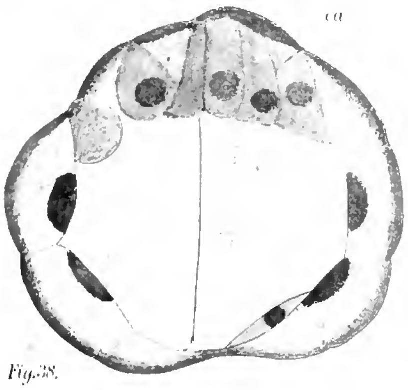

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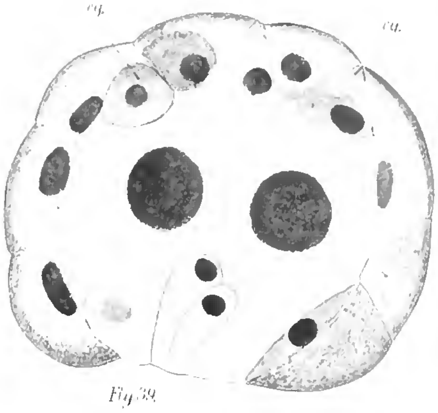

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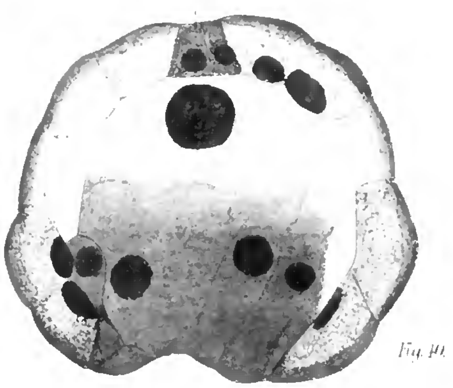

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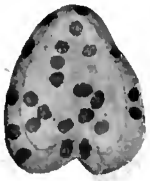
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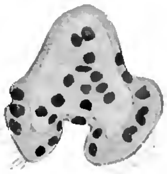
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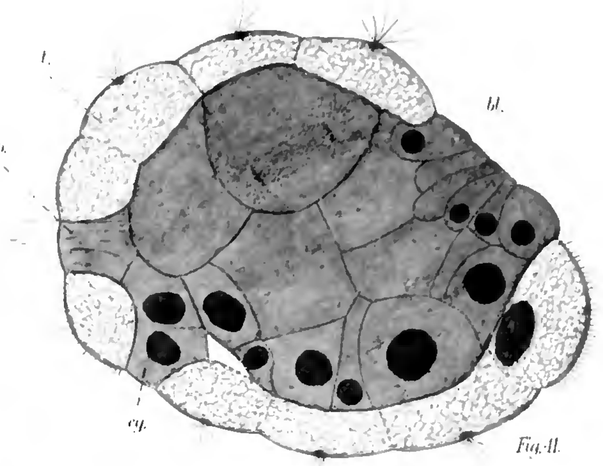

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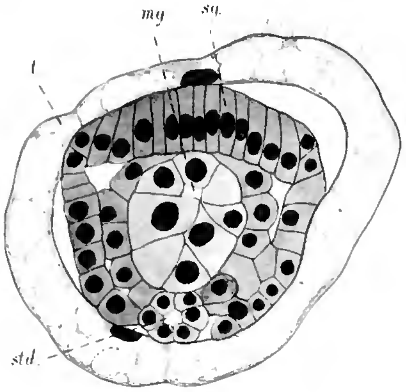

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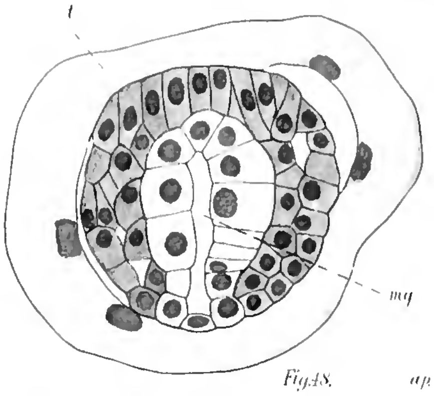

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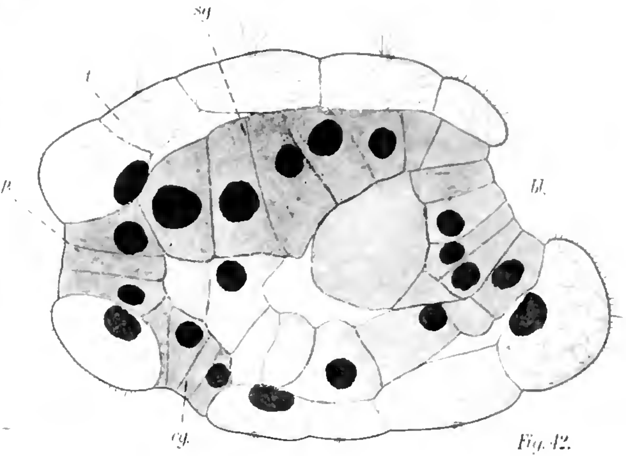

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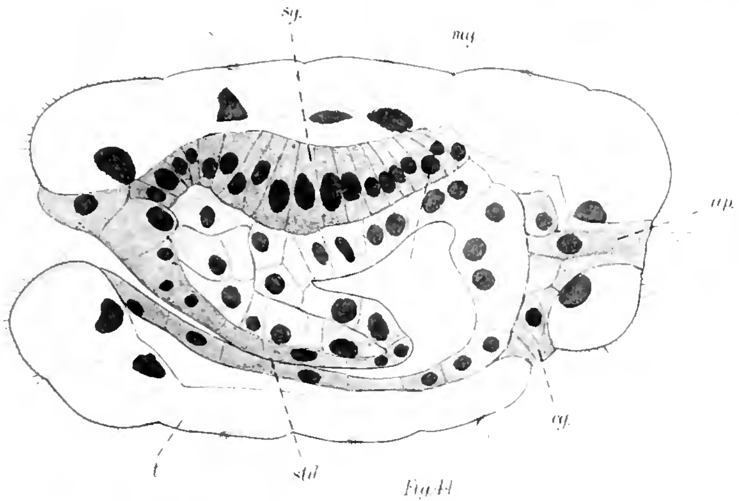

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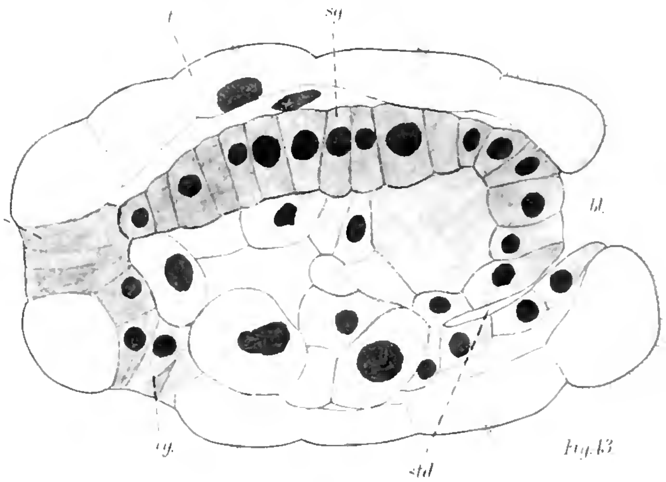

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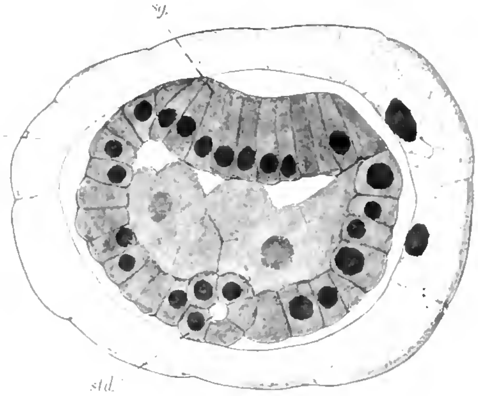

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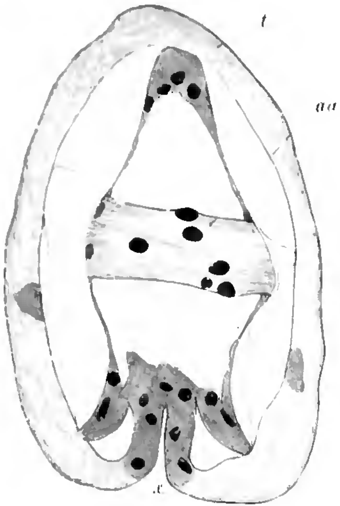

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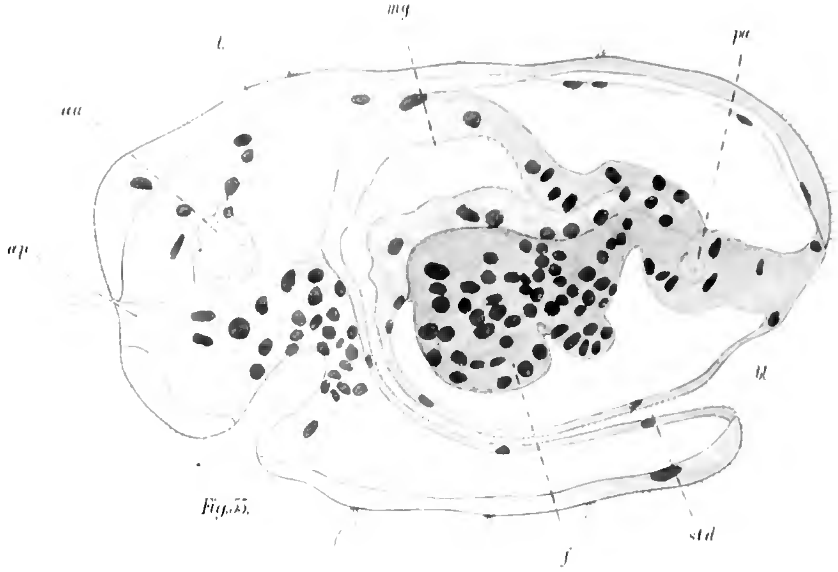

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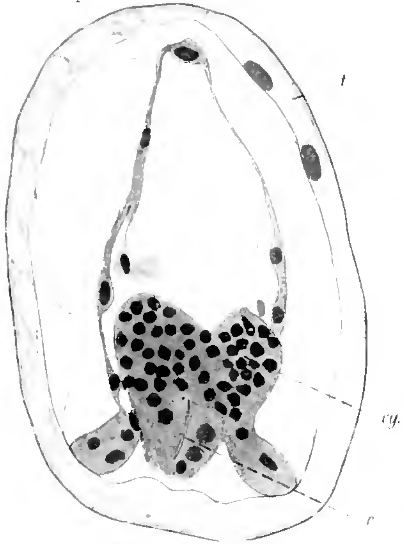

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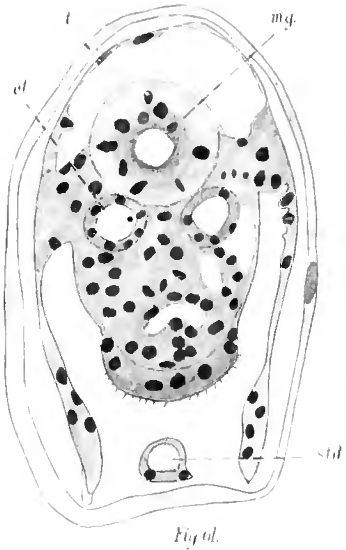
Fig. 60.



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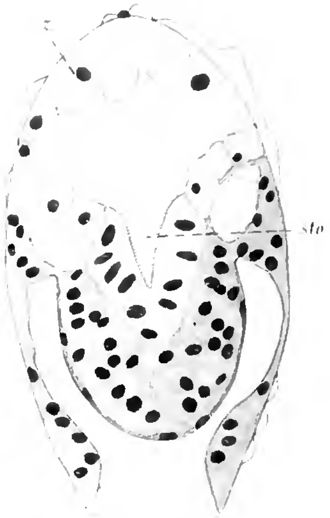

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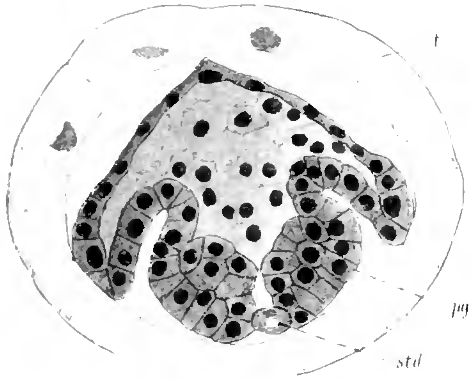

Fig. 57.

Fig. 62.

Fig. 64.

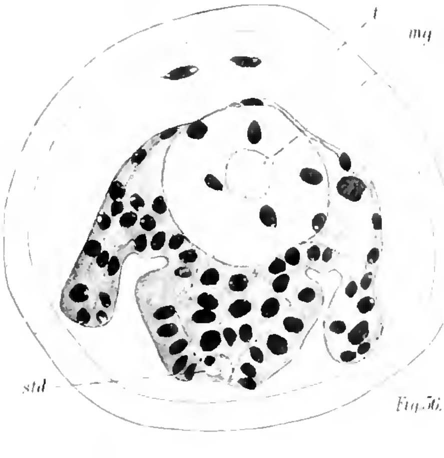

Fig. 56.

Fig. 63.

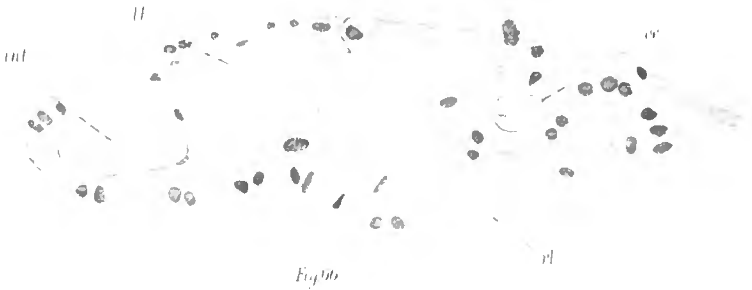

Fig. 66.

PHYSIOLOGY AND HISTOLOGY OF THE CUBOMEDUSÆ

INCLUDING

DR. F. S. CONANT'S NOTES ON THE PHYSIOLOGY

A DISSERTATION PRESENTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS HOPKINS UNIVERSITY FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

BY

E. W. BERGER

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This Memoir is a continuation of the work upon the Cubomedusæ which was begun by the late Dr. FRANKLIN STORY CONANT, and it contains his notes of physiological experiments, as well as new results which have been obtained by Dr. E. W. BERGER from the study of material which had been collected by Dr. CONANT, who had hoped to make it the object of further study.

In order that this work may be made public as a continuation of Dr. CONANT'S researches, his sister, GRACE WILBUR CONANT, has, with the coöperation of other members of his family, made an adequate and generous provision for its publication.

For this gift, which is at once a contribution to science and a memorial of an able and promising investigator, lately student and fellow in this institution, the Johns Hopkins University returns its grateful acknowledgments.

DANIEL C. GILMAN, *President.*
W. K. BROOKS, *Professor of Zoölogy.*

CONTENTS.

INTRODUCTION.

This paper may be regarded as a continuation of the Cubomedusan studies pursued by Dr. F. S. Conant while in Jamaica, in 1896 and 1897, with the Johns Hopkins Marine Laboratory. His systematic and anatomical results have since been published as his Dissertation ("The Cubomedusæ") by this University. Conant described this paper as Part I, hoping soon to add a second part on the physiology and the embryology, for which he had some notes and material at hand. Returning, however, to Jamaica with the laboratory, in 1897, he continued his physiological experiments, and preserved material for histological purposes. Upon the untimely death of Conant, his material and notes were placed in my hands by Professor Brooks, to whom I here take the opportunity of expressing my appreciation and sincere thanks for the honor thus conferred and for the many favors received.

In this paper I shall note at some length Conant's physiological results and append his notes. I shall also add my results on the histology of the eyes and the sensory clubs in general, with some few facts on the histology of the tentacles. The embryology will be reserved for a future paper.

The forms used in the physiological experiments were Charybdea Xaymacana, one of the two species (see Literature V, a and b) first found and described by Conant; Aurelia aurita; Polyclonia and Cassiopœa. The greater number of Conant's notes are on Charybdea, and were left by him just as taken at the time of experimenting. Many of these notes are highly interesting and in the main fit in well with Romanes'[I] and Eimer's[IV] results.

Dr. Conant's work on Charybdea, in 1897, was wholly done at Port Antonio, Jamaica. At first Conant had only varying success in obtaining Charybdea, scouring the harbor and neighboring water at all hours, only to obtain but few specimens. It was on the forenoon of August 7th, while we were dredging at the head of East Harbor with a steam launch, that many Charybdeae were brought up in the dredge. This gave Conant a clue to their whereabouts and to the means of obtaining them, and from that time on he was able to obtain them in abundance. His first physiological experiments were begun on August 4th and continued thereafter at intervals of several days until his departure from Jamaica on September 6th.

Dr. Conant usually performed his experiments during the second half of the forenoon, after the animals had stood for a few hours in the laboratory.

The building that was rented at Port Antonio for a laboratory had, in the basement, a photographer's dark-room, which was of great service to Conant in his experiments.

The experiments on Aurelia, in 1897, were also performed at Port Antonio, between August 6th and 9th. The experiments on Cassiopœa were probably made at Port Antonio, where specimens were occasionally obtained.

The notes on Aurelia and Polyclonia, in 1896, were taken at Port Henderson, between May 12th and June 27th.

In his notes Conant speaks of Polyclonia and Cassiopœa. It is at present undetermined whether he really had both forms or whether he uses the two names for the same form. It seems likely that in 1896 he thought the form to be Polyclonia, while for some reason, in 1897, he supposed it to be Cassiopœa. I have examined several specimens of these medusæ brought from Port Antonio and find that they all have twelve marginal bodies and twenty-four radial canals, according to which (V, Haeckel's System), they should be Polyclonia. Conant, however, speaks of removing sixteen marginal bodies, which seems to indicate that he had Cassiopœa. A careful classification of this form of medusæ found about Jamaica seems to be a desideratum. I suppose, however, that for our purpose in this paper it will make little difference which name is used, the two forms being so similar in form and structure. I have, therefore, decided to retain both the names used by Conant.

For the complete anatomy of Charybdea the reader is referred to Dr. Conant's dissertation, "The Cubomedusæ" (8b), or the *Johns Hopkins University Circulars* (8a), both published by the Johns Hopkins Press. But, for the convenience of those who may be less familiar with Cubomedusan anatomy, the following brief summary of the anatomy of Charybdea is given:

The Cubomedusæ, as the name implies, approximate cubes, with their tentacles (four in Charybdea) arranged at the four corners of the lower face of the cube. These tentacles are said to lie in the interradii. Half way between any two points of attachment of the pedalia (the basal portions of the tentacles) and a little above the margin of the bell (cube), in a niche, hang the sensory clubs, one on each side, four in all. Each sensory club hangs in a niche of the exumbrella and is attached by a small peduncle whose axial canal is in connection with one of the four stomach-pockets and in the club proper forms an ampulla-like enlargement.

Each club is said to lie in a perradius, and, like the tentacles, belongs to the subumbrella. This is shown by the course of the vascular lamellæ, bands of cells that, stretching through the jelly from the endoderm to the ectoderm all around the margin, form the line of division between sub- and exumbrella.

Each club has six eyes. Two of these on the middle line of the club facing inwards are called the proximal and distal complex eyes, to distinguish them from the four simple eyes that are disposed laterally, two on each side of the line of the two complex eyes. All of these eyes look inwards into the bell cavity through a thin transparent membrane of the subumbrella. Besides the eyes and the ampulla already mentioned, a concretion fills the lowermost part of the club, and a group of large cells, having a network-like structure and called network cells by Conant, fill the uppermost part of the club between the proximal complex eye and the attachment of the club to its peduncle (Plate II, Fig. 13). What is evidently nerve tissue, fibers and ganglion cells, fills the rest of the club, with two groups of large ganglion cells disposed laterally from the network cells. A sensory (flagellate) epithelium covers the club.

Most Cubomedusæ, among them Charybdea, have a velarium (comparable to the velum of the Hydromedusæ), a membrane of tissue that extends inwards at right angles all around the margin. This velarium, like a velum, has a central opening through which the water is expelled from the bell-cavity when the animal pulsates. In the perradii and in the angle between the velarium and the body wall, are the frenula, which give support to the velarium much like brackets support a shelf, except that here the brackets are above the shelf instead of below.

In the upper part of the bell is the stomach, with the phacelli in its interradii, and continued ventrally into the manubrium, or the proboscis. The cavity of the stomach is continued in the perradii through the four gastric ostia into the four stomach pockets, which occupy the sides of the bell and extend to the margin. Immediately below the gastric ostia, and in the bell cavity, are the suspensoria, one in each perradius. These support the floor of the stomach much as the frenula support the velarium, except that the suspensoria are placed under the shelf (to continue Conant's figure) and not above it as are the frenula.

A nerve ring, underneath the epithelium of the subumbrella, passes from near the origin of each pedalium at the margin to the origin of the peduncles of the sensory clubs, a little above the margin, giving off a branch to each club. Eight ganglia are found in the course of this nerve. The four pedal ganglia lie near the bases of the pedalia, and are hence interradial; the four radial ganglia lie near the bases of the peduncles of the clubs, and are perradial. A small nerve, radial nerve, can be traced a short distance upwards from each radial ganglion. Underlying the epithelium of the frenula and the suspensoria are ganglion cells and nerve fibers in larger numbers than elsewhere (excepting the ganglia mentioned) in the subumbrella. Otherwise, ganglion cells and nerve fibers underlie the epithelium of the subumbrella, including the inner surface of the velarium, as also do muscle fibers, except in the perradii and in the region of the nerve, where the latter become interrupted.

PHYSIOLOGICAL.

CHARYBDEA.

Light and Darkness--Experiments 1-9, 10, 33, 34.—As already stated in the Introduction, a part of Conant's experiments were performed in a photographer's dark-room, with the animals in a deep glass jar. In the dark a fair proportion of the animals became nearly quiescent on the bottom, but upon lighting a lamp many started up immediately, while others took a longer time to come to the surface and swim. These experiments were tried a number of times and on different occasions with very similar results. Some medusæ, however, tried immediately after being brought in, seemed not to react so well upon being placed in the dark-room, nor would they become quiescent. This, probably, was due to the fact that the animals had not yet recovered from the effects of being caught and placed in new surroundings. (Experiments 1, 2, 3.)

Other experiments (4–8, 33, 34) were tried by carrying the jar with the animals from the weaker light of a room into the more intense light of outdoors or into direct sunlight. The usual result was an inhibition of pulsation and a settling to the bottom, while the medusæ immediately became active again upon returning with them to the room. These results were so marked that no doubts can be entertained as to their cause, though some exceptions occurred in which animals placed in the sun continued to swim on the surface or soon recovered pulsation. In some experiments, too, no animals responded to the inhibitory stimulus of the brighter light or all very soon recovered. (See, however, Temperature.)

Reducing the light by placing a coat over the jar produced the same effect in some experiments (8, 9, 10) as did reducing the light in other ways, while removing the coat produced the same effect as exposure to brighter light. In these instances it appears to be the transition from weaker to stronger light that inhibits pulsation, rather than the actual intensity of the light; and *vice versa.* It must be noted, too, that when left for some time in any one place the animals changed, some coming to the surface and others going to the bottom.

These experiments show beyond doubt that Charybdea is sensitive to light, and that it is moderate light that stimulates the animals to activity, while darkness and strong light inhibit activity. While the individual exceptions, as Conant himself suggests, are well explained on the supposition of individual diversity, yet it appears that other conditions, such as the time of day, temperature, etc., may have been responsible for some of the exceptional experiments in which no animals responded as expected.

While light of any intensity seems to have stimulated Romanes'[I] Sarsia and Tiaropsis (Hydromedusæ) to activity, we note that it is moderate light that stimulates Charybdea. This fact is evidently correlated with the circumstance that Charybdea usually lives upon or near the bottom.

It may further be added in regard to Romanes' Tiaropsis polydiademata, that when it was suddenly exposed to light it went into a spasm preceded by a long latent period during which there was a "summation of stimulating influence" in the ganglia. Sarsiæ would congregate toward the source of light and in general were more active in light than in the dark, while sudden darkness often inhibited a swimming bout. Romanes proves for Sarsia that the marginal bodies are the seat of luminous stimulation and that it is the light rays and not heat rays that stimulate. He also remarks that he has obtained similar results on the covered-eyed (Scyphomedusæ) medusæ, namely, that they respond to luminous stimulation.

It may here be of interest to note a few observations made by myself at Wood's Holl, Mass., on a beautiful Olindiad, which is abundant in the Eelpond at the above place. I found that in a room, in the ordinary light of evening, the animals swam actively; but the moment the electric light was turned on they stopped swimming and settled to the bottom or attached themselves to a branch of some weed or stem suspended in the water. This was the result in every trial. It is found, further, to be little active during the brighter parts of the day, when one must dip quite deep with a net in order to obtain it. A similar observation is also made by Murbach[II], who further states that this medusa may be deceived into laying its eggs by placing it in the dark.

One cannot help but remark how analogous is the behavior of medusæ, in respect to light and darkness, to the behavior of many of the higher animals,—and medusæ are among the most lowly organized of the animal creation.

Were one to conclude from the behavior of Charybdea in light and darkness in the laboratory, that it remained on or near the bottom in the daytime but became more active near or at the surface evenings, nights and early mornings, one would probably not be far from the truth. Dr. Conant, while towing near the bottom with a weighted net, in water four to five feet (1.2–1.5 m.) deep not far from shore and deeper farther out, found Charybdea in abundance mornings and afternoons, but very few in the evening. In the evening some few were usually taken in the surface tow. (See Introduction, Occurrence and Activity.)

Again, who knows but that Charybdea is active during the day, on the bottom where it was dredged (the light there would only be moderate), and quiet at night. This supposition would seem to be true, at least, for those forms of Cubomedusæ that live in deep water. We can hardly suppose that they should regularly rise to the surface from great depths and become active. This much we do know that bright light inhibits Charybdea's activities, while it probably would not be active in perfect darkness.

I do not know just what interpretation to put upon Conant's finding Charybdea at Port Henderson at the surface during the early part of the forenoon, before the sea-breeze roughened the water ("Cubomedusæ" p. 7). This fact hardly fits in with my conclusions above. Perhaps Charybdea's habits vary with its habitat.

Finally, while I find no experimental evidence in Conant's notes about what parts of Charybdea are sensitive to light, yet it would seem preposterous, from histological evidence and from Romanes' results on Sarsia, to doubt that the eyes of the marginal bodies are the seat of this stimulation.

Dr. Conant further experimented by cutting off certain organs and parts from the Cubomedusan bell. These excisions consisted chiefly in cutting out the concretions of the sensory clubs, cutting off the whole club, eliminating a part or whole of the margin and the velarium, cutting the bell into sectors, excising the stomach and parts connected with it, and other parts.

Concretions—Experiments 10, 11.—The four concretions were removed from each of four animals. Two of these (Experiments 10, and another (X), not appended, to save space) seemed to be little if at all affected by the operation. One of the two (10) swam actively, at first up and down more changeably than those intact, but later mostly near the surface. The other one also swam actively and showed nothing to indicate weakened sense-perception. The other two (11) did not stand the operation well, as Conant remarks, and immediately went to the bottom, where they remained, one swimming, while eight hours later one was still in good condition.

Several attempts with stronger light by removing the coat from the jar made no difference in the behavior of 10; it continued to swim as heretofore. Upon a final trial, however, with removing the coat, it went to the bottom, thus showing a possible reaction to light; but when next seen it was keeping to the bottom.

That the concretions should function as organs of light sensation, as the first of the above animals might seem to indicate, I believe is out of the question.* The fact, too, that this same animal (10), together with another (X), swam actively, immediately changing their course upon coming to the surface, in reality behaving quite as normal animals, hardly permits us to conclude from the behavior of the other two (11) that the concretions function directly as organs of equilibrium or space relations. May these concretions not function simply as weights for keeping the sensory clubs with their eyes properly suspended? Since these concretions lie at the lowermost part of the clubs and in closed sacs and unsupported by cilia, it would seem that the above suggestion as to their being weights is not improbable. Direct observation (Experiment 20) by Conant shows, furthermore, that the clubs always hang with a tendency for the concretions to be lowermost, regardless of the position of the animal.

Again, while they may function as weights, as just explained, the fact that the epithelium of the clubs is flagellated (a flagellum, continued as a nerve fiber, to each cell—see Histology), the supposition lies near that these flagella are the ones influenced by the concretions as the clubs bear against one side of the sensory niche or the other.

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* It was at one time supposed that the concretions in the marginal bodies of medusæ represented lenses and the surrounding nerve tissue the optic nerve, a supposition so highly improbable that it never gained any acceptance. (Ib., p. 41, note.)

A somewhat similar view seems to be held by other observers and is noted by Lang in his text-book ("The outer epithelium of the auditory body carries the auditory hairs"). It seems, then, that in functioning as weights for suspending the clubs, they may also serve at the same time for making the pressure of the club against the niche greater than if they were absent, and thus in part serve in equilibrium. On this supposition we should expect, furthermore, that after the removal of the concretions the animal would be little, if at all, affected, since the clubs themselves, without the concretions, would still be of sufficient weight to be influenced by gravity and thus to bear against the walls of the sensory niche. It must be noted, however, that Conant's experiments upon equilibration in Charybdea are negative. Also, that Charybdea has any auditory sense is negatived by two attempts of Conant's with a violin—one attempt with the violin near the animals, and another with it in contact with the dish. (From an unpublished note.) Hence, some other word such as sensory or equilibrating should perhaps be substituted for "auditory" in the above quotation.

Removing the concretions from Aurelia gave negative results very similar to those on Charybdea. (Experiment 42.)

Sensory Clubs—Experiments 12–19, 20, 24.—The entire sensory clubs were removed from a number of animals. A paralysis of pulsation followed by a rapid recovery was the usual result. In some instances, however, there was no paralysis, while in others no recovery followed paralysis. This is true in a general way whether one club only or all were removed. While no permanent paralysis followed the removal of one or two clubs, yet permanent paralysis did occur after the removal of a third club, as, of course, also after the removal of a fourth. It is evident, too, that as the removal of the clubs progressed recovery seemed to be weaker after each cutting, except in one case when pulsation seemed to be quickened after the removal of a second club. The pulsations after recovery seemed to be not so strong and regular, often quite feeble, and in one instance in groups. Pieces of tissue with a club attached and pulsating regularly, ceased pulsating after removal of the club, in one instance, however, still giving occasional contractions.

These results are quite the same as those of Romanes[I] on Aurelia, Cyanæa, etc., and of Eimer[IV] on Aurelia, Rhizostoma, Cotylorhyza, etc.* In these forms Romanes sometimes obtained complete paralysis after the removal of the sensory clubs only, as also after the removal of the whole margin, though this was not marked in Aurelia. In Cyanæa and other forms motor centers seemed to be more abundant than in Aurelia, so that paralysis was oftener followed by recovery. He concludes that while the principal motor centers reside in the lithocysts, other centers doubtless exist that may function vicariously, but that the centers of the margin are more definitely limited to the marginal bodies in the Scyphomedusæ than in the Hydromedusæ, in which the whole margin seems to be replete with centers. He feels positive, furthermore, that no motor centers exist in Aurelia's margin outside of the marginal bodies (lithocysts). Eimer's results are essentially the same as Romanes', so that for a more detailed comparison of the two, Romanes' works should be consulted.

Romanes' conclusion for the Hydromedusæ is that the motor centers are not so definitely localized in the marginal bodies, but in the margin generally, the excision of the marginal bodies alone producing only partial paralysis, as would also the removal of the margin from between the marginal bodies, but not so marked. For the Hydromedusæ he concludes, then, that all the centers of spontaneity are definitely localized in the margin, but not limited to the marginal bodies. To this he mentions one exception, namely, *Staurophora laciniata*, in which another center is found near the margin and two others in two opposite arms of the proboscis.

I made the remark in an abstract (VI) on Conant's notes that Romanes did not obtain recovery of pulsation after removal of all the lithocysts in Aurelia. As noted above, he did obtain recovery, so that Conant's results on Charybdea and also Aurelia (see Polyclonia and Aurelia) are quite in agreement with Romanes.

The paralysis following the removal of the clubs in Charybdea is evidently, primarily, the result of a loss of a part of its nervous mechanism (motor centers), and, secondarily, of nervous shock, and points to the existence of a definite nervous mechanism in the clubs. The histological evidence is here, as usual, corroborative of the physiological.

Another interesting phenomenon observed after the removal of

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* Eimer's results I get from Romanes and Hesse$^{\text{III}}$.

one or all of the clubs was the strange behavior of the proboscis. This would reach from side to side, expanding and contracting its lips as if trying to grasp something. This behavior is very similar to that of the proboscis of *Tiaropsis indicans* when Romanes stimulated any part of its subumbrella, or of *Limnocodium sorbii*, a little fresh-water medusa, when he stimulated its margin or the region of the radial canals. (Ib., p. 242.)

I may add that I observed a very similar movement of the proboscis of the Olindiad, before mentioned. When I pulled off pieces of its gonads by means of quick jerks, with a small forceps, it would continually reach toward the injured part of its subumbrella. This medusa is generally quite active with its proboscis and can occasionally be seen to reach with it.

Romanes states in one place that the proboscis is not affected by the excision of the margin. This is evidently not the case in Charybdea, in which excision of the sensory clubs (which really belong to the margin—see "Cubomedusæ") decidedly stimulated the proboscis to active movements. This, furthermore, points to the marginal bodies as being organs of considerable importance in giving information in the life of Charybdea. In Romanes' Sarsia and other medusæ, however, the proboscis did respond to the stimulation of the tentacles and the marginal bodies, as also would the bell respond to a stimulation of the proboscis (manubrium), thus showing a reflex nervous connection between these regions of the bell, similar to that described for Charybdea.

Velarium and Frenula—Experiments 18, 29, 30, 41c.—"The power of originating contractions" to use Conant's own words, "evidently resides in the velarium or in ganglion cells of the frenula, just as it does in the proboscis and the floor of the stomach." Isolated pieces of the velarium contracted by themselves as did the whole velarium when all other tissue had been removed. An isolated velarium with the margin and the pedalia attached gave irregular contractions. When the pedalia with the *interradial ganglia* were removed it still contracted; and when all the other tissue was cut off contractions continued.

Cutting the velarium caused the *pedalia* to be strongly contracted inwards so that the tentacles were brought inside the bell. Cutting away the velarium did not interfere with the pulsations of the bell, but progress was much retarded.

Cutting the frenula caused the pedalia to contract but seemed not to affect the ability to swim. Comparing the velarium of the Cubomedusæ with the velum of the Hydromedusæ, I recall no observations similar to the ones here noted, though it seems that the two may have quite similar functions. It seems somewhat probable that the velum, and also the velarium, may function in obtaining food,—and this besides their function in swimming. Their probable function in swimming, as is well known, is evidently to narrow the mouth of the bell and thus to cause the water to be forced out in a smaller but more rapid stream, giving the animal a steady and more prolonged movement through the water at every contraction of the bell. In regard to taking food, I observed that a small crustacean, in the process of being swallowed by an Olindiad, seemed to be held by the velum being firmly contracted about it while the proboscis was working itself over the crustacean. It would seem, furthermore, that my supposition is supported for Charybdea by the fact that the pedalia and tentacles were contracted so as to be brought inside the bell when the velarium was cut. The stimulus of cutting the velarium may be comparable to a stimulus from some object touching it, and thus cause the pedalia and tentacles to come reflexly to aid in capturing or holding the object, a fish, crustacean, or such, to be captured.

Pedalia, Interradial Ganglia, Tentacles—Experiments 15, 23, 27–31, 41b.—When the pedalia were removed, the power of the animal to guide itself was completely gone. When one pedalium was cut the others contracted, while stroking the outer edge of the pedalia, touching the sensory clubs, or sharply pricking the subumbrella, often produced the same result. (See also Nerve.) The upper part of the subumbrella seemed not so sensitive and more seldom produced the reflex of the pedalia, while the base of the stomach did not give it at all. Stroking the outer edge of the pedalia of *Tripedalia cystophora*, the second of the two species of Cubomedusæ described by Conant, also caused the pedalia to be contracted inwards. I may note here that the muscle fibers under the ectoderm of the pedalia are specially well developed at and near the inner and outer edges, both in Charybdea and Tripedalia. On the flattened sides of the pedalia the muscle fibers are fewer.

When the pedalia were cut off far enough up to remove the interradial ganglia, coördination was not affected and the animal could pulsate well enough but with little progress. (See above under Velarium and Frenula.)

An isolated tentacle is capable of squirming contractions, and when stimulated at either end, it would contract wholly or in part only.

The pedalia, then, it would seem, serve also as a steering apparatus, for which they are admirably fitted, considering their blade-like thinness.

Considering, now, the reflexes noted under this head and the preceding one, we find that there is an intimate nervous connection between the velarium and frenula, subumbrella, sensory clubs, nerve, and a single pedalium, on the one hand, and the pedalia on the other hand. This is born out fully, furthermore, by the histological evidence —(See Introduction and "Cubomedusæ"). Considering the subumbral plexus of ganglion cells and fibers, including the velarium and the frenula, which is in connection with the nerve ring and this again with the sensory clubs and the interradial ganglia at the bases of the pedalia, we have a basis for these reflexes. While Conant failed to demonstrate nerves ("Cubomedusæ") from the interradial ganglia to the pedalia, yet, that a nervous connection exists between the pedalia and the bell is well shown by his physiological experiments. I have, furthermore, demonstrated ganglion cells under the ectoderm of the tentacles (see Histology).

Romanes obtained quite similar results in the Hydromedusæ. He found that when a tentacle of Sarsia was slightly stimulated, it alone would contract, but when it was more strongly stimulated the other tentacles also would respond as also the manubrium. I find no evidence in Conant's notes of any such response of the manubrium of Charybdea, except when the clubs were cut off.

The reflex obtained on stimulating the subumbrella of Charybdea, when the pedalia would contract, is somewhat different from that obtained by Romanes, who found that the most sensitive part of the subumbrella in producing a reflex of the margin was at the junction of the manubrium to the bell and that the subumbrella below this point did not give the reflex.

Stomach, Suspensoria, Proboscis, Subumbrella—Experiments 12, 18, 19, 24–26, 29, 31.—The proboscis and the stomach with the phacelli when cut out, contracted with or without the lips removed. The isolated lips also contracted (twitched).

Pieces of the sides connected only with the stomach and suspensoria, or with the margin (Experiment 47 (?)) twitched spontaneously, but seldom did so when these were removed. In one instance the whole side was cut out so as to exclude the radial ganglion but still connected with a portion of the suspensorium. This pulsated, or contracted, but on being halved transversely, the lower half ceased to contract while the upper half connected with the suspensorium, continued to contract.

Cutting off the whole stomach end of the animal excited to very rapid pulsations of the remaining part, with the stream of water stronger out the aboral end than past the velarium.

Conant says, "It seems I get no good evidence of the subumbrella without connection with special nerve centers being able to contract by itself." The piece in which he did get contractions he suspects may have been intimately associated with some part of the frenula or the suspensoria. In Polyclonia no such doubt exists, for small pieces of subumbrella were seen to contract. A small piece of subumbrella of Charybdea with a sensory club attached could contract by itself.

From the above it would seem that a center capable of inciting to contractions resided in the suspensoria as well as in the sensory clubs, and this may be one of the centers that becomes potent upon the removal of the clubs. This is further supported by Conant's observation (Introduction and "Cubomedusæ") that an extra large number of ganglion cells is found under the epithelium of the suspensoria. A somewhat similarly located center of spontaneity described by Romanes for *Staurophora laciniata* (Hydromedusa) has already been noted.

As to the rapid pulsations of the bell after cutting out the stomach end, this also is similar to Romanes' results on Aurelia and other Scyphomedusæ, when he cut off parts of the manubrium or an aboral ring out of the bell. In these instances, however, Romanes soon obtained a slackening of the rhythm following the temporary acceleration. The temporary acceleration he attributes to the stimulus of cutting, and the slackening to a lack of some afferent stimulus from the removed tissue. Conant obtained the same results on Polyclonia by removing the oral arms (see Polyclonia) but says nothing about a slackening of the rhythm in Charybdea. I believe the increased rhythm in Charybdea was in part due to the decreased amount of labor necessary to force the water out of two openings instead of one, namely, past the velarium. Just how much this observation bears upon Romanes' theory of rhythmic contraction, that the rhythm is due to an alternate exhaustion and recovery of the contractile tissue, as opposed to the ganglionic theory of rhythm of physiologists, one does not wish to speculate much. Yet, I feel that the observation rather supports this theory. The tissue having to do less work, would become less exhausted at each contraction and require less time for recovery and hence have a more rapid rhythm.

I here sum up Romanes' theory in a few words. The ganglia liberate a constant and comparatively weak stimulus, one perhaps about minimal. This stimulus sets off the contractile tissue; but as the tissue contracts and becomes exhausted the constant stimulus becomes, in relation to it, sub-minimal, and it does not contract again until it has recovered and the stimulus is again strong enough to set it off. The ganglionic theory of rhythmic contraction supposes that the ganglia liberate stimuli to the contractile tissue at successive intervals. Romanes had this theory suggested to him by the rhythmic contractions he succeeded in obtaining by subjecting deganglionated bells to a continuous but weak faradic stimulus, or by placing them into weakly acidulated water, or into 5 per cent. glycerine. Romanes claims that his theory better explains muscular tonus and the contraction of involuntary muscle. He does not, however, hold this theory to the exclusion of the ganglionic theory, since only too often does he speak in terms of the latter. He further brings in his support the fact that the frog's tongue, in which no ganglia have been demonstrated, can be made to contract rhythmically when subjected to a weak and continuous stimulus. He also calls attention to the rhythmic contractions seen in the Protozoa, the snail's heart, etc. Finally, physiologists are much inclined to explain the rhythmic contraction of the heart and other involuntary muscles, in part, at least, as due to a property of the contractile tissue.

Margin, Radial Ganglia, Nerve—Experiments 18, 21–23, 30.—Complete removal of the margin did not stop pulsation; but the removal of the radial ganglia stopped it permanently. While this experiment seems to have been tried only once, yet, taking into consideration the results of other operations, it would seem that the principal centers of spontaneity reside in these ganglia. (It should here be remembered that the interradial ganglia were probably removed at the removing of the margin.)

Cutting the nerve in the eight adradii caused the *pedalia* to bend inwards at right angles to their normal position but did not in the least affect the coördination of the sides. When, however, the sides were cut in the eight adradii to the base of the stomach, coördination for the main part ceased, and each side pulsated in its own rhythm.

I have said that the principal centers of spontaneity reside in the radial ganglia. Upon further thought this hardly seems warranted. No doubt, among the principal motor centers must be placed the ganglionic masses of the clubs, and the radial ganglia, together with the homologous interradial ganglia, represent centers of equal value. I speak of these two sets of ganglia as homologous, since strictly speaking, they both belong to the margin, and the clubs at whose bases they lie probably represent modified tentacles. Conant's experiments leave us in the dark as to the function of these ganglia. Next in order, it would seem, are the ganglion cells in the suspensoria, as is suggested by the contractions of an isolated side with a portion of a suspensorium attached. (See previous head.) While we have seen that the frenula and the velarium can contract by themselves, yet, I find no evidence that these can impart their contractions to any adjacent tissue.

Conant's results on cutting the nerve eight times and then continuing the cuts to the base of the stomach are quite the same as Romanes and Eimer obtained upon Aurelia. Romanes, however, concludes that in his Sarsia, Tiaropsis, etc., coördination was broken when only short incisions were made in the margin. Charybdea appears, then, to agree with Aurelia rather than with the Hydromedusæ. Yet, since Romanes at first obtained similar results to those of Charybdea on Sarsia, but on further experimenting concluded that coördination had really been destroyed at the first cutting, we cannot speak with certainty that coördination had not been destroyed in Charybdea before the cuts had been continued to the base of the stomach. I say not with certainty, because the injury to the bell being slight, coördination may have been maintained on the principle of a simultaneously (simultaneous for the octants) alternate exhaustion and recovery of the contractile tissue on the principle of Romanes' theory.

Stimulation.—Romanes found when he stimulated a deganglionated bell of a Hydromedusa, that it responded by a single contraction, while that of a Scyphomedusa responded with several quite rhythmic contractions. Charybdea in this respect agrees with the Scyphomedusæ. Romanes' results were also verified on Aurelia. (Experiments 12c, 15, 50, 51.)

Activity of Charybdea.—In speaking of the activity of Charybdea, I cannot do better than refer the reader to the notes. (Experiment 41.) Conant remarks in his dissertation what an active swimmer Charybdea is, and this is further borne out by his later observations.

Temperature.—Ice in the water seemed to have no effect, except when held against an animal, when a slowing of pulsation followed in a few instances. On some pulsating actively in the sun the temperature of the water was found to be 92° F. (Experiments 33–35.)

Conant does not tell us how cold the water became when he placed ice in it, but judging from his results, it seems that he might have obtained a decided slowing of pulsation if the water in which the medusæ swam had been permitted to approach anywhere near the freezing point, say 35–40° F. Romanes obtained decided slowing of pulsation, and even complete inhibition, on a bell of Aurelia, as also a lengthening of the latent period on some strips cut from a bell of Aurelia, by lowering the temperature of the water. Replacing Aurelia in warmer water had the effect of immediate recovery and increased rhythm. In Aurelia, raising the temperature increased the rhythm but diminished it when the temperature of the water became 70–80° F. After a slowing of pulsation due to such a rise of temperature, it would not quicken again when the animal was placed in water of its normal temperature. Romanes explains this by supposing that the tissue of the medusa had been permanently injured by the abnormally high temperature. It would be interesting to observe how the tropical Aurelia behaved under such treatment, seeing that Charybdea pulsated actively and without apparent injury in water at 92° F. *Limnocodium,* noted by Romanes, and probably a tropical species, lived happily in water at 85° F. in the lily house of the Royal Botanical Society. The temperature of the water could be raised to 100° F. before it proved fatal to this medusa. Such facts point to a decided difference in the constitution of the protoplasm of tropical and temperate medusæ. Romanes' Sarsia became frantic when placed in milk-warm water.

While writing the above, I was led to wonder whether the temperature of the water may not have been the stimulating influence in those experiments on light (previously noted) in which the medusæ continued to swim actively in the sunlight.

Food and Feeding.—See Experiment 36.

I again make note of a few observations made by myself on the Olindiad. A crustacean became entangled in the tentacles of a medusa; apparently this wished to retain it, for the proboscis reached in the direction of the crustacean, which, however, got away. I then placed, by means of a needle, another small crustacean against one of the tentacles. This was seized but not retained, for the animal pulsated and it was washed away by the water. Twice I saw a good-sized crustacean in the proboscis. In one instance the velum appeared to hold the part of the crustacean not yet in the proboscis. I noticed another with a crustacean wholly in the proboscis, which was much lengthened out, the upper part of the crustacean being in the stomach. The next morning the crustacean was wholly in the stomach and the proboscis normal. At 5.30 P. M. the crustacean was ejected, nothing but the shell and some rubbish remaining.

These medusæ seem to pay no attention to being touched by one of their kind, except to give a pulsation or two.

The proboscis appears very "intelligent" in its actions.* First, some of the tentacles can be seen to contract and to bend inwards, then the side next the tentacles contracts and the proboscis is seen to reach in that direction. I could not see, however, what the irritant was.

Occurrence of Charybdea—Experiments 37–40.—Dr. Conant's remarks ("Cubomedusæ") on the occurrence of Charybdea at the surface of quite shallow water and near the shore (which is quite at variance with former observations, that the Cubomedusæ are essentially deep-sea forms) are further borne out by his observations at Port Antonio. As already noted in the Introduction, Charybdea was here found in abundance in quite shallow water and near shore, but on the

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* By no means do I wish to attribute intelligence to these animals.

bottom instead of at the surface as at Port Henderson. It is possible that the animals had been active near the surface earlier in the morning and that some unknown conditions determined their settling to the bottom earlier in the former place than in the latter.

Conant's conjecture, "whether these were their natural conditions, or whether the two forms," Charybdea and Tripedalia, "were driven by some chance from the deep ocean into the harbor and there found their surroundings secondarily congenial, so to speak," seems to be borne out in favor of the former supposition (for Charybdea at least),—that these are their natural conditions and that Charybdea Xaymacana is essentially a shore form.

Aurelia and Polyclonia (Cassiopœa)

Experiments 42–53.

Many of the observations on these forms relate to the rate of pulsation. In an Aurelia, following the removal of a lithocyst, there was a pause followed by pulsations. In about two minutes rhythmic pulsations were renewed. Four minutes after the operation there were nineteen pulsations to the half minute, while twenty minutes after there were only nine, and these in groups of six and three. The normal rate of pulsation was twenty-five to the half minute.

Polyclonia behaved much in the same manner as Aurelia. Upon the removal of lithocyst pulsations continued, but in groups with short pauses. The normal rate of pulsation was twenty-seven to the half minute, while three minutes after the operation it was seventeen, and eleven minutes after, fifteen to the half minute. The tissue connected with a removed lithocyst gave contractions. Placing a Polyclonia in fresh sea-water more than doubled the rate of pulsation, which, however, soon fell to the normal rate, and lower in one instance. In small individuals the rhythm is decidedly more rapid than in those of larger size. The few observations on this point would seem to show that it is in inverse proportion to the squares of the diameters of the bells.

The removal of a single oral arm or of the whole eight, in Polyclonia, had much the same effect as the removal of a lithocyst: there was a decided slowing of the rate of pulsation, while the immediate effect of cutting was an acceleration or a return to near the normal rate. About a day later this same animal had quite regained its normal rate of pulsation and continued to live over two weeks. A long latent period followed the cutting of an arm, before the stimulation of cutting manifested itself.

An Aurelia, with all its lithocysts removed, still gave spontaneous and coördinated contractions after allowing time for recovery from the operation. This was the result in one instance, while in several others only a few contractions were observed. Removal of the sixteen marginal bodies (lithocysts) in a Cassiopœa produced paralysis for a time but recovery soon followed. A Polyclonia with its entire margin removed was paralyzed but had so far recovered in a day as to be able, at intervals, to give spontaneous pulsations.

The removed margin of a Polyclonia pulsated vigorously. This margin was then split so as to make a ring within a ring but connected at one point by a small bridge of tissue. The waves of contraction, which always originated on the ring with the lithocysts, passed the bridge to the inner ring quite as Romanes experienced. The outer ring was next split so as to separate the exumbral portion from the subumbral, when it was found that the contractions always originated from the latter. Seven days after its removal, this same margin was still alive and pulsating vigorously, and broken-off pieces of the subumbral portion were pulsating by themselves. Fifteen of the ganglia were removed. It was then found that while most of the pulsations originated at the remaining ganglion, now and then contractions originated in other parts where no ganglion remained. Two days later this margin was still alive with contractions originating as often from other parts as from the ganglion. A similar observation was made on a margin of Cassiopœa.

A Polyclonia with the eight lithocysts of one side removed, to compare with a normal one, gave no evidence of affected coördination.

An oral lobe from an Aurelia could give contractions some minutes after removal.

In another Aurelia a circular cut was made about the base of the oral lobes through the epithelium of the subumbrella. The animal could pulsate well enough but coördination seemed a little affected, while in another one with a like cut but semicircular, no effect was noticed.

These results on the removal of the lithocysts (and margin in Polyclonia) in Aurelia, Polyclonia and Cassiopœa agree quite with those on Charybdea and, of course, also with Romanes' and Eimer's results as to paralysis and recovery following the removal of the lithocysts, or margin, in Aurelia, Cyanea, etc. I recall no similar observations, however, on removing a single lithocyst, and the question of an explanation for the slowing of the rhythm thus brought about arises. Romanes gives as an explanation for the slowing of the rhythm (Aurelia, Cyanea, etc.) following the temporary acceleration upon removing the manubrium or a portion from the center of the bell, as due to a lack of an afferent stimulating influence upon the ganglia from the excised tissue. May a similar explanation not serve to explain the slowing following the removal of a single lithocyst, above noted? The removed lithocyst could no longer give its efferent stimulus to the remaining ganglia nor to the tissue, so that the former would have a weaker stimulating influence, in consequence of which the latter (the contractile tissue) would be deprived of a part of the original stimulus of the remaining ganglia as also of that of the removed ganglion. The whole would thus result in giving to the contractile tissue a weaker stimulus, which, again, would require longer and greater recovery on the part of the tissue in order to be set off by the stimulus at hand. This explanation is given on the basis of Romanes' theory of rhythmic contraction previously explained.

Of course, it may be suggested that the musculature had lost tonus, due to the lack of influence of the removed ganglion (lithocyst), in consequence of which there was a lowering of irritability on the part of the contractile tissue. This would require a greater summation of stimulating influence (Ganglionic theory of contraction) on the part of the remaining ganglia to set it off. Again, the loss of irritability on the part of the contractile tissue may have been due to a lack of nutritive influence from the removed ganglion.

Romanes' explanation, that the slowing of the rhythm following the removal of the manubrium and central parts of the bell in Aurelia and Cyanea is due to a lack of an afferent stimulus on the ganglia from the removed tissue, likewise explains the similar results obtained by Conant by removing the oral arms from Polyclonia.

The fact that a margin of Cassiopœa and also of Polyclonia, connected with but one ganglion, often originated contractions in other parts as well as from the ganglion, seems to show that motor centers resided in the margin outside of the ganglia. This would be somewhat at variance with Romanes' conclusion, that no such centers existed in the Scyphomedusæ. Conant does not state whether the Polyclonia margin in question was kept in fresh sea-water or whether the water was not changed during the seven days. If the latter is the case, then some poisonous compounds may have been formed that acted as a stimulus much as weakly acidulated water served Romanes in producing rhythmic contractions in deganglionated bells.

Again, while it is true that no ganglia are known to exist in the margins of the Scyphomedusæ outside of the ganglia in the marginal bodies, yet, ganglion cells and nerve fibers are found in the subumbral part of the margin as well as in the rest of the umbrella. And as I know no reason why scattered ganglion cells may not function as ganglia, it is possible that the contractions in question were spontaneous.

Finally, is it possible that the remaining ganglion originated the contractions in different parts of the margin, thus acting at a distance from the points at which contractions originated? Romanes gives an instance in which he believed to have evidence that this was the case. Upon a final consideration I am inclined to this latter explanation.

SUMMARY.

Summing up for Charybdea, we have seen that it is very sensitive to light, strong light as also darkness inhibiting pulsations, while moderate light stimulates it to activity. Also, a sudden change from weaker to stronger light, or *vice versa*, may inhibit or stimulate to activity respectively. This behavior of Charybdea seems to be correlated with its habit of life on the bottom. We have no reason to doubt but that the eyes of the sensory clubs are the seat of light sensation.

The experiments on equilibration are negative, giving us no certain light on the function of the concretions, though it appears that they may serve, in part at least, for keeping the sensory clubs properly suspended. Their function in giving the animal sensations of space relations is not, however, excluded.

Excision of the sensory clubs demonstrates that they are the seat of important ganglionic centers, the removal of which results in temporary paralysis and weakness. That they also are the seat of organs (eyes, network-cells, concretions) that are of importance in giving information in the life of Charybdea, is evident from the reaching motions of the proboscis after the removal of the sensory clubs. Other centers of spontaneity in their order of importance probably are: the radial ganglia (one experiment); the interradial ganglia (?); the suspensoria, as shown by their supplying stimuli to isolated pieces of the sides connected with them; the frenula and the velarium, the latter of which gave contractions when removed with the frenula or in pieces only. No evidence is given that the frenula or the velarium can impart their contractions to other tissue, though this seems probable for the former. The proboscis can also contract of itself.

Reflexes between the velarium, frenula, subumbrella, sensory clubs, nerve, and any one pedalium, on the one hand, and the pedalia on the other hand, are very common, and point to the pedalia with the tentacles as organs of defense and offense. The pedalia serve also as rudders in swimming.

Finally, as judged by the results in this paper, Charybdea seems to occupy, physiologically, a position intermediate between the Hydromedusæ and the Scyphomedusæ. In its great activity as a swimmer, in its response to light, and in its reflexes it is Hydromedusan, while in the paralysis and recovery following the removal of its marginal bodies, as also in its response with several pulsations instead of one, when a deganglionated bell is stimulated, it is Scyphomedusan.

The observations on the Discomedusæ, Aurelia, Polyclonia, Cassiopœa, demonstrate the existence of motor nerve centers in the marginal bodies; but that other centers are present is shown by the recovery of pulsation following the removal of the marginal bodies or the margin. These results are mainly confirmatory of those of Romanes and Eimer. They differ from these in the fact that margins of Polyclonia and Cassiopœa, with only one ganglion attached, originated contractions distant from the ganglion. Removing of a single lithocyst resulted in a slowing of pulsation, as did also the removal of the oral lobes, though the immediate effect in the latter case was an acceleration. Isolated pieces of the subumbrella could contract.

DR. CONANT'S NOTES.

Below follow Dr. Conant's notes. They are printed about as Conant left them. Their order of succession, however, has been changed to bring similar experiments together, while useless and often repeated ones have been omitted, and short elliptical sentences completed. Where the present writer wished to add any explanation, the same has been placed in brackets.

CHARYBDEA.

Light and Darkness.—1. Eight medusæ, in a deep glass jar and covered by a black coat, except one inch around the top, were placed in the dark-room.

a. When light from a lamp was thrown on the surface (one inch) layer, the animals were active near the surface; when the light was withdrawn, one or two were on the bottom and not moving but were probably pulsating.

b. After four or five minutes in the dark, three or four besides a feeble one are on the bottom. It took about two minutes to get them all to swim [by the lamp]. Of the three on the bottom, one, at any rate, was not pulsating. [Three other attempts like a and b were made, with very similar results.]

2. Experiment No. 1 was repeated several weeks later. Four in a large round glass dish were placed in the dark-room. A lamp being held to the dish all but one were found to be on the bottom. That one quickly went to the bottom, while two of those on the bottom quickly came to the top. In two or three minutes the one that had gone to the bottom began to pulsate and at about the same time the other one that had remained on the bottom also began to pulsate, while the two that had gone to the top stayed there swimming very actively. [Repeated with like results.]

3. Fresh ones did not show the reaction to light after darkness so well as did those in the experiments previously recorded. They were experimented with about nine A. M., while usually they were tried later in the day. I had rather suspected from previous work that they would not react so well when fresh.

4. a. In walking with the jar (1) of jelly-fish of experiment 1 from the dark-room to the back porch of the laboratory (fifty steps), in the bright sun and a cool breeze, all were found upon entering the laboratory door to have settled to the bottom and most of them to have ceased active swimming. In five minutes two or three were swimming somewhat, and in five minutes more all but one or two (eight in all) were swimming.

Walking with the jar about the laboratory did not suffice to make any change in their swimming, nor did blowing on the surface make any appreciable change.

b. Upon taking the jar to the back porch and placing it on the stone or cement flags, in the shade and a cool breeze, in four minutes time all were on the bottom not even pulsating.

Upon replacing them on the laboratory table all began to swim about at once. [Repeated.]

c. The jar (1) was placed on the back porch again; in fifteen seconds three were on the bottom; in one-half minute all but one. In three or four minutes all were on the bottom, but two were swimming lively and the others pulsating. In another minute all were swimming.

d. The jar (1) was tried again, not resting it on the flags but holding it by my hands on the sides. The effect was just as quick; they stopped pulsating at once. By the time I had got back to my table in the laboratory, one was at the surface and another arrived just as the jar was set down.

[Several other experiments of an order similar to those just noted were tried, with very similar results.]

5. Two buckets stood side by side in the laboratory. One bucket (1) had more Charybdeas in it than the other bucket (2), and also had more since brought in (about an hour). The water of one (1) was also more discolored and with more organic matter (sea weed, etc.). In the laboratory the animals were active on the surface of both buckets. Placed in the sunlight on the porch, no breeze, the sun slanting so that one side of the water in the buckets was bright while the other side was shaded, the jelly-fish in (1) went mostly to the bottom, while those in (2) seemed unaffected though some showed a tendency to go to the bottom after a longer exposure. The experiment with (1) was repeated and it took some five minutes for them all to go to the bottom. In a few minutes after replacing them in the laboratory several were active again on the surface.

6. Jar (a) with five large ones stood on my table; they were quite active. Placed in the sun (no breeze), on the porch, one or two sank to the bottom at once and the others seemed to slow their activities somewhat but not very markedly. In a few minutes all were swimming, apparently more actively than before, in the bright sunlight.

[In other experiments Conant shows that it is not the stimulus of walking that causes them to swim when carried into the room, for they would not swim when he walked with them on the porch. Also, he shows how they may change, some swimming, others not, when left for some time in any one place.]

7. In a tumbler were two pulsating very vigorously. Placed in the bright sunlight, very little breeze now and then, they showed no change whatever.

8. Some in a jar were covered with a black coat. The coat was taken off, and almost immediately they stopped pulsating, or pulsated but feebly, and sank to the bottom. The coat was put on again with one part near the bottom of the jar exposed. Almost at once, the animals, which were quite motionless, pulsating but little, resumed pulsation, which became more and more vigorous, and quickly swam to the top again. It seems plainly to be a reaction to light. [Such experiments as this were repeated at different times with very like results.]

9. A bucket with several bobbing actively on the surface was set out in a smart shower, and the animals continued bobbing on the surface as before. I could not see that they made the slightest attempt to go below.

There can be no doubt but that there is an individual difference in sensitiveness to the reaction of light after darkness. E. g., I just removed the coat from a dish with four in it; one went to the bottom at once, another presently, a third remained active at the surface, the fourth when noticed was on the bottom.

There is also a difference in the length of time they stay on the bottom as well as in the quickness in the response to light. Some recover very quickly, should say in less than a minute, and at once become very active. Some stay for a long time and only resume activity upon the coat being placed over them. Perhaps this explains some of the observations in Experiment 1.

Sensory Clubs.—10. All four concretions were removed and the animal stood the operation well. It swam more restlessly, however, than others did in the same surroundings. It seemed at first to show a trace of loss of sense-perception. It swam up, and down again, more changeable than those intact, which stay rather more constantly either on the bottom or at the surface. This may, however, have been due solely to the restlessness of the animal after the operation. Later it swam actively for by far the most part on the surface only, which points to the truth of the preceding statement.

It showed no reaction to *light*. A coat placed over the jar was removed, when it was found to be on the surface and it remained there. This was twice repeated. I noticed specially that on pushing the bell above the surface of the water it at once turned and went deeper as the normal animal does. Finally, given another trial with removing the coat from the jar, it went to the bottom as the normal animal usually does. After this, when next seen, it was keeping to the bottom. [This experiment was repeated on another occasion with almost identical results, no loss of sense-perception being noticeable.]

Sometimes it seemed as if access of *light* at removing the coat acted as a stimulus to one or more of those that were quiescent on the bottom. This was noticed again on the following day.

11. Two more were operated upon. These did not stand the operation well and stayed on the bottom, one swimming, while eight hours later one was in better condition (pulsating) than two left in the same dish for comparison.

12. a. Three clubs were cut off leaving only the stalks. A temporary paralysis of the power to swim was the immediate effect. Later it partially recovered this power. The proboscis, which was previously quiet, now showed convulsive twitchings and movements. It continued for some time to move to one side and then the other (after short pauses of varied length) as if to grasp some object. The lips of the *proboscis* were also moving and at times expanding. Often the movements were towards the side on which the club was uninjured.

b. The fourth club was next removed. A temporary paralysis as before resulted, followed by a quick recovery of pulsation; but the animal was now much weakened. The movement of the proboscis continued—shortening, lips expanding, moving to this side or that. The pulsations of the bell were kept up even when too weak to swim.

c. The sensory niches of this same animal were treated with 2.5 per cent. acetic acid by means of a pipette. The stalks of all four clubs showed white. Pulsations ceased. The velarium showed feeble local contractions. The movements of the proboscis and suspensoria drawing down the stomach continued. Upon stirring the animal it gave rather feeble, somewhat convulsive pulsations with local (fibrillar) contractions; the pulsations in some cases were pretty well coördinated, but were more on the twitching kind.

13. Three clubs were removed. The animal pulsated well, only a little less strongly, perhaps. After a minute or two the fourth club was removed. It pulsated almost immediately, perhaps thirty seconds after the operation. It swam very well and pulsated feebly five hours after the operation.

14. One from jar (a) (Experiment 6) was operated upon. When the first club was cut off there was a paralysis of pulsation followed by a quick recovery. Cutting off the second club seemed to stimulate pulsation, the third to diminish it; after cutting off the fourth club it still pulsated. When placed in a large jar it pulsated on the bottom, but not strong enough to swim. The pulsations were fairly regular and sometimes seemed to occur in groups of two, but these groups were not well marked.

15. Another one from jar (a) was taken. One club was cut out, upon which there was a very temporary paralysis followed by good pulsations afterwards. The *proboscis*, as in all cases noticed, gave active movements to this side and that side. These movements of the proboscis were often very quick and definitely directed as if a well defined stimulus were given. After the operation one *pedalium* contracted so as to be at a right angle to the main axis of the bell; shortly a second pedalium also contracted. Placed in a small round dish the animal swam actively.

A second club was removed, and it swam as well as before. After fifteen minutes it was not swimming but pulsating against the jar. Upon stirring it a little it swam vigorously ten to fifteen strokes and then stopped. It seemed weak and its movements appeared not so definite, though this might be due to weakness.

A third club was removed. The only change seemed to be rather greater weakness.

After about five minutes the fourth club was removed. Paralysis of pulsation followed. It had the power to contract its *pedalia* when these were rather vigorously stimulated with a needle. It also gave one feeble pulsation when so stimulated.

16. The sensory clubs were removed from another. After removal of the third one it still pulsated actively, but stopped completely and apparently for good after the removal of the fourth club. Another

one stopped pulsating apparently for good upon removing the third club.

17. All four sensory clubs were removed from one, cutting as high up as possible so as to remove the endodermal tract of nerve fibers of the peduncle. It pulsated afterwards apparently the same as if the stalks had been left intact.

18. A small piece surrounding a sensory club and including the *margin* can contract by itself. The piece observed pulsated with quick pulsations and rhythmically but intermittently. After a fresh cutting away of such a piece, the portion of the *velarium* attached was seen to contract rhythmically, while the rest of the *subumbrella* was not so seen. The part of the subumbrella above the radial ganglion that was cut off did not contract by itself. The same portion of the velarium cut off did give contractions.

19. A sensory club with the surrounding region cut out pulsated rhythmically; when the club was cut from the end of its stalk pulsation stopped. This observation was repeated on another, and contractions were seen after the removal of the club. A piece of the *subumbrella* wall from the same animal gave contractions now and then even after an hour.

20. The normal position of a sensory club seems to be with the concretion almost at the lowermost end; often with it certainly lowermost, but probably oftener with the perpendicular passing through the center of the attachment of the club to its peduncle and just by the inner edge of the concretion. The eyes point inwards.

When the animal is on its side the concretions are always quite lowermost. When the animal was inverted the tendency was for the concretions to be lowermost. In this position the eyes may point in several directions. In one instance those of one club pointed rather outwards, while of two other clubs they pointed more in the plane of the body wall. (See also Experiments 24, 29.)

Nerve.—21. Cutting the nerve eight times, once on each side of each sensory club, produced no loss of coördination in pulsating. The animal was weakened, however, by the operation, which was made drastic to insure cutting the nerve; but it was still able to swim. This experiment was repeated four times.

22. That coördination was continued after the nerve was cut was proved beyond doubt by cutting from the edge up (eight times)

so as to perfectly separate the sensory clubs and the pedalia. Pulsations continued synchronously in all four sides—not the slightest evidence that one side contracted out of time with the others.

23. The eight cuts were made as in the preceding experiment with no loss of coördination noted. When the cuts were carried up to the base of the stomach, however, coördination ceased. The four side pieces seemed to contract each in its own time. Only two sides could be observed at one time, and they at any rate did not contract synchronously. One side often gave two contractions while the other side rested or gave one.

Yet, a little later, three of the sides at any rate showed a pretty good coördination. The fourth was smaller and did not seem to get into the game much—it went more on its own schedule. The four pieces were then cut apart and placed together under a dissecting microscope. No coördination at all could be made out. No evidence, therefore, of any definite rate of pulsation inherent in the sensory clubs.

Cutting the nerve causes the *pedalia* to forcibly contract inwards.

Side, Subumbrella.—24. A whole side was cut out, the transverse cut being above the sensory organ so as to take off [leave off] the radial ganglion also. This pulsated, or rather contracted, nicely. The upper end had been cut just through the *suspensorium.* It especially gave twitchings like the twitchings of the stomach. The piece was then halved transversely, when the upper part containing the portion of the suspensorium twitched as before while the lower part was not seen to contract again. This was repeated with the same result, except that a portion of the lower part gave a slight contraction several times. The part that contracted was at the upper end of the piece, *i. e.*, nearest the *suspensorium.* The contractions were also more longitudinal than transverse, as the regular contractions would be.

The piece connected with the sensory clubs of course pulsated nicely. Upon cutting off the sensory club from the stalk, pulsation ceased, but twitching of the *velarium* continued. This was repeated with the same effect.

In the same animal, in cutting off the sides, the stomach was left, the cut being through the gastric ostium. The floor of the *stomach* was now cut off by cutting out the four interradial points of attachment. The stomach and the proboscis gave vigorous contractions and tied themselves all up so that I could not cut off the proboscis.

The four pieces of the floor of the stomach left on the interradii gave contractions nicely. The phacelli continued their squirming movements.

25. Cutting off the whole aboral end of the animal excites to very rapid pulsations of the remaining part. The stream, as shown by particles in the water, is apparently stronger out the aboral end than past the velarium.

It seems that I get no good evidence that the subumbrella is able to contract of itself without connection with special nerve centers. In the one case noted (Experiment 31) I could not be sure but that the part that contracted was intimately associated with the suspensorium or frenulum.

26. A piece of the subumbrella cut off and having, so far as I could determine, no connection with ganglia, frenula, or suspensoria, gave contractions. Another piece was not seen to contract.

A small piece of the subumbrella connected with a club can contract. The proboscis can give contractions of itself when cut off with the base of the stomach. Even a cut-off lip can twitch by itself. A portion of the subumbrella by itself also showed twitchings. (See also Experiments 18, 19, 25, 26, 29, 47, 49.)

Pedalia, Velarium, Radial and Interradial Ganglia.—27. The pedalia with their tentacles were cut off at their bases to insure cutting out the interradial ganglia. The animal could pulsate well enough, but intermittently and without much progress (the velarium, of course, being injured). Cutting one pedalium caused the others to contract.

28. When the pedalia were cut off from one, the power of direct motion was entirely gone. It swam in circles, turned summersaults, changed its course continually, the oral end getting ahead of the aboral end, or trying to do so. The whole power of balancing was gone. It seemed excited by the operation and swam continually. [Repeated.]

29. The pedalia can be made to contract inwards by stroking their outer edge with a needle. This was noted last year and has been seen several times this year. Their inner edge is not so sensitive.

Touching a *sensory club* caused the pedalia to contract inwards in two cases.

The pedalia could be made to contract by giving the subumbrella a prick,—generally a rather severe one was necessary. The upper part of the subumbrella seems not so sensitive as the lower part and the proboscis, and the base of the stomach did not give any reflex at all (two specimens). One of the two could be made to give the reflex only with much difficulty. This was a very lively one. It would even stand severe pricks on the nerve, or even through the region of the sensory clubs, without contracting the pedalia or stopping pulsations.

Cutting the frenula seemed not to affect the ability to swim well. Cutting in this region brings about the reflex of the pedalia.

In the preceding fish the *velarium* was cut away wholly in some places, in other places it was left only as ragged strips. The pedalia became very strongly contracted and the *tentacles* were brought inside the bell. Pulsations that seemed strong produced much less progress than with the velarium intact. [Repeated.]

30. One with the whole *margin* cut off still gave pulsations. Upon the removal of the region of the *radial ganglia*, however, pulsations were seen no more.

The *velarium* in the above continued to give twitchings. The four pedalia were cut off with plenty of the tissue at their bases to insure the removal of *interradial ganglia*, and twitchings of the velarium with irregular contractions continued. No full contraction all around the velarium was noticed. When all the tissue was trimmed off as nearly as possible down to the *velarium*, the latter still gave twitchings and irregular contractions as before,—even more so as if excited by the operation. The power of originating contractions evidently resides in the velarium or in the ganglion cells of the frenula just as it does in the proboscis and the floor of the stomach.

Small pieces cut from between the pedalium corners and the frenula, so as to have tissue on them from neither, could contract by themselves. (See also for Pedalia, Experiments 15, 23, 41b; Velarium 18, 41c.)

Tentacles.—31. A cut-off tentacle can contract by itself, sometimes with squirming contractions. A prick at either end can produce a forcible contraction. A slight prick at the distal end may produce a local contraction. The proximal end is more sensitive, but this difference is not very marked. One with only the tentacles removed seemed to be a little less able to guide itself well.

Proboscis, Stomach, Phacelli.—32. The lips of the proboscis are highly contractile by themselves. The movement of the stomach and the phacelli goes on, after the lips are cut off, with increased vigor, due to the stimulus of shock. The vigor and frequency of their contractions, however, diminish quicker than that of the cut-off lips. (See for Proboscis, 12, 15, 18, 26, 29; Stomach, 18, 24, 29, 31; Phacelli, 18, 24, 31.)

Temperature.—33. Temperature does not seem to have much effect. Some placed in a tumbler half full of water, in the bright sunlight, swam vigorously over three-fourths of an hour. The water was quite warm to the hand.

34. The above experiment was repeated with the same results. A thermometer placed in the water with them showed 92° F.; hung in the sun near by, it showed 94° F.

Ice in the water did not stop their pulsating temporarily or permanently, except that it did for a short time after being held against one. Even then it took some time (fifteen to twenty pulsations) before it produced any effect.

35. Ice placed in the water again showed no marked effect. They swam as lively as ever. Some, after pulsating against the ice for a little while, seemed to be less vigorous, but quickly recovered in another part of the jar. Others did not seem to be the least bit affected by contact with the ice.

Food and Feeding.—36. I tried to feed one. A red and a white copepod were put into the subumbrella cavity. No attempt to eat it was observed in either case, though the copepods remained in the subumbrella cavity for some time.

Animals found in the stomach of Charybdea: small fish were most frequently seen; at another time a small stomatopod; again, a small polychæte; small shrimps; amphipod.

Those taken on August 16th (3 to 4 P. M.) seemed to have, for the most part, food in the stomach, and this more so than those taken in the morning.

Occurrence of Charybdea.—37. In the first tow on the bottom (with a net made of mosquito-netting and weighted with rocks in order to sink it) the haul was forty. I do not think that we could have been towing more than four or five minutes. The time was about seven A. M. A light breeze was blowing and there had been a heavy shower a half-hour previous.

38. The usual time of towing was about 6.30 to 7.30 A. M. The water was four to five feet (1.2 to 1.5 m.) nearest shore but deeper farther out. At this time of day one could count on getting plenty of the larger sized (15 to 20 mm.), many small ones, but very few of the smallest. This was the experience of several mornings.

On August 12th I towed about nine A. M., and got but few of the larger sized, many small, ones, and very many of the smallest.

The next day (7.00 to 7.45 A. M.) those obtained were mostly of the larger size. On the same day (3 P. M.) others of the party towed at the same place and obtained but few.

On another day I towed in the afternoon (3 to 4 P. M.) and obtained great numbers as I usually did in the morning.

39. We towed about 7.30 to 8.30 at night. Very few Charybdeæ were taken. On this evening we towed five times in the same locality, and obtained but seven or eight specimens. Towing with the same net on our way home, it was filled with Aureliæ and five or six Charybdeæ. It seems as if Charybdea came to the surface at night. Those towed in the evening were dead the next morning.

The next morning Richard, our colored attendant, towed from 5.30 to 6.30. There were heavy showers. The usual find of large and medium ones was obtained. There were only two with planulae.

40. The material of September 2nd was obtained about six A. M. They were mostly of large size. In all only fifteen or twenty were taken. Richard explained the small number by saying that the bottom had changed in the locality where we usually towed and that he got no weeds in his net, but mud.

The next day more were brought in by Richard (6.30 A. M.) There were rather more than yesterday but the quality was the same. There were three with planulae.

On another morning Richard brought in a great many, about a hundred. Among these there were three with planulae (light-colored and budding); on a previous day there was one with the reddish-brown kind and with a mouth.

Activity of Charybdea.—41. a. About five o'clock in the morning a Charybdea was taken in the tow. It was in good condition swimming incessantly round and round without change of direction, in a jar of about twenty centimeters in diameter. It came to the surface every now and then, after eight to fifteen pulsations. The tentacles and the phacelli were of a lilac shade. If a pencil was placed in its way it would pulsate against it repeatedly without any effort to dodge around it.

6.58 A. M., 124 pulsations were counted to the minute.
8.00 " 124 " " " " "
9.25 " 136 " " " " "
10.15 " 131 " " " " "
11.00 " 146 " " " " "

At 10.15 it went around the dish in eight seconds, taking eighteen or nineteen pulsations. If a bright platinum spatula or a black pencil was placed in its circuit it would repeatedly butt against it each time it came around. After the second or third pulsation against it, however, it seemed to have some sense to change its direction.

b. The *pedalia* have no perceptible action of their own. They move inwards slightly toward the axis at each pulsation, but scarcely as much as one would suppose from their attachment to the pulsating margin. It seems as if they were for "winging" the moving animal more than for anything else.

c. The *velarium* is loose and it flaps. It seems to take part in swimming something more than the passive diaphragm function,—i. e., it straightens out during the recovery after each contraction of the bell.

AURELIA AND POLYCLONIA.

[The following experiments were performed at Port Henderson, Jamaica, in 1896.]

42. May 12th. An *Aurelia* was pulsating normally at the rate of twenty-five or twenty-six pulsations to the half-minute. One lithocyst was cut out, when a few contractions, evidently caused by the stimulus of cutting, followed; then, rest. In the first minute there were only about five pulsations. In two or three minutes rhythmic pulsations were resumed. Four minutes after the cutting there were nineteen pulsations to the half-minute. About twenty minutes after there were nine to the half-minute, in groups of six and three.

A *Polyclonia*, about four and one-half inches (115 mm.) in diameter, gave twenty-six or twenty-seven regular pulsations to the half-minute. After one otocyst was removed, pulsations continued, but in groups with intervals of pause: *e. g.*, thirteen, pause; ten, pause; six. Three minutes after the removal of the lithocyst there were 5, 3, 1, 3, 5, or seventeen pulsations to the half-minute. Eleven minutes after the operation there were fifteen to the half-minute. The removed lithocyst and surrounding tissue gave contractions.

43. May 13th. The *Aurelia* was in rather poor condition but would pulsate upon being stirred. The other seven lithocysts were removed when only a few contractions originated thereafter.

The *Polyclonia* was in good condition, but was pulsating only intermittently when first seen in the morning. When the remaining seven lithocysts were cut out and no more pulsations were observed, the oral arms could still move.

May 14th. Both were found dead upon returning in the evening.

44. May 15th. An Aurelia and a Polyclonia were taken in the morning. The *Aurelia* was two and one-half to three inches (62.5-75 mm.) in diameter, with three tufts of phacelli, three oral arms and seven lithocysts. The *Polyclonia* was normal and seven or eight inches (175–200 mm.) in diameter.

In the *Aurelia* all the lithocysts were removed. Spontaneous and coördinated contractions could still occur after time had been allowed for the shock from the operation to pass away. The next day the animal was still alive and pulsating, but ragged, and the next day following was quite dead.

In the *Polyclonia* the normal rhythm was fourteen pulsations to the minute. Some pulsations were apparently quicker than others and the intervals were not the same. Thirteen, ten, and twelve pulsations were also counted. After putting the animal into fresh sea-water, it pulsated thirty-three to the minute. Six minutes later it was still pulsating at the same rate, while in four minutes more eleven pulsations, many of which were in groups of two, were noted. In five minutes more it pulsated eleven times to the minute with only one double pulsation. One *oral arm* was then cut off and the rhythm counted about one minute afterward—fourteen pulsations, then a pause of fifteen seconds, then two pulsations, in all sixteen to the minute were counted. About ten minutes later there were eight pulsations, two or three minutes later only three, while in two or three minutes more only three. There was a long latent period—two or three seconds—before the stimulation of cutting off the arm made itself evident in the rhythm.

A second oral lobe was removed. Then there followed twenty-four pulsations, a pause of two seconds, and two pulsations, in all twenty-six pulsations to a minute. The rate of pulsation soon fell to the previously abnormal low rate.

Third lobe removed: 21 pulsations in first half minute and then 16, or 37 per minute.

Fourth lobe removed: 17 pulsations in first half-minute plus 13 gives 30 for the minute.

No difference in the coördination of the animal was shown as a result of the removal of one-half the number of oral arms.

Fifth lobe removed: 17 pulsations plus 15 equals 32 to the minute.

Sixth lobe removed: 17 in first half-minute plus 4 in the second half-minute gives 21 pulsations for the minute.

Seventh lobe removed: 17 plus 9, or 26 per minute.

In all these instances the rhythm in the second half of the first minute was irregular and intermittent.

Seventeen and then seven pulsations were provoked after the animal had become quiescent, or nearly so, by merely handling it.

45. Eighth oral lobe was removed and pulsations stopped. The next day the animal was in good condition. The pulsations counted in the evening were 12, 14, 14, 11, per minute. The rhythm was not regular; there was a tendency to groups of twos, threes, or more, but no prolonged intervals of rest were observed. When placed into fresh sea-water, the pulsations were fourteen to the half-minute or twenty-six to the minute; seventeen to the half-minute, and thirty-three to the minute were also counted. This specimen gave spontaneous contractions during two weeks, after which it was thrown out, the aboral end being eaten through and little or no regeneration having taken place.

46. Two more were operated upon: A. Its rhythm was 18, 14, 17. Its entire margin was cut off. The separate pieces of the margin pulsated, 6, 7, 4, 6, 7, 9. The animal seemed paralyzed by the operation; it responded by a contraction now and then to stimulation but gave no spontaneous pulsations. B. Its rhythm was 17, 15, 12, 12. All its *oral arms* were removed. Its rhythm was only raised to seventeen and not perfect. In twenty-five minutes it had fallen to eleven, in four hours to ten pulsations [per minute].

May 22nd. A and B are living as also the pieces of the *margin* of A; all are giving spontaneous pulsations now and then at comparatively long intervals—even A, with its margin removed.

May 26th. Everything is still living. The one with the margin cut (A) counted sixteen and nineteen pulsations per minute, though this was not kept up all the time.

June 2nd. A and B and pieces are still living and contracting spontaneously. It is now two weeks, and they were thrown out eaten through at the aboral end with little or no regeneration.

47. The margin was cut off another one (C) and it was then paralyzed. The margin contracted vigorously by itself. The margin was next split, but a connection of about one-half an inch wide was left between the two rings. Over this bridge the contractions passed from the outer and inner ring. The inner ring did not originate any contractions. Both rings were then cut near their connecting bridge of tissue and the larger ring with the marginal bodies was split longitudinally so as to separate the exumbral from the subumbral portion. It was found that the contractions started only from the subumbral portion while the exumbral portion did not contract at all.

June 5th. Five of the eight small pieces of C were not seen to contract either to-day or yesterday. A slow rotary motion was observed in some of the pieces suggesting ciliation, but no cilia or currents pointing to ciliation were seen with a low power. C was seen to pulsate spontaneously. Possibly it did yesterday but it was not watched closely. A piece of the subumbral surface of C broken off (not from the margin) was found to contract spontaneously.

48. June 6th. In a fresh one (D) from Port Royal, the eight lithocysts of one side were removed in order to compare its movements with an intact one. Coördination was apparently unaffected.

June 9th. The margin of C is still pulsating vigorously. Parts of the subumbrella broken loose from the strip pulsated by themselves now and then. Fifteen lithocysts were removed, leaving only one at the end of the strip. It was found that with this single ganglion (lithocyst) left, and originating most of the contractions, now and then a contraction would originate at another part of the strip where there was no ganglion. Three days later contractions originated as often from other parts as from the ganglion.

Cassiopeia.

[The remaining experiments were all performed in 1897, at Port Antonio.]

49. Removal of the sixteen marginal bodies caused paralysis for a time; then recovery followed.

Contraction was limited to the subumbrella.

A portion of the *subumbrella* not from the margin can contract by itself as well as a portion of the margin with the marginal bodies (lithocysts).

In the *margin* cut off as a strip with only one marginal body attached at one end, contractions sometimes started from the opposite end.

Aurelia.

50. Size, seventeen or eighteen millimeters. Pulsations, thirty-two. Lithocysts, nine. The operation consisted in the removal of the concretions with as little injury to the pigmented parts of the marginal bodies as possible. One whole marginal body, however, was removed in the operation. Soon after the operation the pulsations were 28, 26, 20, 20, per minute.

Another one; size fifteen millimeters. Pulsations were forty per minute. The operation consisted in the removal of the concretions and pigmented parts of the marginal bodies with as little injury to the adjoining parts as possible. After the operation it seemed as if the intervals between the pulsations were irregular,—not a series at regular intervals. An hour or so after the operation the pulsations were very intermittent. During the afternoon it was not seen to pulsate except when it was stirred up, when six or seven vigorous pulsations followed. These, however, were rather aimless.

51. One sensory club (marginal body) was cut out, including its basal part also. In one or two other cases more or less injury was done to adjoining parts also. Pulsations ceased upon the removal of the last club, but upon placing it in an aquarium and allowing it to come to rest for two or three minutes, pulsations were now and then seen. In the evening, this one and another did not pulsate except when stirred, when they pulsated with good progress.

52. A circular cut, about two inches in diameter, was made through the epithelium of the subumbrella around the base of the

oral lobes. The animal pulsated well enough, but the contractions seemed not so simultaneous in all parts of the margin as normally. After a few days it had partly regenerated but died. One of the oral lobes cut off had some power of contraction, and this some time after the operation. A similar cut, but semicircular, made no difference between the contractions of the two halves.

53. The whole region of the sensory clubs was cut out when the animal was not seen to pulsate again, except in the evening, when pulsations were observed. The oral lobes also moved.

HISTOLOGICAL.

Method.—The following results on the histology of the sensory clubs, their eyes, and the tentacles, as already noted, were obtained from some of Dr. Conant's preserved material. These results relate almost wholly to Charybdea, with only a few references to Tripedalia, noted in their proper place.

A portion of this material was killed after keeping the animals in the dark for some time, for the purpose of discovering any changes in the pigment of the eyes. I believe that a retraction of the pigment of the long pigment cells that project between the prisms and pyramids of the vitreous body in the retina of the distal complex eye is very evident in eyes killed in the dark. (But more on this below.)

I obtained my best results from the material preserved in saturated corrosive sublimate, to which had been added (5 to 10 per cent.) acetic acid. This also was Conant's experience in his previous work on Charybdea and Tripedalia.

My best sections were obtained by embedding the sensory clubs in celoidin, passing the little blocks of celoidin with the sensory clubs into chloroform until perfectly transparent, and then into paraffine. I then cut sections as we ordinarily cut paraffine sections, mounted and stained them on the slide. My purpose in using this method was to avoid the displacement of the vitreous bodies of the eyes during embedding and cutting. This object was fully realized and more besides. Since the sections cut by the celoidin-paraffine method gave me so decidedly the best differentiation of the axial fibers of the retinal cells, as also of the cilia, basal bodies, etc., I am inclined to believe that the celoidin was in part responsible for this differentiation.

Most of my series were cut 4 μ in thickness. All in all I cut sixty-five clubs besides making some maceration preparations from material preserved for that purpose. These sixty-five series represent material from fourteen bottles. As a whole, my material was good, but the material from one bottle was decidedly superior for showing the axial fibers of the prisms and pyramids of the retinal cells. This shows the advantage of plenty of material. It will be evident that I had plenty of material.

I found iron-hæmatoxylin the most satisfactory stain. I stained for a shorter or a longer time—one-half to several hours and longer—and then washed out the sections until under a low power of magnification they appeared quite unstained, the nuclei and a few other parts only appearing darkly stained.

Depigmentation I practiced but little. I obtained many of my series almost wholly unpigmented, especially those I cut last. Others, of course, were very heavily pigmented. I am not certain but that alcohol slowly dissolves out the pigment after a long period of preservation. Slight variations in the technique of killing and preserving may also, perhaps, determine the stability or solubility of the pigment, as, of course, also the condition of the pigment at the time of killing.

Anatomy.—For a short epitome of the anatomy of a Cubomedusa and of a Cubomedusan sensory club see p. 2 of the Introduction.

The Distal Complex Eye—General.—The distal (larger) complex eye (Fig. 7) and the proximal (smaller) complex eye (Fig. 13) are so named to distinguish them from the lateral simple eyes of the clubs. The distal complex eye consists of the following parts: a cellular cornea, continuous with the epithelium of the sensory club; a cellular lens (externally cellular and internally often quite homogeneous) immediately beneath the cornea; a homogeneous capsule just internal from the lens, and evidently a secretion from the lens cells; a vitreous body composed primarily of prisms and pyramids just beneath the capsule; and a retina of pigmented cells, with subretinal nerve tissue, ganglion cells and fibers. To my knowledge all observers (except Carrière, who missed the capsule) are quite agreed on the anatomical structure of the distal complex eye as also on the proximal complex eye and the lateral simple eyes.* It is on the histological structure of some of the various parts that differences exist.

Cornea.—Little need be said on the cornea except that it consists of flattened cells applied to the outer surface of the lens. It is continuous with the epithelium of the club and evidently a modified portion of this epithelium (Fig. 7). All observers conform to this statement.

The Lens.—The lens is of cellular origin, but in its interior the cells are often so changed—absence of nuclei, cell walls, and protoplasmic structure—as to make a mass quite homogeneous and structureless. While this internal mass sometimes shows practically no structure, yet at other times it is found broken up into masses much the size and shape of cells but without nuclei, while again, cells with nuclei may be quite evident. This occasional breaking up of this mass is evidently predetermined by its original cell structure. Iron-hæmatoxylin stains this inner mass very dark and it is difficult to wash out the stain. Borax carmine and Lyons blue give the best results on the lenses. In figure 7 the lens of the distal complex eye is shown as quite homogeneous internally, while in figure 13 (proximal complex eye) it is drawn cellular. In this latter lens the inner cells are quite round and nucleated as they may also appear in the distal eye. What I have said applies equally to the lenses of both complex eyes, though the cellular nature of the inside of the lens is more readily demonstrated in the proximal eye.

It appears that it is in younger specimens that the central mass of the lens shows the cellular structure best, and that as the animal grows older this structure is more and more lost until no trace

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* Haake[2] says that in the adult *Charybdea Rostonii* the vitreous bodies of the complex eyes are absent but present in the young. It is difficult to explain this observation except on grounds of imperfect preservation of the adult material, for in all observations on other forms a vitreous body is described. Haake evidently did not use sections, and for this reason his results must be regarded as of doubtful accuracy. Haake also says that the simple lateral eyes of the clubs are absent in the adult, but present in the young.

of it remains. As concerns most of my series I could not well determine which were from younger and which from older individuals, yet, several series of quite small (5 mm.) and therefore young animals, in which the eyes were so small that the lenses were compassed into less than half a dozen sections, the cellular structure of the lens was very evident.

The external cells of the lens form a spherical shell (both complex eyes) which, in section, shows as a hollow ring (Figs. 7, 13). The thicker ends of these cells lie at the inner (toward the capsule) half of the sphere and the cells taper toward the corneal surface, dovetailing laterally with their immediate neighbors as also distally with those from the opposite side of the sphere. The thicker inner ends of the cells contain the large nuclei with nucleoli. At a point (*Figs. 7 and 13) on the inner (next the capsule) surface of the lens the cells only approximate each other and thus leave a place which is easily broken through, as is shown by portions (drops, probably representing cells or portions of cells) of the mass within the lens becoming squeezed out into the substance of the capsule and the vitreous body, and found occasionally also among the cells of the retina. A considerable portion of the inside of the lens may be found thus squeezed out, and its path can often be traced. This phenomenon is evidently brought about by a contraction of the shell of the lens during fixation and before the inside of the lens has become hardened.

In origin the lens is evidently ectodermal, originating from an ectodermal invagination which becomes pinched off as a hollow sphere, the outer (*i. e.* next the cornea) half of which becomes the lens, the inner half the retina (*i. e.* vitreous body plus the so called retina). (See Retina.) The transition from retinal to lens cells is quite readily made out at the lower side of Fig. 7, but the corresponding structure on the upper left side is not so manifest. It is further evident that the lens is again an invagination into this sphere, and the point at which the lens cells approximate (where the central mass of the lens may be squeezed out as above described) represents the place of pinching off of the original lens-retina sphere. It appears, then, that the lens is formed in the lens-retina sphere in the following manner: The cells of the secondary invagination going to form the lens begin to lengthen distally (*i. e.* toward the cornea) during their invagination to form a hollow sphere, at the same time dovetailing with each other and budding off cells to form the inside of the lens (Figs. 7, 13).

At the lower side of the lens, near the margin of the retina, the cells of the lens are slightly indented or pushed inwards (Fig. 7, ind.). I believe this to be due to the weight of the lens in the normal position of the club, when the lens rests against the margin of the retina and the capsule and adjacent tissue.

Anticipating the description of the retina, it may here be added, that the retina is formed from the inner half of the lens-retina sphere. The cells of this portion of the sphere become differentiated into prism cells, pyramid cells, and long pigment cells, while laterally, beyond the margin of the vitreous body, they are differentiated into pigmented iris cells (Figs. 7, 6a).

Above are my results on the lens. Haake[2] speaks of the lens as consisting of a cellular "Kern" with a covering of lamellated cells. Carrière describes it as cellular and filled internally with a "Gerinsel," or coagulation. Carrière and Haake are each in part right. Claus describes it as wholly cellular. Schewiakoff regards the lens as wholly cellular, and like Claus has not noted that internally this cell structure may be quite obliterated. Schewiakoff regards the lens and retina as formed from an invaginated sphere, and shows the transition from the lens cells into retinal cells as I have figured. Conant also gives the structure of the lens for the complex eyes as cellular but missed the change of structure that the interior of the lens may undergo.

The Capsule.—The capsule of the lens (Figs. 4, 7) lies immediately below (inward from) the lens. In structure it is homogeneous, except for certain fibers from the long pigment cells of the retina that traverse it, while sometimes also other fibers can be seen which, possibly, are branches from the fibers just mentioned or continuations from the fine fibers of the prism cells of the retina soon to be described. I have, however, no evidence that the fibers from the prism cells extend beyond the prisms in whose axis they lie. The capsule lies very closely applied to the lens, never becoming separated from it in sections, and is, hence, regarded as a secretion from the lens cells. Just what its function may be is difficult to surmise. The proximal complex eye possesses no capsule. I have thought, however, that if the lens should be adjustable, the capsule might serve as a protection to the prisms of the vitreous portion of the retina during the adjusting movements of the lens. (But more on this below.) To my knowledge all previous observers are quite agreed on the structure of the capsule. Carrière and Haake, however, missed it altogether.

Retina.—While I have enumerated (following previous observers) the vitreous body and the so-called retina as distinct parts, yet, as the sequel will show, they are, histologically, different parts of the same thing—namely the sensorium proper of the eye—and I propose to use the term retina for both taken together, while I retain the expression vitreous body (as hitherto used) for the vitreous portion of the retina. This simplifies matters; and using a word that is already used for analogous structures of other eyes (vertebrates, anthropods, molluscs) is conducive to clearness. I have been tempted, furthermore, to use the words *rods* and *cones* for the prisms and pyramids that I find in the vitreous bodies of the retinas of the complex eyes. But since the prisms in reality approximate prisms and the pyramids pyramids, in their shape, I have decided to retain the words prism and pyramid for these structures. The former of these terms (prism) was first used by Conant in his description of the complex eyes.

What I shall call the retina, then, in the distal and proximal complex eyes of Charybdea, consists of three kinds of elements: the prism cells, the pyramid cells, and the long pigment cells. (Figs. 4, 7, 22, prc, pyrc, lp.) We may also describe the retina as composed of three zones: the vitreous zone (vitreous body of authors), the pigmented zone, and the nuclear zone. (Figs. 4, 7, 22, vb, pz, nz.)

The cells composing the retina form a single layer in the shape of a hollow cup, into which cup the lens with its capsule fits. (Fig. 7.) This single layer of cells takes in the thickness of the vitreous zone, the pigmented zone, and the nuclear zone. Indeed, the distinctions vitreous zone (vitreous body), pigmented zone, and nuclear zone characterize three topographical regions of the retinal cells.

That the retina is made up of three kinds of cells is most readily demonstrated in transverse sections through the vitreous body. Fig. 1 is such a section, taken quite near the pigmented zone (at about the level x, Fig. 4). Three different kinds of areas are readily made out in such a section. The more numerous areas (pr) are transverse sections of the distal prisms of the prism cells, the less numerous and lighter areas (pyr) are transverse sections of the pyramids of the pyramid cells, and the large oval heavily pigmented areas (lp) are the transverse sections of the long pigment cells. The dots within the two first named areas represent fine fibers in the axes of the prism and pyramid cells, to be described below. The presence of three kinds of cells can again be readily seen in such Figs. as 4 and 7, in which the elements of the retina are cut parallel to their long axis. (Fig. 22.) Again, a transverse section through the most distal part of the pigmented zone of a slightly pigmented retina (Fig. 2) also shows us the presence of three kinds of elements. The larger and more heavily pigmented areas (lp) are the long pigment cells; the smaller, lighter areas (pyrc) with a central dot are the pyramid cells, and the more numerous dots, with no definite polygonal areas outlined about them (prc), belong to the prism cells. Thus, I believe, we have conclusive evidence of the existence of three kinds of cells in the retina of the distal complex eye.

(a) The prism cells are the more numerous, and, as the name implies, end distally in a vitreous polygonal prism (Figs. 4, 7, 22, pr). The prismatic structure of the vitreous body is also shown in Figs. 10 and 11, which are drawn from a macerated preparation of Conant's. (See the descriptions of these figures.)

In Figs. 4 and 7 the prism cells correspond to the cells with the darker nuclei (npr); in Fig. 2 they are represented by the dots without defined polygonal areas about them (prc), and in Fig. 1 by the most numerous areas (pr). These cells, then, consist of a centrad portion with nucleus, a pigmented portion with granules of a dark-brown pigment, distal from the nucleus, and a distal vitreous prism which extends to the capsule of the lens.

In the axis of each prism is a fine darkly-staining fibril extending the entire length of the prism. I found no good evidence that this fiber extends into the capsule. Centrad this fiber is continued through the pigmented part of its cell and approaches to or near the nucleus (Fig. 2, dots without defined polygonal areas; Fig. 7, part of retina left unpigmented). In some instances I could trace this fiber quite to the nucleus, while in others it ended before reaching the nucleus or a little to one side of it. I am inclined to believe, however, that it extends past the nucleus and is continued as a nerve fiber. I believe this to be so because the fiber is evidently sensory, and *a priori* we should expect it to be so continued. Further, I find decided evidence in sections of the simple eyes to show that the fibers there extend past the nucleus into the subretinal tissue where I could not trace them farther. (Fig. 16.) Again, that the flagella of the epithelial cells of the club are also continued into the cells, in some instances could be traced past the nuclei (Figs. 12 and 26), and the fact, too, that the retinal cups of the eyes represent invaginated epithelium (the axial fibers of the prisms are hence cilia?)—all this leads me to believe that the axial fibers of the prism-cells extend centrad past the nuclei through their cells and are continued as nerve-fibers. (See below under pyramid-cells and under epithelium). Immediately upon entering the pigmented part of its cell the axial fiber of a prism-cell has a dumbbell-shaped enlargement which lies quite at the distal edge of the pigmented part of the cell (Fig. 7, unpigmented part of figure). This, of course, can be seen only in unpigmented retinas. This dumbbell-shaped body, (Basalkörperchen of Apathy), which name I give it, since it evidently is homologous to the basal bodies described by others for the cilia of epithelia, can be most beautifully seen as two minute spheres lying close together and in line with the nucleus. These two little spheres of the basal bodies put to the test the highest powers of the microscope; but, when, after a prolonged and careful study, one satisfies himself of their existence and exact shape, the very difficulty with which they are resolved adds a zest to be appreciated. The length of a basal body is about one-fifth to one-fourth that of the nuclei of the prism-cells.

The structure of the nuclei of the prism-cells is that of a dense network (Figs. 4, 7, npr) which stains dark with hæmatoxylin. A nucleolus can often be seen in these nuclei. In some few series, again, these nuclei did not show a network-like structure, but the chromatin was arranged in masses (Figs. 5, npr). These nuclei can usually be distinguished from those of the other cells of the retina by their denser, darker-staining network (Figs. 4, 7, npr), or as shown in Fig. 5 (npr). Their denser structure and staining capacity are a distinguishing characteristic of the nuclei of the prism-cells. I must add, however, that not in every series is this apparent.

That portion of a prism-cell that contains the nucleus rarely contains any pigment; and when pigment is present, I believe that it has been dissolved in from the pigmented zone. The nucleus, again, lies a little centrad from the pigmented part of its cell, so that an unpigmented zone is seen in .the retina between the pigmented zone and the row of nuclei (Figs. 4, 7, 22).

Centrad the prism-cells are continued as a single process (Figs. 6, b, c, d, and 8a, b, c, d). In some sections I thought I could trace these processes to the basement membrane, but I could not satisfy myself that such appearances were not due to artificial splitting in the tissue. Schewiakoff makes a similar remark about his supporting cells, which cells I believe are the same as my long pigment cells, but these do not extend to the supporting lamella.

At the margin of the retina the cells do not develop prisms but remain pigmented and form an iris (Fig. 7), which was so named by Claus and also described by Schewiakoff. These cells also assume a somewhat different shape (Fig. 6a). This cell (Fig. 6a) is seen from its broader side with which it is applied to the capsule or the lens. Schewiakoff figures similar cells. That the cells of the iris are prism cells without the prisms does not necessarily follow. They simply represent cells of the retinal cup that have become differentiated to serve as an iris.

As to the exact origin of the prisms, and pyramids (to be described below), it is difficult to say anything definite. If the so-called basal bodies of the axial fibers are really homologous with the basal bodies of flagella, then it would seem that they (the prisms and pyramids) are secretions comparable to cuticular secretions.

(b) The pyramid-cells, like the prism-cells, are differentiated into three regions: a distal vitreous pyramid, a pigmented part, and a centrad part with nucleus. The pyramids are seen in transverse section in Fig. 1 (pyr) and in longitudinal section in Figs. 4 and 7 (pyr).*

Each pyramid extends between the bases of the prism-cells about one-third to one-half the depth of the vitreous body (Figs. 4, 7, 12 (pyr). The pyramids are also a shade lighter than the prisms,

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*In the series from which Fig. 3 is taken the pyramid-cells are not so readily demonstrated. Indeed, I missed them altogether at first in this and some other series and supposed that there were only two kinds of cells (19), but upon a careful re-examination I could demonstrate them to my satisfaction. They did not show, however, in the particular section of Fig. 3, so that they are not indicated in this figure.

which fact is characteristic. In the axis of each pyramid is a darkly-staining fiber quite like the one described for the prism-cells (Figs. 1, 4, 7, 22). That this fiber extends distally beyond the limits of the pyramids I could not determine, but I do not think that it does. Centrad this fiber extends into the pigmented portion of its cell quite to or near the nucleus as was described for the fibers of the prism-cells (Figs. 7, 22). Whether or not these fibers extend past the nucleus and become continued as nerve fibers, the same course of reasoning holds as was given for the fibers of the prism-cells. Each of these fibers possesses a basal body just on its entrance into the pigmented part of the cell (Fig. 7), but I could not determine that it was dumbbell-shape. In form it represents an enlargement of the fiber itself, which gradually tapers again to its normal size. The continuations of these fibers within the pigmented parts of the pyramid-cells, as also the basal bodies, could only be demonstrated in unpigmented series.

Patten[5] describes axial fibers extending centrad through the rods (vitreous portions) of retinal cells ("retinophora") into the region of the nucleus and past the nucleus (arthropods and molluscs). My retinal cells (prism and pyramid cells) evidently correspond to Patten's retinophora, but I find no evidence that one of my retinal cells represents more than a single cell, while Patten gives evidence that his retinophora are made up of two cells closely applied to each other as twin cells. If this were also true for the retinal cells that I have described, I believe my macerated preparations would have shown it. Schreiner[12b] and Hesse[13] also figure and describe axial fibers for the rods of the visual cells in polychætous annelids, and Schreiner[12a] also for molluscs. Neither of these observers finds the fibers to extend distally beyond the rods nor centrad toward the nucleus as Patten and myself show. Neither Schreiner nor Hesse figures these cells as twin cells as Patten does, so that to my knowing Patten stands alone in this respect. Andrews[14] describes and figures rods for the visual cells of polychæte annelids but no axial fibers. He was the first to describe these rods in annelids.

The pigmented zone of the pyramid cells, in heavily pigmented series, is filled throughout with dark-brown pigment granules, and is quite like that of the prism cells (Figs. 4, 7). In transverse sections, however, through the most distal part of the pigmented zone, of unpigmented series (Fig. 2), lighter areas with central dots could occasionally be demonstrated, which areas are the pyramid cells. In Fig. 2, the more definite polygonal outline as well as the lighter shade of these areas was a distinguishing feature. The difference in shade was not wholly due to a difference in pigmentation but to a structural difference.

The nuclei of these cells are usually a little larger than those of the prism cells and are filled with a finer and less dense network (Figs. 4 and 7, npyr), in consequence of which they present a lighter appearance in sections when examined with a high power. It will be seen in the figures (4, 7) with what regularity these lighter nuclei lie opposite the pyramids. Some few exceptions occur. These are probably due to the fact that a nucleus or pyramid was not differentiated by the technique. If this opposition between the pyramids and the lighter nuclei were all, I believe it would be sufficient evidence for associating these lighter nuclei with the pyramid cells.*

(c) The *long pigment cells* are about as numerous as the pyramid cells. In these cells, as in the prism and pyramid cells, three regions can be distinguished: the region of the nucleus, a pigmented region (the distal half of which extends between elements of the vitreous body), and a distal rod-like portion, or fiber, which is continued between the prisms into the capsule of the lens (Figs. 4, 7, 9). The pigmented portion is about twice the length of that described for the other cells, and also often of greater diameter, so that in transverse sections (Figs. 1, 2, 3) these cell-areas are larger than those of the other cells. As nearly as I could determine, these cells are pigmented just like the other retinal cells described. In quite unpigmented series, however, they often contain more pigment than the other cells do

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*I go into this at some length because the cell-walls in the series that showed the nuclei best differentiated as lighter and darker ones did not show well, and there might be some doubt that these lighter nuclei belonged to the pyramid cells. I could, however, in many instances, trace the axial fibers of the pyramids through the pigmented zone to these lighter nuclei (as already noted) which fact can leave no doubt but that some of these nuclei belong to the pyramid cells. (Similar nuclei, however, are found to belong to the long pigment cells, to be described below.) Centrad these pyramid cells are continued into a single process just as the prism cells were shown to be (Fig. 7). Figures 6, 8, 9, and 21 show samples of all the pigmented cells found in macerated preparations, and none of these (except Fig. 9, long pigment cells) show more than a single centrad process. Hence, I conclude that centrad both the pyramid cells and prism cells are continued as a single prolongation.

(Fig. 2). Distally, the pigmented part becomes narrowed to a strong pigmentless fiber (Figs. 3, 4, 7). This fiber stains quite dark with iron-hæmatoxylin and appears homogeneous. It passes between the prisms into the capsule, where it usually bends in a direction toward the margin of the capsule (Fig. 7) and passes diagonally across this to the lens. In sections, a space is often seen about these fibers in the vitreous body, which I regard as a shrinkage space (Figs. 3, 4), since it is not evident in all series (Fig. 1). In Fig. 7, I have assumed that these spaces are due to shrinkage and have not indicated them. Also, in this same figure I have assumed that the spiral appearance of the fibers (Fig. 4) is due to a shortening of the prisms during fixation, and have drawn them straight. At the lens these fibers seem to end. In a few instances they were seen to branch upon reaching the capsule (Fig. 4). In Fig. 9, also, which shows some of these cells from a macerated preparation by Conant, the rods show evidence of branching at their distal terminations. In the same preparation I thought I could see that a fiber became expanded into a membrane spreading over one of the lens-cells. I could not satisfy myself, however, that this was the actual condition of things. Judging from Fig. 9, one might conclude that all the fibers are branched distally; yet, if such were the case I should have seen more of it in sections, but branching as seen in Fig. 4 is the exception. Hence, if all these fibers do branch, I am inclined to believe that it must be among the bases of the lens-cells. Or, if the fibers do expand into membranes to cover the lens-cells (I could not explain purpose), the evidence in Fig. 9 may be nothing more than fragments of this membrane left attached to the ends of the fibers. As is seen in Fig. 7, most of these rods end opposite the cells of the lens, and not usually between two adjacent cells as Schewiakoff has described for Charybdea marsupialis. The nuclei of these cells are like the nuclei of the pyramid cells (Figs. 4, 5, 7, 9) and often have a nucleolus.* Centrad these cells are continued into a number of processes as is seen in Figs. 5, 7 and 9. How far the several centrad processes extend and where they end I cannot say; but, as seen in Fig. 5, they soon taper to a thin end which I suppose may be continuous with a nerve fiber. I believe Schewiakoff was mistaken when he stated that these cells extend to the basement membrane.

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* I have been able to demonstrate nucleoli in all the different nuclei of the cells of the sensory clubs.

I have found no evidence in these cells of the existence of an axial fiber such as I have described for the prism and pyramid cells. I find no definite arrangement of the nuclei of the retina into definite layers, but the nuclei of the three kinds of cells lie quite mixed, sometimes one kind lying deeper than the other as can be seen in the figures. Again, they may lie quite at the same level. (This point will be referred to later.)

It is these long pigment cells that I believe retract their pigmented part from between the prisms and pyramids when the medusæ are placed in the dark, protruding with their pigment when placed in the light. Fig. 5 is a section from a slightly pigmented retina killed in the dark. The parts of the cells projecting beyond the pigmented zone, and which would lie between the prisms and pyramids (here not shown) of the vitreous body are seen to be narrower than in sections from retinas killed in the light (Figs. 1, 3, 4, 7) and the cells themselves appear in a condition of retraction as is shown by their large centrad portions with the nuclei, which latter, also, here lie at quite a lower level than the other nuclei. (The pyramid cells were not shown in this series.) I occasionally found appearances like Fig. 5 in retinas killed in the dark (indeed, in some the pigmented portions in the vitreous body were much thinner and more retracted than in Fig. 5). Yet this appearance was not of sufficiently general occurrence to leave no doubt as to its significance. As positive evidence, however, I cannot give it any other interpretation than the one given—that the cells retract themselves with their pigment when in the dark. Again, it must be added that the nuclei of these cells may occasionally lie quite deep even in retinas killed in the light. Indeed, like structures in different retinas may vary considerably in size and shape. None of my darkness retinas, however, showed such a large proportion of the pigmented parts of the long pigment cells projected between the prisms and pyramids as did the light retinas. I examined and tabulated all my series with respect to the extent the long pigment cells were projected into the vitreous body, and I found that those which showed these cells with their pigment least projected between the prisms and pyramids to be those that had been killed in the dark. I thus feel satisfied that the pigmented parts of these cells become in part or quite completely retracted from between the prisms and pyramids of the vitreous body when in the dark, but just how this is accomplished—whether the whole cell with its nucleus takes up a deeper position, the cell substance at the same time collecting in the region about the nucleus, as shown in Fig. 5 and the diagram (Fig. 22), I cannot with certainty state. It would seem, too, as though the pigment became less in the cells exposed to darkness, for I rarely, even in the most retracted heavily pigmented series, saw the pigment to extend farther towards the nucleus than commonly. The time of keeping in the dark, prior to fixing, varied from three-fourths of an hour to one and one-half hours. I could not bring the amount of retraction into relation with the time of exposure, except that in general the retinas longest exposed showed the greater amount of retraction.

(d) The tissue underlying the retina is described by former observers (Claus, Schewiakoff, Conant) as composed of nerve-fibers and ganglion cells. I cannot give it any other interpretation, but I must add that the supposed ganglion cells are seen only as nuclei, no cell bodies ever being demonstrable in any of my sections. Conant also recognized no cell bodies. Occasionally, as in Fig. 7, long fibers could be traced for some distance in this subretinal tissue, in some instances quite to or from a visual cell. Pigment was not regularly observed in this tissue, as Schewiakoff describes, and when present I believe it has been dissolved in from the pigmented zone.

(e) Schewiakoff describes the retina (my pigmented and nuclear regions) as composed of spindle-shaped visual cells (my pyramid cells?) alternating with pigmented supporting cells (long pigment cells), with the nuclei of the former lying more centrad than those of the latter. The visual cells are pigmented only at their periphery, or surface, leaving an unpigmented axis, while the supporting cells have pigment throughout their whole substance within the pigmented zone. Distally, the visual cells have hyaline rods, or fibers, which extend into spaces in the vitreous body, and pass through this and the capsule to the lens. The vitreous body is described as homogeneous, except the spaces for the visual rods, and a secretion from the retinal cells.

It will thus be seen that my results are quite different from those just described. I find the vitreous body to be composed of prisms and pyramids with axial fibers, while the long pigment cells (supporting cells of Schewiakoff) are continued into the vitreous body, and becoming narrowed into a non-pigmented fiber, extend to the lens as described. The prisms and pyramids are, further, the distal continuations of cells whose pigmented and nuclear parts lie in the so-called retina, but which, together with the vitreous body, I have named the retina proper. Conant has so summarily disposed of Schewiakoff's distinction between retinal cells based on pigmentation and location of nuclei, that I need not say more. Schewiakoff's Fig. 18 corresponds to my Fig. 1. In this figure he shows the vitreous body as homogeneous with pigmented areas (my long pigment cells) and with spaces with his visual rods. It is quite evident that his spaces with the visual rods correspond to my lighter areas with central dots; *i. e.* my pyramids of the vitreous body are the same as the spaces shown in his Fig. 18. It is quite evident that Schewiakoff mistook the lighter areas for spaces. That they are not spaces can readily be seen by comparing them with real spaces. It is, of course, possible, too, that the reagents had dissolved the pyramids, leaving only the axial fibers with a little pyramid substance about them, and that this is what Schewiakoff saw. I often found small circular spaces in the centers of the pyramid areas, as also in the prism areas (Fig. 3), which might be taken for hyaline visual rods, fibers, in transverse section, but in such spaces I could usually see a small dot to one side of the space that I take to be the rod (fiber) proper. Fig. 14 also shows such small circular spaces that have very much the semblance of hyaline rods. This figure is a transverse section of the vitreous body of the proximal complex eye, in which no long pigment cells or pyramid cells are present, but it serves well to illustrate the point. The above explanation also accounts for the large size of the visual rods (fibers) in Schewiakoff's figures. That the fibers of the pyramid cells (visual rods of Schewiakoff) do not extend to the lens is quite evident in my Figs. 4 and 7.

Again, since the long pigment cells are often not seen to terminate in a fiber, but a part of the fiber can often be seen in the distal part of the vitreous body and in the capsule, it will be quite readily seen how Schewiakoff should associate his visual rods, or fibers, with these distal parts of the fibers of the long pigment cells and suppose his visual rods to extend to the lens.

Again, since the long pigment cells sometimes cannot be seen to terminate distally in a fiber, while the vitreous body at the same time may be broken away from the pigmented zone (Fig. 4), it is quite evident how Schewiakoff should have interpreted the parts of the long pigment cells in the vitreous body as conical pigmented caps placed opposite his supporting cells (long pigment cells).

Finally, since Schewiakoff had only twelve marginal bodies to study, and since this tissue is difficult to preserve properly, I do not believe that I am doing Schewiakoff any injustice by explaining away his results as I have done. This fact remains, that Conant and myself agree in all points in which we differ from Schewiakoff.

To Conant belongs the credit of having first demonstrated the prismatic structure of the vitreous body, and he also regarded the prisms as a part of the retinal cells. H. V. Wilson[15, 8b] suggested, however, some years prior to Conant, that the vitreous body might be of a prismatic structure. Conant had evidence also of both the prism and pyramid fibers, as is well shown in his figures of transverse sections but he found his evidence too meager to make any very definite statements. Indeed, Conant concludes that there are three kinds of fibers in the vitreous body and complains of finding but two kinds of cells in the so-called retina (pigmented and nuclear zones) to which to refer them. He saw the pyramids with their axial fibers as lighter areas in transverse sections of the vitreous body (his Figs. 64 and 68, and my Figs. 1, 4 and 7), but suggests that they may be the same as the long pigment cells, the cells having only to project themselves or their pigment in order to become long pigment cells. This suggested to him to preserve material both in the light and in the dark. I do not think Conant's supposition to be a fact, for I find the pyramids in specimens preserved in the light as well as in the dark. It is, of course, possible that the pyramid cells are in a stage of structural transition to the long pigment cells, for, besides their pigmentation, they also have like nuclei. Furthermore, I held for a long time with Conant that there may be only two kinds of cells in the retina, but I soon found the pyramids so definitely shown as to leave no doubt but that they represented a third kind of cell. For me it remained to first definitely see all the fibers in the vitreous body as also the pyramids in sagittal sections.

Conant describes the long pigment cells with their fibers extending between the prisms of the vitreous body quite as I have described, and in this my work is only confirmatory of his. Conant does not, however, describe the several centrad processes of these cells, nor is he clear that their distad processes extend to the lens, though he speaks of fibers within the capsule.

(f) What, now, is the function of these three varieties of cells of the retina? Schewiakoff regards his visual cells (pyramid cells), as the name implies, as having a visual function. That they have such it seems reasonable to suppose, since they have an axial fiber in their pyramids. If the pyramid cells are visual cells, it appears that the prism cells also are such. Indeed, since these are the only ones present in the proximal eye and the more numerous ones in the distal eye, and like the pyramid cells have an axial fiber in their prisms, it seems that they are the visual cells *par excellence* of the Cubomedusan eye. Also, the analogy between the prisms and pyramids on the one hand, and the rods and cones of the vertebrate eye on the other hand, does not seem to be so far fetched. It may be of interest, here, to briefly consider Patten's theory of color vision.[5b]

The gist of Patten's theory is this: In the eyes of certain molluscs and arthropods, in the parts of the retinal cells corresponding to my prisms and pyramids, he not only finds an axial fiber (or fibers) but finer fibrils that extend at right angles from these axial fibers to the surface of the rods (I shall here, for convenience, call the prisms, pyramids, etc., rods) where they probably become continuous with other fibrils in the surface of the rods. These fibrils from the axial fibers are arranged in superimposed planes, and if I understand rightly, an axial fiber with its radiating fibrils may be compared to the axial wire with its radiating bristles of a brush used for cleaning bottles, provided the bristles of such a brush be arranged in superimposed planes. The lateral arrangement of the fibrils will, of course, be modified according whether a rod is circular, hexagonal, square, etc., in transverse section. It will also be remembered (p. 49) that Patten describes the retinal cells studied by him as composed of twin cells, and he gives the name *retinophora* to a pair. The system of fibers and fibrils in the rods he names a *retinidium*. Centrad the axial fibers are continued past the nucleus as a nerve fiber. The fibrils extending laterally in superimposed planes from the axial fiber of a rod, Patten supposes to be the ones stimulated by the incoming rays of light, the retinophora being so arranged that the light rays entering them are parallel to the axial fibers or perpendicular to the lateral fibrils of the retinidium. Again, since the rods are usually the shape of truncated pyramids or cones the lateral fibrils, which are perpendicular to the axial fibers, are of different lengths accordingly as they are situated at the larger or smaller end of a rod. Patten assumes similar fibrils to exist in the rods and cones (particularly the cones) of the vertebrate eye, and he thus makes a general application of his theory. He supports himself in this rather sweeping generalization by the claim to have demonstrated the twin-cell nature of the cones in amphibia and fishes.

For illustration, Patten supposes that if red light only were admitted to the retinophora this would stimulate the fibrils near the broader end of the cone (but that all the fibrils of the retinidium would be stimulated a little) and that we would thus have the sensation of red light. Likewise, if violet light only were admitted, the fibrils at the narrower end of the cone would be stimulated, and we should have violet light. Similarly, if light including all the different wave lengths of the spectrum were admitted, all the lateral fibrils would be stimulated and the sensation of white light produced. The method of stimulation need not be that of a vibration of the fibrils.

Certain grave objections may be raised against such a theory, the most serious, perhaps, being the fact that no such fibrils as Patten has described have as yet been demonstrated for the eyes of those animals that we know have color vision. Yet, as a whole, the objections are perhaps no more serious than any that can be brought against other theories of color vision. What Patten's theory does do, —it gives us a definite mechanical basis to work from, and if these fibrils should be demonstrated for the rods and cones of vertebrates, physiologists would then have a mechanical basis for color vision quite as they now have for hearing. As Patten says, the problem is primarily a mechanical one. However, the theory cannot well pass for more than a suggestion, a stimulus for future work, and in this lies its present value.

It is quite evident that my results for the retinal cells of Charybdea are, if any thing, a support to Patten's theory. While I have not been able to demonstrate the fibrils that are the essential to Patten's theory, yet I have demonstrated the axial fibers of the rods, and if these fibers should be continued as a nerve fiber to some central ganglion (as I believe is reasonable to suppose, see p. 47), I do not see how we can avoid the conclusion that these axial fibers of the prism and pyramid cells are somehow concerned in vision. In Patten's theory these fibers would represent a conducting element, the real sensory element (fibrils perpendicular to these axial fibers) not having been demonstrated by me.

I have recently read in a short review of Patten's theory[9] that the evidence we at present have points to the tips of the cones (vertebrate eye) as being the seat of the sensation of red. This would be exactly the converse of what Patten's theory supposes. Whether or not this objection is a real one, future investigation only can determine.

Hesse[13] regards the axial fibers that he describes for the rods in worms as the primitive fibers of Apathy. In this I agree with him, regarding the axial fibers I have described as "Primitivfibrillen." Further, I believe, if I understand Apathy rightly, that the fibrils described by Patten as extending laterally from the axial fibers correspond to Apathy's "Elimentarfibrillen."

It is the long pigment cells that are the puzzling element. Since there can be little doubt but that these cells can project and retract their pigmented parts (as already described), it would seem that a part of their function is to check the diffusion of light in the vitreous body when exposed to strong light. This function would be quite analogous to that of the pigmented cells of the vertebrate retina, which in light become projected between the rods and cones. Similar observations have also been made on the compound eyes of arthropods by Herrick[10] and by Parker[7], who find that the distal retinula cells of Palaemonetes project themselves distad in the dark, thus surrounding the vitreous cones with a cylinder of pigment, while (Parker) the pigment of the proximal retinula cells migrates centrad and the accessory cells move distad; in light the reverse takes place. Other observations of this kind are not wanting for crustacea, insects and arachnids. To my knowledge, the pigment changes that I have described are the first of their kind for medusae.

I suggested while describing the capsule, that the lens might be adjustable. That the fibers of the long pigment cells extend to the lens is my principal reason for this. May these cells not represent ganglion cells and their distad fibers nerve fibers? That they are not sensory (*i. e.* are stimulated by light waves) seems to be suggested by their not having any axial fiber and in having several centrad processes. These facts suggest that they are not sensory but the center of a reflex mechanism.* When the sensory cells proper are stimulated, the impulses are conducted centrad into some nerve center (it may be the nerve tissue underlying the retina, or other nerve centers such as the two groups of ganglion cells in the upper part of the club, or the radial ganglia) from which center, again, impulses return over fibers leading to the long pigment cells causing them to project their pigment, and conducting the impulse to the lens, to produce a change in its adjustment. Since these cells are not so numerous as the prism and pyramid cells taken together, but in turn have a number of processes continued centrad (the sum of which processes approximates the number of sensory cells, prism and pyramid cells) it appears that these cells are admirably adapted to function in just such a mechanism as I have described,—each long pigment cell serving a number of its immediate neighbors.

Further, we may conceive each of the centrad processes of the long pigment cells as receiving a fiber from one of the sensory cells directly as well as indirectly, as just described. While I have been able to demonstrate only a single centrad process for the sensory cells (prism and pyramid cells), yet this does not exclude the possibility of a nerve fibril passing out from such a centrad process to one of the processes of the long pigment cells, and it seems possible that this constitutes the reflex mechanism. That nerve fibrils ramify in ganglion and sensory cells, and may even leave these cells to join those of other cells, has been well demonstrated by Apathy,[6] so that my finding only a single process of the visual cells leading centrad without giving off lateral fibers cannot be a serious objection. Again, fine nerve fibers coming off from the main centrad process of sensory cells in medusae have been figured by other observers, among whom I mention the Hertwigs. Careful macerations at the seashore would probably demonstrate them for Charybdea.

Hesse thinks that the eyes of the Alciopidæ are adjustable. He

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*It may be objected that my criterion, the presence of axial fibers, is not necessarily characteristic of visual cells. However, the great general occurrence of such axial fibers (Patten,[5] Grenacher,[16] Schreiner,[12] Hesse,[13] myself, in simple complex eye, see below, and perhaps others) in eyes in which the retina has only one kind of cells, would seem to indicate that they are quite characteristic of visual cells. Note again that in the proximal eye of Charybdea there is only one kind of cells and with axial fibers.

describes what he supposes to be muscle fibers just exterior (distal) to the lens, and believes that a contraction of these fibers would have the effect of forcing the lens nearer the retina, or *vice versa.* His supposition, like mine, needs experimental verification. Hitherto the only instance known of accommodation in the eyes of invertebrates was that described by Beer[17] for Cephalopods.

The Proximal Complex Eye.—With four exceptions, the description and discussion given for the distal complex eye also holds good for the proximal complex eye (Fig. 13). The four exceptions are: the absence of a capsule to the lens; the absence of the long pigment cells; the absence of the pyramid cells; and the different relative position of the lens and retina. This eye, then, has a cornea continuous with the epithelium of the sensory club, a lens, in structure and probable origin quite like that described for the distal complex eye, and a retina of prism cells with axial fibers for the prisms. Since Conant[8b] has described this eye quite fully, and discussed Schewiakoff's conclusions at length, I shall be brief. Suffice it to say, that Schewiakoff describes two kinds of cells (supporting cells and spindle-shaped visual cells) for the retina of this eye just as he described for the distal complex eye. The vitreous body he likewise describes as being homogeneous and with spaces for the visual rods (fibers) of the visual cells. It is evident that Schewiakoff has interpreted the structure of this eye from analogy with his results on the distal complex eye. Claus likewise has described two kinds of cells for the retina, and the vitreous body as homogeneous. Conant and myself find only one kind of cells in the retina of this eye. The pigmentation that Schewiakoff describes for the vitreous body I believe to have been dissolved in from the pigmented zone of the retina, for I find no regular pigmentation in the vitreous body. Haake's observation, previously noted (p. 42), applies also to the proximal complex eye.

Conant's evidence for the axial fibers of the prisms was clearly insufficient, so that he did not in this respect complete his Fig. 69. I republish this figure with the prism fibers drawn (Fig. 13).

Since the long pigment cells are absent my reasons for supposing the lens of this eye to be adjustable vanish.

Finally, a word on the origin of the lens and the relative position of the lens and retina. The lens and retina in this eye are evidently not developed from an outer and an inner half, respectively, of the invaginated and pinched-off lens-retina sphere (as is true for the distal complex eye) but from proximal and distal halves respectively. It is also quite easy to understand the connection of the lens in this eye with the supporting membrane. Since the cells of the ectoderm of the club can in many instances be seen to extend to the basement membrane, or supporting lamella, the cells of the lens, which arise from the ectoderm, simply remain in connection with the basement membrane, this becoming thickened to form a support for the lens. That the lens of the distal complex eye has lost its connection with the basement membrane is evidently due to the fact that the lens is formed from the outer half of the lens-retina sphere. The cells of the lens are by this so far separated from the basement membrane as to lose their connection with it. Schewiakoff also notes the fact that the lens and retina of the proximal complex eye are developed from proximal and distal halves of the lens-retina sphere. He further supposes that the portion of the basement membrane that acts as a support to the lens takes the place of the capsule in the distal complex eye. This latter supposition I do not think probable, since the supporting lamella does not form a distinct covering to the lens on its retinal side.

The Simple Eyes.—Since the shape and position of these eyes have already been described (Claus, Schewiakoff, Conant), I shall not tarry long in this respect. Speaking generally, these eyes are flask-shaped (Fig. 12), the proximal pair quite so, while the distal pair are drawn out in the transverse diameter of the club. These eyes are invaginations of the surface epithelium and the shape of the cells lining these invaginations is quite like that of the epithelial cells, except that their distal portions (bordering the lumen of the invagination) are heavily pigmented. The proximal walls (Fig. 12, left side) of the distal pair are heavier pigmented than the distal walls and the proximal pair of eyes. Schewiakoff calls attention to this point. The pigmentation is, furthermore, not only heavier, but the pigmented portion of each cell is much longer in the proximal walls of the distal eyes (indeed, the cells are longer) than in the distal walls. The significance of this I do not understand. Indeed, I am inclined to believe that in life all these eyes are pigmented quite alike and that it is the reagents used that alter or dissolve the pigment in certain places. Yet, the fact that the cells of the proximal walls of the distal eyes have their pigmented portions nearly double the usual length, shows some deeper significance.

I also note here the small secondary, non-pigmented invagination into the tissue of the clubs from each of the distal simple eyes. Schewiakoff describes this invagination, and it extends in a proximal and dorsal direction (dorsal-side of club opposite complex eye) from the dorsal sides of the distal simple eyes. The cells of these invaginations are not pigmented, but quite like the other pigmented cells in shape, and like these with distal flagellate fibers. I do not see the necessity of assuming, however, that these secondary invaginations are the real sensitive parts of these eyes, while the pigmented parts serve as an iris, as Schewiakoff does in his general discussion.

The histological structure of both pairs of simple eyes is the same. Sections and macerations give me evidence of only one kind of cells, all pigmented alike (except, of course, the non-pigmented secondary invaginations just noted). The cells in these eyes are very closely crowded so that their nuclei lie at several different levels. That they all extend to the lumen of the eyes and are all pigmented could be demonstrated with certainty in many sections, when some of these cells whose nuclei lay most centrad could be followed with the greatest nicety to the lumen (Fig. 12). Macerations (Figs. 8, unlettered cells 21) also show cells with very long cell bodies pigmented at their distal ends and occasionally with a distal process or fiber. While there are, therefore, spindle-shaped cells found, yet they are in every other respect alike, and their differences of shape and position of nuclei are simply the result of crowding. There is, therefore, no evidence of supporting (pigmented) cells and spindle-shaped visual cells (pigmented only externally) as Claus and Schewiakoff have described and which Conant and myself cannot corroborate.

Distally, the retinal cells of the simple eyes have each a fiber (flagellum) that extends into the lumen (Figs. 12, 15, 16, 21). Each flagellum has a dumbbell-shaped basal body just on its entrance into its cell quite like the basal bodies described for the visual cells of the complex eyes (Fig. 12, part left unpigmented). Each flagellum, or fiber, can usually be seen to extend into the cell. In one series I found appearances like Fig. 16, which is a drawing of a part of a section through one of the proximal simple eyes. This section is quite in the angle between the proximal complex eye and the group of network cells in the upper part of the club. In this series I could very definitely trace the distal fibers of the retinal cells centrad, past the nucleus and into the subretinal nerve-tissue. These fibers could be so easily followed that no doubt can exist as to the fact noted. It thus appears that the axial fibers just described pass centrad through the cells and are continued as nerve fibers. On the evidence of such sections as Fig. 16 I have indicated these fibers as extending centrad through their cells. The lumen of the simple eyes is filled with a homogeneous vitreous secretion. This is often incomplete in some parts; occasionally the secretion shows a formation of globules, but all this I believe to be due to the action of reagents. Indeed, I have found simple eyes in which hardly any secretion was present, while others showed an almost completely filled cavity. In that portion of the vitreous secretion just outside the mouth of the distal eyes I occasionally found numbers of very darkly staining granules. I suspect that these are either bacterial or algal organisms.

As already noted, Claus and Schewiakoff describe two kinds of cells for the retinas of these eyes which neither Conant nor myself can demonstrate. Further, I believe I have shown that only one kind exists. If any doubt should still exist, a section like Fig. 25 (which is from the epithelium of the club, but similar smaller areas with central dots could often be demonstrated in transverse sections of the retinal cells of the simple eyes) I believe should be convincing. Schewiakoff further describes flagella for the retinal cells (his visual cells) of the simple eyes quite as I have described them for all the cells. The pigmentation that Schewiakoff mentions as occurring in the secretions within the lumina of these eyes I believe to have been dissolved in from the pigmented zones. I find no definite pigmentation in these vitreous secretions. These secretions are evidently products of the retinal cells and have been so regarded by former observers.

Lithocyst and Concretion.—The cavity filled by the concretion is lined in places by a single layer of cells, two of which are shown in Fig. 7. This fact has been noted by both H. V. Wilson and Conant. Such cells are evidently remnants of the cells that formed the concretion. The supporting lamella completely surrounds the cavity of the concretion.

The concretion filling the lithocyst has the shape of a hemiprolate spheroid cut in the plane of the axis of revolution. Whether it is of endo- or of ectodermal origin, I believe developmental studies only can determine. Tests made in the Chemical Laboratory show the presence of calcium sulphate with perhaps a very small trace of phosphate.* Nitric acid slowly dissolves these concretions, but I believe Claus was mistaken when he said that they dissolve with an evolution of gas. I watched them dissolve under the microscope, and never could see the least bit of gas formed. If Claus's observation is correct, then the composition of the concretions of C. marsupialis is different from that of the concretions of C. Xaymacana. The concretions, further, were dissolved out of the material preserved in formaline and in osmic acid solutions. For dissolving them in situ I used either nitric or hydrochloric acid, or both. A slight husk remains after all the lime is dissolved.

The Epithelium of the Clubs.—The epithelium is thickest on the dorsal side of a club. The thickening here, as in several other places, seems to be due to a crowding of the cells, in consequence of which the nuclei come to lie at different levels, but I believe that all the cells quite reach the surface. The cells with their nuclei nearest the surface are pyramidal in shape, with the bases of the pyramids toward the surface, while those cells whose nuclei lie deeper (where several layers of nuclei occur) may be spindle-shaped (Figs. 12, 23, 24, 26). Centrad these cells are continued into a single process, which often seems to extend to the basement membrane (Figs. 7, 12, 13, 23, 24). Where the epithelium covers the region of the concretion, the cells become flattened and with the long axis of their nuclei parallel with the surface of the club (Fig. 7). The same holds true for the corneal epithelium (Figs. 7, 13).

It is a significant fact that in many places the nuclei form only a single layer, and in such places one cannot speak of spindle-shaped cells. I cannot find any evidence of sensory and supporting cells as Schewiakoff describes. The fact that spindle-shaped cells may exist is simply a physical consequence of their being closely crowded. Conant arrived at the same conclusion.

But I have another and better reason for supposing the existence

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* Mr. J. C. Olsen, of the Chemical Laboratory, kindly made these tests for me.

of only one kind of cells in the epithelium. In a tangential section taken just through the tips of the epithelial cells (Fig. 25) I find polygonal areas with a central dot. This section does not at all agree with Schewiakoff's Fig. 8, in which he figures two kinds of cells. In Fig. 25 there can be no evidence of two kinds of cells, unless both kinds have like flagella, for these dots are the transverse sections of flagella continued within the cells (Fig. 26).

The epithelium, then, is flagellate, a flagellum to a cell. Whether there are flagella on the epithelium covering the region of the concretion, I could not determine. But I believe that in all other parts, excepting, of course, the corneas, it is flagellated. The fibers (flagella) of the simple eyes are evidently the flagella of the invaginated epithelium. Each flagellum has a basal body, and I could in many instances determine that it was dumbbell-shaped (Fig. 12). This fact was not always evident, however, and it was only occasionally that I felt sure of it. Often the flagella showed only a general thickening within the cells (Fig. 26) while, again, the thickening (basal body) might be quite localized near the surface of the cell. Each flagellum extends into its cell, and occasionally I could trace one clear past the nucleus into the subepithelial nerve-tissue (Fig. 26), just as I did for the axial fibers of the retinal cells of the simple eyes. In those instances in which I could do this, the fibers could so clearly be traced that little if any doubt can exist. I have thus made bold and have drawn the flagella as continued through their cells into the subepithelial nerve-tissue for all the cells of the epithelium of Fig. 12.

A word on the epithelium covering the network cells of Fig. 13. Conant and Schewiakoff here describe fibers from the supporting lamellæ that pass in bundles in among the network cells. These fibers are supposed to be a part of the supporting lamella which reaches out to be a support for the epithelial cells. (Schewiakoff also describes similar fibers for other parts of the epithelium.) Now, as Conant himself shows in Fig. 13, these coarse fibers are not of the same consistency and staining capacity as the supporting lamella. I found them to stain just like the intracellular parts of the flagella or like the central continuations of the axial fibers of the cells of the simple eyes. I could, also, occasionally trace them to the surface of the epithelium, and beyond, when they became continued as short blunt processes or flagella (Fig. 13). I, therefore, conclude that they are sensory fibers like those I have described for the other epithelial cells. Yet, that they pass to the supporting lamella, just as Conant shows in Fig. 13, would seem to indicate that they are fibers from the supporting lamella or processes of the epithelial cells. While this stands as an objection to their being sensory fibers, yet I cannot explain away their being continued distally as a flagellum, except I assume this continuation to be an artefact. This does not seem probable. Perhaps they serve both purposes; namely, that the cell body with its axial fiber is continued to the supporting lamella, the cell proper ending there, while the axial fiber is continued as a nerve fiber. I believe this to be the proper explanation.

The epithelium of the peduncle is quite like the epithelium of the club just described. Sections through the tips of the epithelial cells of the peduncle and also sections sagittal to the axis of these cells give sections like Figs. 25 and 26. I, therefore, conclude that this epithelium is a sensory flagellate epithelium like that of the clubs. Nerve tissue and unstriped muscle fibers underly the epithelium of the peduncles. Claus and Conant also describe a small ventral endodermal tract of nerve tissue, which according to Conant is connected with the endodermal nerve tissue found in the region of the radial ganglia.

To sum up, the epithelium of the club and the peduncle is a flagellate sensory epithelium whose flagella are continued through the cells as nerve fibers into the nerve tissue below. *A priori*, judging from the mass of nerve tissue underlying the epithelium, we should expect the epithelium to be one strictly sensory. What sense it serves is difficult to surmise. In the physiological part of this paper I suggested that it might be tactile, serving in connection with the lithocysts in giving the animal sensations of space relations.

Claus mentions having seen patches of flagella on the epithelium of the clubs. Schewiakoff supposes that his spindle-shaped sensory cells have only a single flagellum, while his supporting cells have many cilia. In the latter supposition he was evidently mistaken. Conant (from an unpublished note) saw the flagella of the epithelium on the living object and does not think that there could be more than a single one to each cell. He also concludes from living specimens squeezed out under a cover-glass, that there is only one kind of cells in the ectoderm.

Cilia and flagella extending into the cells to which they are attached are described by a number of observers.

I shall not endeavor to discuss the subject further, but shall append the literature on the subject that has come to my notice. (See Literature). Some of these observers ascribe a nervous function to these centrad continuations. I am inclined to believe that they represent the primitive fibrils of Apathy, whether the cilia or flagella are motile or sensory. I should mention, however, that Apathy has traced the "Primitivfibrillen" to be continuous with cilia, and also traces them into the sensory rods of the sensory cells in the sense organs of leeches. Eimer also describes cilia as continued centrad.

The Network Cells and the Multipolar Ganglion Cells.—Conant is the first to accurately describe the true structure of the network cells (Fig. 13) that fill the upper part of the club between the proximal complex eye and the attachment of the peduncle. I cannot add anything to Conant's description. As their name implies, they are filled with a coarse network-like structure with a central nucleus and nucleolus. Schewiakoff erroneously described them as ganglion cells and Claus as supporting cells. I have sometimes thought that they are not made up of a network, but of a vesicular structure; *i. e.* the network we see is really produced by the sections of planes that intersect to form little polyhedral cavities. I could not, however, satisfy myself on this point. I further saw similar but smaller cells, with a finer network, disposed in small groups laterally and distally from the attachment of the peduncle to the club.

What the function of these network cells is can only be guessed. In size and shape they somewhat resemble some of the cells found in luminous organs. Conant, however, nowhere mentions that Charybdea is luminous.

Lateral to the larger group of network cells lie two groups of large multipolar ganglion cells (a group on each side). Claus describes these cells, but Schewiakoff does not specially note them, and evidently considered them a part of the network cells, which he erroneously described as ganglion cells.

The Nerve Tissue.—I cannot add anything new on this. It consists of fine fibers and ganglion cells, quite as described by Claus, Schewiakoff, and Conant, and fills the club between the ampulla and the epithelium, except the spaces occupied by the eyes, lithocyst, and network cells. It is likewise present under the ectoderm of the peduncle, where also a small tract is found under the endoderm. (See preceding head, or Claus[3], and Conant[8b]). As already noted, under the distal complex eye, I find only large nuclei to represent the ganglion cells. By saying this, however, I do not wish to dispute their ganglionic nature. The large multipolar ganglion cells I have noted under the preceding topic.

The Supporting Lamella.—The supporting lamella is a continuation, through the peduncle, of the jelly of the bell. It completely surrounds the ampulla and the lithocyst, and also forms a partition between them, so that, as already noted, the lithocyst becomes completely surrounded by it. It also sends a partition ventrally between the complex eyes (Figs. 7, 13). Its thickening to form a support for the lens of the proximal complex eye has already been noticed. I shall limit myself in the discussion of the supporting lamella to the above short resumé, since Schewiakoff gives further detail.

The Endothelium of the Ampulla and the "Floating Cells."—The ampulla is lined by a secreting epithelium. This is shown by the large masses of a secretion within the bases of the cells, and by smaller masses scattered in the central and more distal parts (Figs. 7, and 27, lower half). The section of the cells is such in Fig. 7, that the bases of some (those nearest the supporting lamella) are taken, the central nuclear region of others, and the tips of those farthest from the supporting lamella. The section may be said to be taken diagonally through the bases and central parts of some of the cells, but owing to the curvature of the ampulla wall, through the tips of others. The secretion is a colloid substance, staining yellowish gray with iron-hæmatoxylin, blue with Lyons blue, and reddish with borax-carmine. Sometimes darkly staining rods and fibers of unknown origin could be seen within the larger masses of the secretion (Fig. 7). These rods and fibers could also be seen in spaces within the cells, from which the secretion had evidently been dissolved. I think there can be no question but that the masses described are a secretion. Many series, however, do not show it; indeed, an examination of Conant's slides gave me little evidence of a secreting function, though I could demonstrate it in his sections both within the endothelium and also the floating bodies. The presence or absence of this secretion is evidently correlated with the feeding habits of the animals, or else it would be more generally present.

The endothelium is thickest (the cells are longest) in the upper part of the ampulla where the supporting lamella approaches the lens of the proximal complex eye, and in the lower portion of the ampulla (Fig. 7), in the angle between the concretion cavity and the region of the distal complex eye. In general, the cells are longest in the upper part of the ampulla, while in the lower part, especially where they cover the concretion cavity and the dorsal wall, they may be quite cubical instead of columnar. Often they present a vacuolated appearance at their bases (Fig. 27). Claus and Schewiakoff describe and figure this endothelium, but not in detail. No one, to my knowledge, has described this secretory function.

The nuclei of these cells are peculiar. They may contain a network with a nucleus (Fig. 27). Again, they may show evidence of amitotic division (Fig. 20, h, i, j). Indeed, Remak's scheme (Wilson[18] "The Cell," p. 46) can be quite readily demonstrated. It is, however, such dumbbell-shaped, elliptical, or ringed nuclei as seen in Figs. 7 and 20 that are of special interest.

I have spoken of some of these nuclei as dumbbell-shaped, elliptical, or ringed. This is so, however, only in sections. They are really flattened spheres with a rod of tissue, of the same structure as the nuclear wall, stretching between the poles. One may conveniently compare the shape of these nuclei with that of an apple, the core of the apple representing the rod connecting the two opposite flattened or slightly hollowed poles of the nucleus. For convenience I shall call the rod connecting the two poles the axis of the nucleus. The dumbbell or elliptical shape would be obtained by a meridional section through the axis (Figs. 20, a, b, c, e, g, k, l, m, n, o, 7). Likewise a ringed appearance with a central dot would be obtained by a section parallel with the flattened surfaces or perpendicular to the axis (Figs. 20, d, 7). In a section not strictly meridional the axis would be cut as in Fig. 29, a, or not show at all. As nearly as I could determine, the inside of these nuclei is a vacuole, which the axis penetrates.

The walls and axis of these nuclei have the structure of a very fine and dense network that stains very dark with iron-hæmatoxylin. It stains quite like the reticulum of any nucleus, but is very dense, as though all the reticulum of the nucleus had been crowded together at the surface. Judging from appearances like p (Fig. 20), the hollowing out, so to speak, of these nuclei, would seem to be a process of vacuolation, the reticulum becoming crowded aside to the surface. Bût how, on this view, to account for the formation of the axis, I do not know. Perhaps the axis is formed by a pushing in of two opposite poles of a nucleus, the two invaginations meeting and fusing. On this supposition one might expect the axis to be hollow (cylindrical), but I could not determine that it was. Perhaps the centrosphere (or spheres) (see the next paragraph) has something to do with the formation of the axis (Fig. 20, b, g, e, etc.).

In the nuclei of Fig. 20 with the dark outlines, and of Fig. 7 a small reticular body is seen just opposite one end of the axis, or opposite both ends in g. In d (Fig. 20) this body is seen next the axis just below (outside) the hollow cup represented by the hollow ring. In this instance a central granule is seen in the reticular body, as also in c. I take this reticular body to be the centrosphere, and the central granule in c and d the centrosome. In k, l, m, n, and o (Fig. 20), which are from another series, in which the walls of the nuclei did not stain so dark as in the other nuclei of the same figure, a nucleolus could be definitely seen, indeed, sometimes quite perched upon the wall of the nucleus (k, l). In several instances I could see two nuclei, as in o. But besides these nucleoli, I could in several instances see quite definitely a reticular body (centrosphere) opposite the axis (m, n, o) quite as I described for the nuclei with the dark outlines. In a, b, c, d, e and g the nuclei could not be so readily demonstrated, but I could occasionally see a darker stained body as in a, c and g, that I have no doubt is the nucleolus, which here, again, is perched quite upon the surface of the nucleus. This position of the nucleolus is perhaps due to its having been crowded to one side by the nucleus becoming hollow. It is no uncommon thing, either, to find several nuclei in a single cell, sometimes in process of division or just divided as o and e (Fig. 20), also h, i and j. The whole nuclear phenomenon that I have described seems to be one of division. Perhaps it is somehow associated with the giving off of the secretion of the cells, for these nuclei seem to be found in greatest abundance in those cells in which the secretion is most abundant. In Conant's sections I found but little evidence of these nuclear phenomena as also little secretion, which all goes to show the association of the nuclear phenomenon with the secretion. I have failed to find any descriptions in the literature of nuclei to which I could refer my observations.

The endothelium of the ampulla is flagellated (Figs. 7, 17, 27). It will be seen that there are two slender flagella to a cell. Each pair of flagella has a pair of basal bodies that are longer than thick, and which are continued as a thin fiber towards the nucleus of the cell. That these centrad continuations of the basal bodies extend to or past the nucleus I could not determine. Sometimes the basal bodies with the centrad continuations are pushed quite to one side of the cell (Fig. 27), while in other cells they are applied quite to the distal surface (Figs. 7, 17, 27). Fig. 17, and the part of Fig. 7 that shows these points, are taken just through the tips of the cells. The darker lines within the polygonal areas are the intracellular basal bodies with their centrad continuations, while the thinner lines are the flagella, and are supposed to lie in the plane just below the plane of the figure. In those instances in which the centrad continuations are applied to the distal surface of the cells they could occasionally be seen to bend centrad (Fig. 27b). While these cilia with their basal bodies and centrad continuations are usually separate, as shown in the figures, yet they are at times applied quite closely to each other so that the double nature of the basal bodies and their centrad continuations is not evident. When the intracellular continuations of the cilia become pushed to one side or applied to the distal surface of the cells, I believe this to be due to the turgor of the cells consequent upon the deposition of large masses of secretion within them. But I must add that this explanation is not altogether satisfactory, since in the endoderm cells of the pedalia of both Charybdea and Tripedalia I found like conditions with no evidence of a secreting function. (See below, under tentacles.) No one, to my knowledge, has described the flagellation in detail, although both Claus and Schewiakoff state that the endoderm is ciliated.

The "floating cells" in the stomach pockets and in the ampulla, described by Conant, I believe are in part derived from the endothelial cells of the ampulla. That a portion of them may arise from the ovary, as Conant explains, I do not doubt; I have, further, found a mass of floating cells in a small Charybdea quite as Conant describes for Tripedalia (his Fig. 71). In this Charybdea, however, I could find no traces of any ovary. Conant speaks of larger and smaller floating cells, and that the smaller ones are also found in the males. This latter fact agrees with what I have suggested, that some of the floating cells arise in the ampulla. My chief reasons for my supposition, however, are the following: I find globules of the secretion of the ampulla cells in some of the floating cells and also scattered loosely among them (Fig. 19). These globules in and among the floating cells have the same general appearance and a similar staining capacity as the secretion in the ampulla cells. Again, in spaces within some of the ampulla cells I find bodies resembling the floating cells with lumps of the secretion within them (Fig. 18). The conclusion, therefore, lies near that some of the floating cells originate within the cells of the ampulla, engulf within them some of the secretion, and are then expelled into the lumen of the ampulla. Better said, perhaps, they represent portions of the ampulla cells with some of the secretion. I also found several instances in which a floating cell had the appearance of being expelled from an ampulla cell. Conant suggests for a similar observation that the cells were about to be swallowed by the ampulla cells. I believe, however, that my finding a secretion similar to that within the cells of the ampulla, in some of the floating cells, as also bodies very much like them and filled with secretion within the ampulla cells, together with Conant's finding floating cells in males, and finally the observation that the floating cells are usually quite dilapidated, never showing a healthy cell structure—all this leads me to conclude that some of the floating cells originate from the ampulla cells, and that they have a nutrient function in distributing the secretion. This is quite the reverse of what Conant supposed,—that they were taken in as nourishment by the ampulla cells. I also find what appears to be a secretion in the endoderm of the tentacles of both Charybdea and Tripedalia, and believe this is another source of the floating cells. (See below, under tentacles.)

I also found other very darkly staining bodies (Fig. 19) both within the floating cells and free in the ampulla cavity, and more numerous in the ampulla cells themselves. This again goes to show that floating cells take their origin from the ampulla cells. What these darkly staining bodies are, I cannot say. Perhaps they are something akin to the "Chromatoider Nebenkörper" described by Lenhossek (L), or they represent another kind of secretion. If these floating cells are derived from the cells of the ampulla, the active nuclear division within these also receives an explanation. Some nuclear matter can usually be observed in the floating cells.

The Endothelium of the Peduncle.—The endothelium of the peduncle consists of flagellate columnar cells (Fig. 27, upper half). The cells are vacuolated at their bases like some of the cells of the ampulla, and contain a comparatively large nucleus with nucleolus. The flagella are long and slender, quite like those described for the cells of the ampulla, except that there is only one to each cell. The basal bodies of the flagella are of a peculiar shape. They may be described as a bent spindle, continuous at their distad ends with the cilia and at their centrad ends with a fiber that can be traced quite to the neighborhood of the nucleus. I could not trace these fibers into the basal parts of the cells, except in one instance, and I could not be sure of that (Fig. 27a).

Another interesting observation in connection with the basal bodies is that they are bent in one direction on one side of the canal and in an opposite direction on the other side. In Fig. 27, which represents a longitudinal section of the endoderm and the supporting lamella of the dorsal (*i. e.* farthest from the eyes) side of the peduncle, the distal ends of the basal bodies are bent towards the ampulla, while on the ventral side they would be bent away from the ampulla. This seems to suggest that the flagella move the contents of the canal in one direction on the dorsal side of the canal and in an opposite direction on the ventral side. Conant observed in living material that bodies in the ampulla and the canal were moving about, and that bodies within the tentacles were moving in opposite directions at the same time. This last observation and the histological facts just described, I believe, are mutually corroborative. Again, *a priori*, we should expect some such mechanism as the one described to bring about an exchange between the contents of the ampulla and that of the stomach pockets. I have not as yet been able to demonstrate a similar flagellate mechanism in the tentacles. Flagella and basal bodies are present in the tentacles, but I could not determine that the basal bodies had any definite arrangement like that shown in Fig. 27. (See under tentacles.) I may add, yet, that the cells in the canal of the manubrium have cilia, similar to the ones just described, with large basal bodies, and with centrad continuations. Finally, I am not certain but that these cells form buds at their ends quite like those I describe for the endothelial cells of the tentacles (see below), and that they aid in the formation of the floating cells. I thought I saw such buds just at the entrance of the lumen of the peduncle into the ampulla, but could not find conclusive evidence.

The Tentacles and the Pedalia.—My observations on the tentacles were begun with the object of demonstrating a flagellate mechanism similar to the one described above for the endothelium of the peduncle. While I have failed to demonstrate such a mechanism for the tentacles, yet several interesting points came to my notice. It will be remembered that the tentacles of the Cubomedusæ are not directly attached to the bell, but that a blade-like portion, the pedalium, intervenes between the tentacles and the bell. For figures of the pedalia and the tentacles the works of Haake, Claus, Conant and Maas[22] may be consulted.

The Ectoderm.—The ectoderm of the tentacles is the seat of a number of differentiations. It is quite thick, as the figures (28 and 29) show, and in this respect is very different from the pedalia, on which the ectoderm cells are quite cubical. I found evidence of cilia here and there, but I can add nothing definite about them. Neither can I add any definite statements regarding the ectoderm cells proper, but what I have to say relates to their differentiations.

(a) The *thread cells* are of two kinds, larger ones and smaller ones. This is well shown in Fig. 29, which is part of a transverse section of a tentacle of Tripedalia. Two kinds of nettle-cells are also present in the tentacles of Charybdea, but they were specially well shown in Tripedalia. The structure of these thread-cells seems to be typical, and I have little more to say about them. I wish, however, to call attention to the five or six unstriped muscle-fibers that are attached to their basal lateral parts, and which connect them with the basement membrane (Figs. 28, 29). Claus describes these muscle-fibers and mentions that Fr. Müller has described them before him, but I have not found them mentioned elsewhere in the literature of nettle-cells. Professor Brooks tells me, however, that he has often found them. It would appear from Fig. 29 that they serve to retract the thread-cells from the surface. Claus suggests that the muscles are developed from the cnidoblasts.

(b) The plain subectodermal *muscle-fibers* are of interest. In

Charybdea they lie wholly enclosed within canals of the supporting lamella (Fig. 32, upper part). They run longitudinally, and near the base of each tentacle pass out of their canals and become strictly subectodermal (Figs. 31, 32). This is for Charybdea. In Tripedalia they rarely come to lie in closed canals as in Charybdea. These facts show beyond doubt that these muscles are developed from the ectoderm. Claus has suggested their ectodermal origin, but did not demonstrate it. He also suggested that they become inclosed in canals by the supporting lamella pushing up around them and finally fusing above them. This, I believe, is demonstrated by the conditions in Tripedalia (Fig. 29). Here the canals usually remain open, but occasionally, as in the left-hand canal, one may become completely inclosed. This condition of things suggests the intra-lamellar muscles found in actiniarians. The nuclei found in the canals with the muscle-fibers probably belong to the cells from which the muscles become differentiated. Claus figures these muscle-fibers and nuclei, and it may be added that the supporting lamella he figures, for C. marsupialis, is much thicker than I have figured it for C. Xaymacana and Tripedalia cystophora. The number of muscle-canals also is greater and occupies a much greater depth of the thickness of the lamella. Since Claus gives a figure of a transverse section showing the muscles in their enclosed canals, I have not deemed it necessary to duplicate his figure. In the transition from a tentacle to a pedalium, the muscles are most strongly developed toward and at the edges of the pedalium. This is true for the pedalia in general, and accounts for the readiness with which they can be bent inwards, as noted in the physiological part of this paper.

(c) I have found a single *ganglion-cell* among the cells of the ectoderm of the tentacles. This showed so plainly that I have figured it (Fig. 28). Other ganglion-cells no doubt exist, but could probably not be distinguished from other cells. In its position in Fig. 28 it appears to be associated with the nettle-cell shown just above it. Its position is very much the same as that figured by Lendenfeld (25a).

The Endoderm.—The cells of the endoderm of a tentacle are long and quite slender (Fig. 31). At their bases they are vacuolated quite like the cells of the ampulla and the canal of the sensory clubs. They contain a well-formed nucleus with a nucleolus. In their distal half small light bodies with a dark center are very evident. These bodies are evidently a secretion.

Another peculiar phenomenon presents itself in these cells. The distal part of each cell becomes separated off from its body by what appears to be the formation of a transverse cell-wall (Fig. 31, c–d). I have found the ends of these cells quite separated off in some series. The formation of the walls seems to begin as a thickening at the sides of the cells, and a section through this region, transverse to the cells, would appear like Fig. 30. The dots in the centers of the polygonal areas of this figure are the centrad continuations of the cilia to be described below. As already remarked in describing the endoderm of the ampulla, I believe we here have another place of origin of the "floating cells." The secretion just described moves into the distal parts of the cells prior to their separation (Fig. 31). In some series I could see these secretion bodies much more numerous within the distal ends of the cells than in Fig. 31.

As will be seen in Fig. 31, each of the endoderm cells of the tentacles has a flagellum that extends into the lumen of the tentacle. Each flagellum has a thickening just within its cell, which may be regarded as a basal body. From this basal body, again, a small fiber extends centrad into each cell. It does not appear that the flagella are thrown off with the distal parts of the cells; at all events, I never found them connected with any of the floating cells except in a few doubtful instances.

What I have said for the endoderm of the tentacle of Charybdea applies equally to Tripedalia.

Claus, in his figure of a transverse section of a tentacle of C. marsupialis shows the endoderm as cubical. I cannot explain why there should be such a difference between the endoderm of the tentacles of *C. marsupialis* and that of the tentacles of *C. Xaymacana* and *Tripedalia cystophora.* Claus does not describe the endoderm in detail.

The endoderm cells of the pedalia of both Charybdea and Tripedalia are cubical and possess flagella, basal bodies, and centrad continuations, quite like those I have described for the endoderm cells of the ampulla. The double nature of the basal bodies and the centrad continuations is, however, not so evident. A secretion I did not find. Histologically, therefore, the endothelium of the pedalia corresponds rather with that of the ampulla, and that of the tentacles with that of the peduncle of the clubs.

SUMMARY.

The most important results in the histological part of this paper relate to the structure of the retinas of the eyes of the sensory clubs.

The retina of the distal complex eye is composed of three kinds of cells: two kinds of sensory cells (the prism and pyramid cells), and the long pigment cells (Figs. 1–9). The prism and pyramid cells have each an axial nerve fiber in their prisms and pyramids respectively. These fibers I could, however, trace only to the neighborhood of the nuclei. But since I could trace similar fibers in the retinal cells of the simple eyes (Fig. 16) past the nucleus into the subretinal nerve tissue, I believe that the axial fibers in question also extend centrad as nerve fibers into the subretinal nerve tissue. Other observers also figure such fibers as extending centrad as nerve fibers. The axial fibers of the prism cells have each a dumbbell-shaped basal body at their entrance into the pigmented part of a cell. The evidence for a body of such shape in the pyramid cells was not conclusive, though a basal body for the axial fiber exists. The long pigment cells project or retract their pigment in light or darkness respectively and thus seem to serve to check the diffusion of light in the retina. I have also supposed that these cells may serve for conducting impulses to the lens, and that the latter is adjustable.

The proximal complex eye (Fig. 13) has only the prism cells present in its retina, and not two kinds of cells as Schewiakoff has described (see text, pp. 53, 60, 63) for all the eyes.

The simple eyes (Fig. 12), two on each side of a club, four in all, also have only one kind of cells in their retinas, and each cell has a flagellum extending into the vitreous secretion of the lumen. These flagella could be traced centrad as a nerve fiber (Figs. 12, 16). Similarly, a nerve fiber could be traced centrad from the flagella of the epithelial cells of the clubs. Dumbbell-shaped basal bodies for the flagella of the simple eyes could also be demonstrated, but the evidence for this in the epithelial cells of the clubs was not so satisfactory.

Other points of interest are: A secretory epithelium lining the ampulla of the clubs, and a somewhat similar epithelium lining the canals of the tentacles (Figs. 7, 27, 31); the partial origin of the "floating bodies" in the canals of the clubs and tentacles and the stomach pockets from these epithelia (Figs. 18, 19); two flagella to

each cell of the endothelium of the ampulla and of the pedalia (Figs. 7, 17); the peculiar nuclei in the endothelial cells of the ampulla (Fig. 20); the longitudinal muscles of the tentacles being completely inclosed within canals of the supporting lamella, but near the base of a tentacle becoming subectodermal. This demonstrates their ectodermal origin. In Tripedalia it is seldom that any of these muscles become enclosed as in Charybdea (Fig. 29).

If to the reader my results seem to embody a somewhat heterogeneous detail, he must remember that the work consists partly in corroborating and partly in supplementing the work of previous observers, and that, in general, histological detail does not usually make the most readable paper.

Biological Laboratory,
Johns Hopkins Univ., May, 1899.

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N. See also 6.

REFERENCE LETTERS.

a=flagellum in Fig. 27, that is supposed to extend centrad beyond the nucleus.
b=twin flagella in Fig. 27, of which the centrad continuation is seen applied against the distal surface of the cells and to be continued centrad.
c=capsule of lens.
cf=axial fibers of cells extending centrad.
co=cornea.
concr=concretion cavity.
ec=ectoderm.
en=endoderm.
f=flagella.
flp=distal fiber of a long pigment cell.
fpr=axial nerve fiber of a prism cell.
fpyr=axial nerve fiber of a pyramid cell.
frc=axial nerve fiber of the retinal cells of the simple eyes.
gc=ganglion cells.
ind=impression of the lens probably due to the pressure of weight against the surrounding tissue.
l=lens.
lp=long pigment cells.
m=muscle fibers.
namp=nuclei of ampulla cells.
nc=network cells (Figs. 13 and 16), and nettle cells (Figs. 28, 29).
nf=nerve fibers and tissue.
nlp=nucleus of long pigment cell.
nm=nucleus of muscle cells.
nprc=nucleus of prism cell.
npyrc=nucleus of pyramid cell

nz=nuclear zone.
pr=prism of prism cell.
prc=prism cell.
pyr=pyramid of pyramid cell.
pyrc=pyramid cell.
pz=pigmented zone.
r=retina.
s=secretion in endo. of tent. and ampulla.
sh=shrinkage space.
sec=vitreous secretion in the lumen of the simple eyes.
sla=supporting lamella.
vb=vitreous body or zone.
x=(1) the approximate level at which Fig. 4 should be cut transversely to give Figs. 1 and 3.
(2) the thickening of the supporting lamella in Fig. 13 to support the lens.
*=Point of approximation of cells of lenses in Figs. 7 and 13.

DESCRIPTION OF FIGURES.

ALL FIGURES, UNLESS OTHERWISE STATED, ARE FROM CHARYBDEA.

Fig. 1. This figure represents a transverse section through a portion of the vitreous body of the distal complex eye at about the level x of Fig. 4. Three kinds of areas are seen, namely, the prisms and pyramids with their axial fibers and the distal continuations of the long pigment cells. Towards the lower left of the figure the section is a little more distal than at the right and the transverse areas of the long pigment cells are no more so large as at the right of the figure. The dark granules in the areas of the long pigment cells represent pigment. Camera lucida sketch. ×920. pp. 45, 46, 48, 49, 50, 51, 52, 54.

Fig. 2. This figure is a camera lucida sketch from a section taken transverse through the most distal part of the pigmented zone of a slightly pigmented retina of a distal complex eye. The presence of three kinds of elements is again evident. The dots without the polygonal areas represent the centrad continuations of the axial fibers of the prism cells. The lettering explains the other areas. ×920. pp. 46, 48, 50.

Fig. 3. This is from a section similar to that of Fig. 1, but a little more distal. At the right, the section is more distal than at the left of the figure, in consequence of which the long pigment cells are there taken through their distal fibers. Note the small shrinkage spaces about the axial fibers of the prisms. The white lines bounding the prism areas appear as in nature. The pyramid cells are not shown in this figure. ×950. Camera sketch. pp. 50, 51, 52, 54.

Fig. 4. This figure is from a section taken parallel to the long axis of the cells of the retina of a distal complex eye. It is from a camera sketch, and nothing has been put into the figure except what could be clearly seen. The lateral boundary lines of the prisms are not shown. Note the evidence for the existence of three kinds of cells. ×920. pp. 44–52, 54.

Fig. 5. This figure represents a sagittal section through the nuclear and pigmented zones and the subretinal nerve tissue of a slightly pigmented retina of a distal complex eye, that had been killed in the dark. Camera sketch. The pyramid cells are not shown. ×900. pp. 47, 51, 52, 53.

Fig. 6. These cells are from a preparation by Conant of a sensory club, macer-

ated in acetic acid. Cell a is evidently an iris cell. The others are probably prism cells from the proximal complex eye. ×900. pp. 44, 48.

Fig. 7. In this figure I represent a sagittal section through the distal complex eye. In the middle half of the section, the nuclei, the prism and pyramid cells with their axial fibers, and the long pigment cells with their large distal fibers are all strictly camera lucida sketched. A portion of the pigmented zone has been left unpigmented to better show its structure. At the right and above the concretion cavity is shown a portion of the endoderm of the ampulla. The section is not strictly in a dorsoventral plane of the club, in consequence of which the cells of the ampulla are cut diagonally and through their tips. Note the dumbbell-shaped nuclei of the ampulla cells, as also the masses of secretion. A part of the retina of the proximal complex eye is shown in the upper part of the figure. ×920. pp. 41–54, 63, 64, 68–71.

Fig. 8. These cells are from a macerated preparation. Cells a, b, c, d may be either prism or pyramid cells from the distal complex eye or prism cells from the proximal complex eye. Cells e and f are probably from the right fourth (Fig. 13) of the retina of the proximal complex eye or from the simple eyes. The unlettered cells are probably from the simple eyes. Some of these show a distal process. ×900. pp. 48, 62, 65.

Fig. 9. The cells here figured are long pigment cells from the same preparation as Fig. 6. ×900. pp. 50, 51.

Fig. 10. This drawing shows an end view of a group of prisms from the same preparation as Fig. 6. ×900. pp. 46.

Fig. 11. This group of prisms are from the same preparation as Fig. 6. Two of them are broken off. The fibers seen at the lower end are probably some of the axial fibers. The fiber at the upper end I believe is interprismatic and the distal fiber of a long pigment cell. ×900. pp. 46.

Fig. 12. This figure is a summary of my results on the simple eyes. It is from a camera sketch of one of the distal eyes, but somewhat diagrammatic. The left side of the figure is proximal, the right side distal. ×920. pp. 61, 62, 64, 65.

Fig. 13. Sagittal dorsoventral section of a proximal complex eye. Conant drew and published this as his Fig. 69. Conant's evidence regarding the axial fibers of the prism cells was incomplete; so that, in this respect, he left his figure unfinished. I have drawn in these fibers and republish the figure. At the right of the retina and next the lens (the white space) the vitreous body is incomplete and the fibers from the retinal cells project freely into the space. This part of the retina also remains unpigmented. Like my Fig. 7, this figure evidently represents a section somewhat to one side of a sagittal dorsoventral plane of the club, so that the endoderm cells of the ampulla are cut diagonally or transversely. pp. 41–44, 60, 64–68.

Fig. 14. This is drawn to show how regularly small shrinkage spaces may occur in transverse sections of the vitreous bodies. This figure is from a transverse section of the vitreous body of a proximal complex eye. I believe that these spaces are determined by the axial fibers of the prisms. Prism outlines are not shown. ×950. pp. 54.

Fig. 15. This figure is a drawing of a portion of a transverse section of one of the simple eyes. Note the flagella from the retinal cells. pp. 62.

Fig. 16. The section of the lower left hand corner of this figure is through a portion of one of the proximal complex eyes, and shows the centrad continuation of the axial nerve fibers of the retinal cells. The section is such, that, besides the simple eye, the nuclei of the proximal complex eye (upper part of figure) and two network cells are cut. ×920. pp. 47, 62, 63.

Fig. 17. A transverse section through the tips of the ampulla cells is here shown. To the left is towards the upper end of the ampulla. The basal bodies with the centrad fibers are in the plane of the section, while the flagella are supposed to extend below the plane of the section. ×1350. pp. 71.

Fig. 18. These bodies, from within the ampulla cells, contain some of the secretion of the ampulla cells, and resemble the "floating bodies." ×1350. pp. 72.

Fig. 19. The "floating bodies" here represented are from the ampulla. Globules of a secretion similar to that found in the ampulla cells are seen both within and without the bodies. Note also the two black bodies without the cells and two or three similar ones within the cells. These latter bodies are of doubtful nature. ×1320. pp. 72.

Fig. 20. This figure represents sections of the various nuclei found within the ampulla cells. ×1350. pp. 69, 70.

Fig. 21. These cells are from the same preparation as Fig. 6. They are evidently retinal cells from the simple eyes. The tendency of their pigmented ends to become globular, I believe, is due to their having become isolated before they hardened during maceration. ×920. pp. 62.

Fig. 22. This diagram illustrates the retraction of the long pigment cells. The dotted lines in the vitreous body mark the outlines of the prisms, while the continuous lines represent the axial fibers of the prism and pyramid cells. pp. 45, 46, 48, 49, 53.

Fig. 23. These cells are from the epithelium of a sensory club. They are from the same preparation as Fig. 6. Flagella are not shown. ×900. pp. 64.

Fig. 24. This group of epithelial cells of a club are from the same preparation as Fig. 6. ×850. p. 64.

Fig. 25. This sketch is a transverse section through the tips of the epithelial cells of a club. The polygonal areas are the cells, while the central dots are the centrad continuations (nerve fibers) of the flagella of the cells. ×920. pp. 63, 65, 66.

Fig. 26. The flagella of the epithelium of a club are in this figure seen to extend centrad, some beyond the nuclei. Cell outlines are not shown. ×920. pp. 64, 65, 66.

Fig. 27. The cells of the lower half of this figure belong to the ampulla, those of the upper half to the canal of the peduncle. The right side of the figure is towards the eyes (the ventral side) of the club. Globules of secretion are seen within the ampulla cells, as also a globule without. The ring above the latter globule is probably an empty shell of a floating cell. ×1320. pp. 68, 69, 71, 73.

Fig. 28. This figure is from a transverse section of a tentacle of Charybdea.

The mass with darkly stained granules is the remains of a thread cell. The ectoderm and a small part of the supporting lamella only are figured. Note the large ganglion cell. ×920. pp. 74, 75.

Fig. 29. Part of a transverse section of a tentacle of Tripedalia. The endoderm is not figured. The supporting lamella is seen to be considerably thinner than in Charybdea. Note the subectodermal muscles, as also the muscle fibers to the thread cells. ×920. pp. 69, 74, 75.

Fig. 30. This is a transverse section through the endothelium of a tentacle of Charybdea in the line c d of Fig. 32. The dark lines bounding the polygonal areas are the thickenings of the sides of the walls of the cells in the line indicated. The central dots are the centrad continuations of the flagella. ×920. p. 76.

Fig. 31. This figure is a transverse section through a tentacle of Charybdea at about the middle of Fig. 32, *i. e.* so near to where the tentacle joins the pedalium, that the muscles within the lamella have all come to lie under the ectoderm. The ectoderm is not shown. ×920. pp. 75, 76.

Fig. 32 A longitudinal section through the supporting lamella only, of a tentacle of Charybdea, is here shown. In the upper part of the figure the muscle fibers are seen wholly enclosed by the supporting lamella. In the middle of the figure they are seen to pass out of their canal. In the lower part of the figure, the supporting lamella is seen to bend to the right where it becomes continuous with the lamella of the pedalium. ×920. p. 75.

Fig. 1.

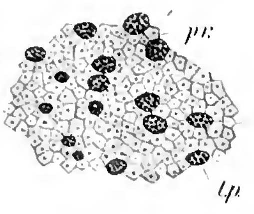
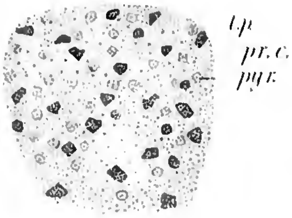


Fig. 2.



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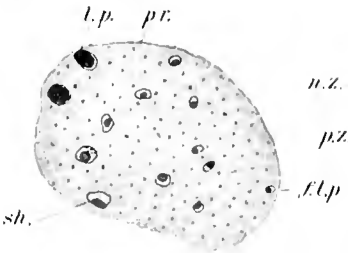

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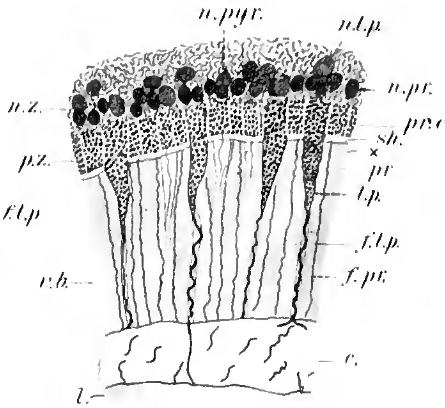
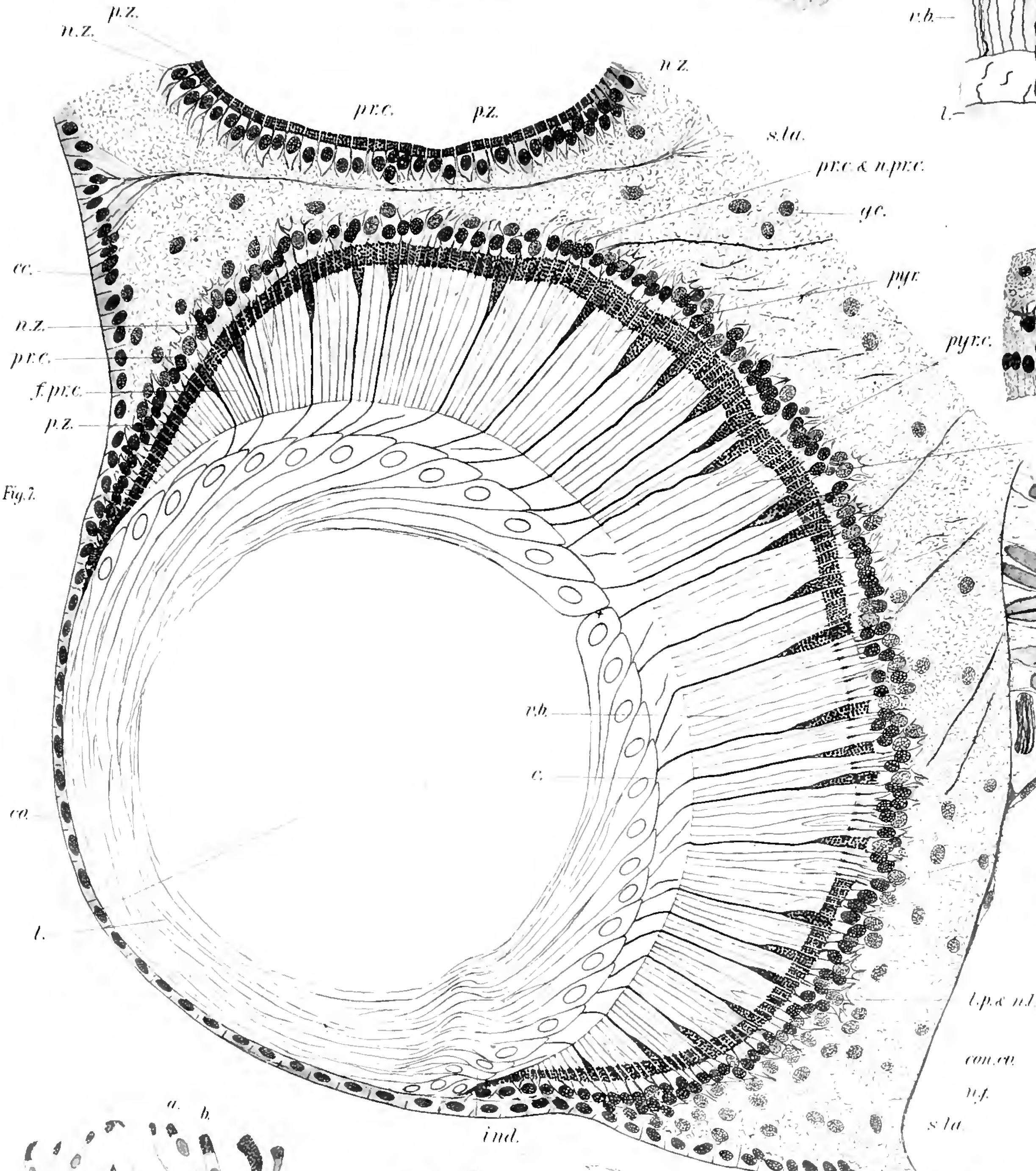
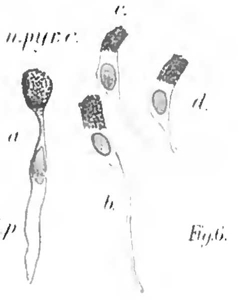


Fig. 5.

Fig. 7.





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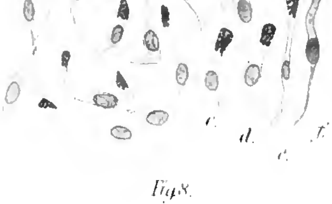

Fig. 8.

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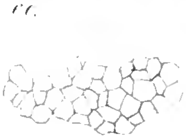
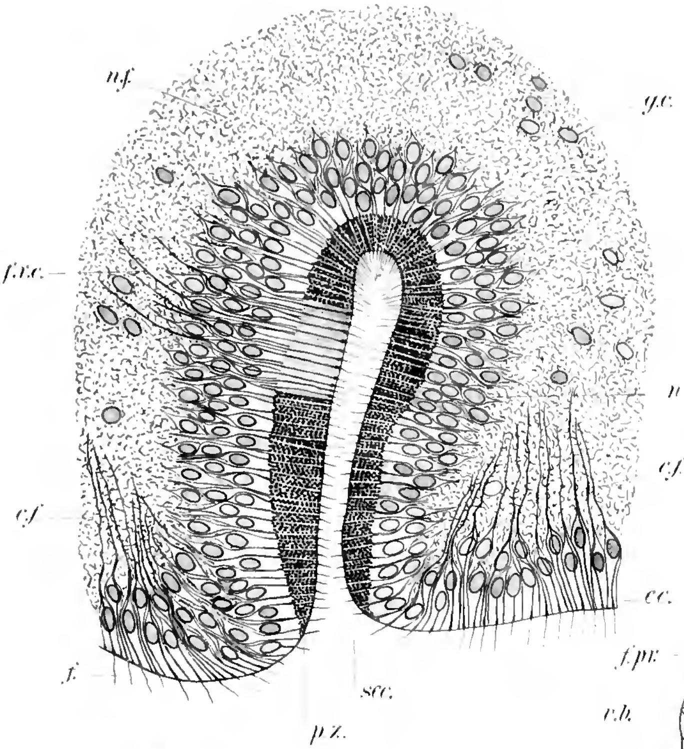


Fig. 10.

Fig. 11.

Fig.12.



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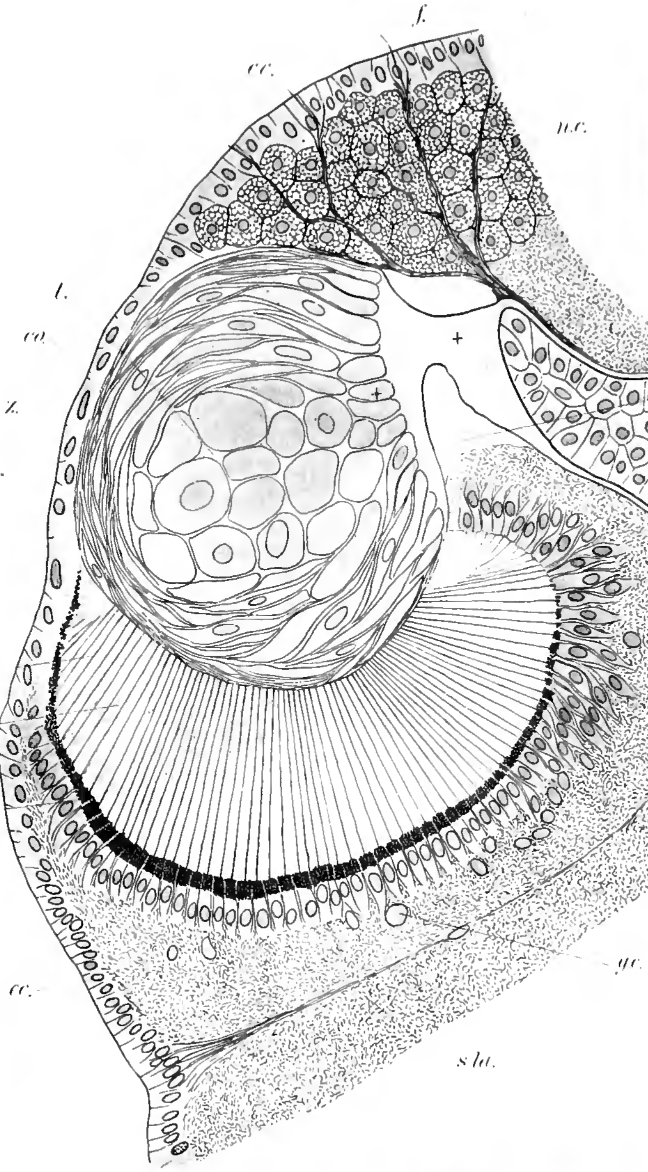

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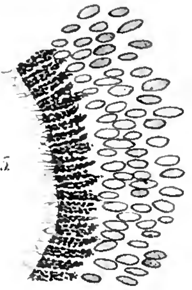

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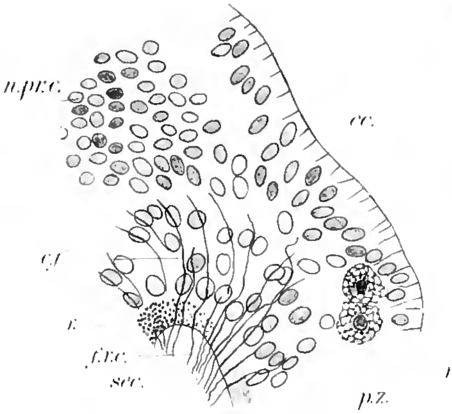


Fig.16.

Fig.21.

Fig.17.

Fig.18.

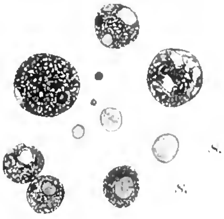
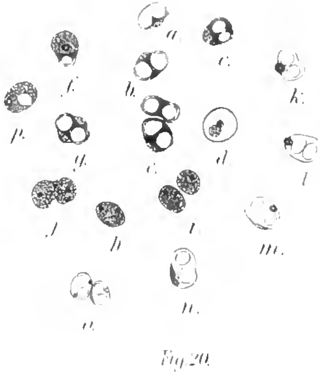


Fig.19.



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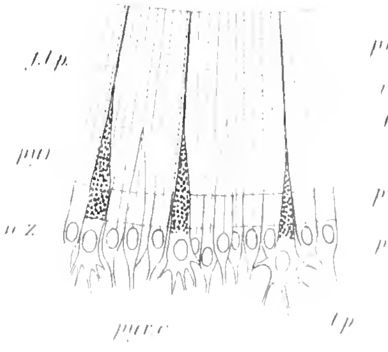


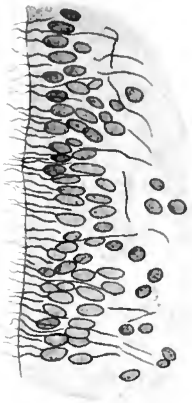
Fig.22.

Fig.23.

Fig.24.

Fig.25.

Fig.26.



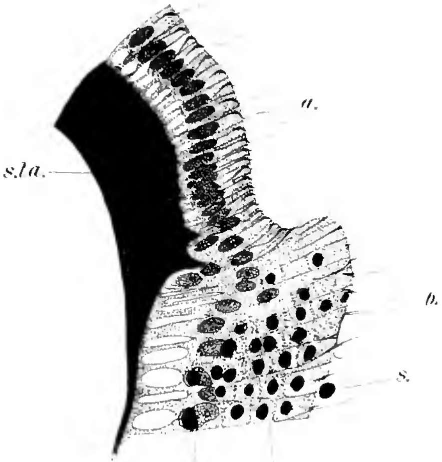


Fig.27.

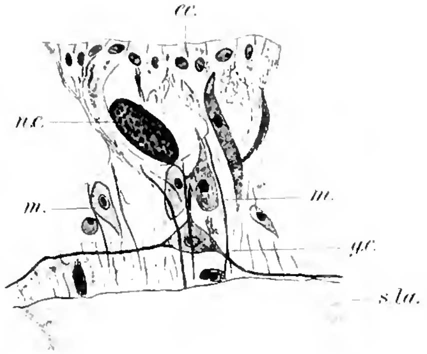


Fig.28.

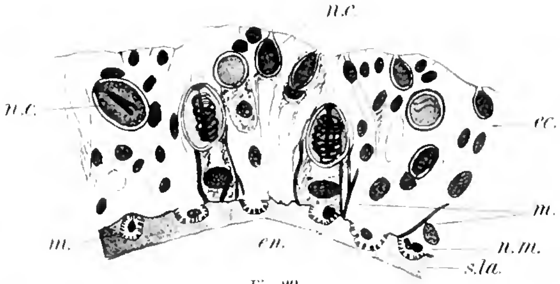


Fig.29.

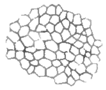


Fig.30.

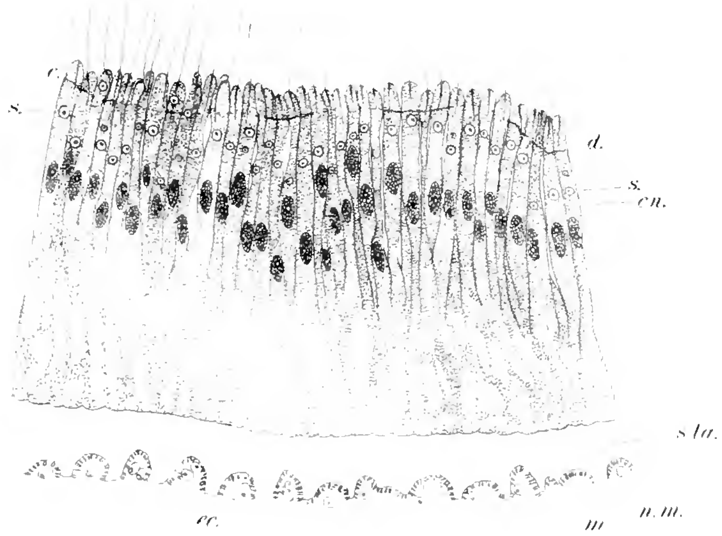


Fig.31.

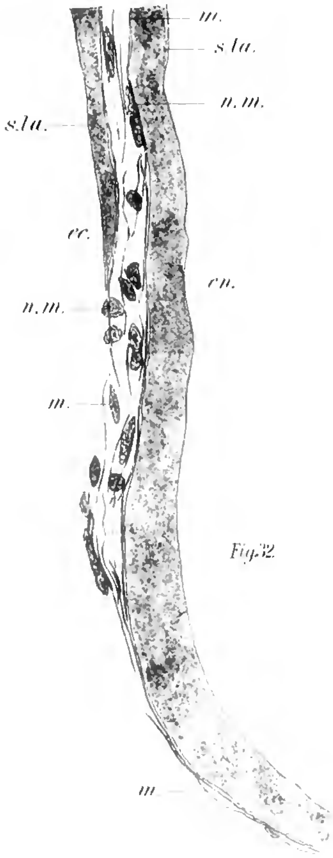


Fig.32.

VITA.

The writer of the foregoing dissertation, Edward William Berger, was born in Middleburg Township, near Berea, Ohio, on November 29, 1869. He is the youngest son born to Karl Gottlob Berger and Christiane Pauline, daughter of Karl Gottlieb Gellrich, who, leaving their home in Silesia, of southeastern Prussia, in 1854, came to make America their adopted country.

The writer's preliminary education was received in the public schools of Lorain, Ohio. In 1886 he entered German Wallace College, of Berea, Ohio, from which institution he graduated in 1891. In 1892 he entered Baldwin University, also at Berea, and graduated in 1894. In the fall of the same year he entered Johns Hopkins University, taking up special studies in Zoology, Physiology, Botany and Chemistry.

Two months of the summer of 1897 were spent in Jamaica with the Johns Hopkins Marine Laboratory, and two months, in 1898, at the United States Fish Commission Laboratory, Wood's Holl, Mass. The writer has twice held a University Scholarship.

BIOLOGICAL LABORATORY,
JOHNS HOPKINS UNIVERSITY, *May*, 1899.

Memoirs from the Biological Laboratory
OF THE
JOHNS HOPKINS UNIVERSITY
IV, 5
WILLIAM K. BROOKS, EDITOR

OPHIURA BREVISPINA

A DISSERTATION PRESENTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY
THE JOHNS HOPKINS UNIVERSITY

BY

CASWELL GRAVE

(Reprinted from the Memoirs of the National Academy of Sciences)

BALTIMORE
The Johns Hopkins Press
1900

As my name appears upon the title-page of this memoir, it is proper for me to state that my share in the work has been that of the instructor under whose direction the work has been done. The discovery that this Ophiuran is of peculiar interest and that it is unusually favorable for the study of the problems of the morphology of Echinoderms, was made by Dr. Grave; and the results which are here detailed are his work.

W. K. Brooks.

CONTENTS.

OPHIURA BREVISPINA.

By W. K. Brooks and Caswell Grave.

INTRODUCTION.

During the summer of 1898 it was my privilege to occupy the table of the Johns Hopkins University in the United States Fish Commission laboratory at Woods Hole, and while here I rediscovered the peculiar Ophiuran larva, which was first found and figured by Krohn (7).

Finding the larvæ he described in the open sea Krohn did not know to what species they belonged; but the larvæ, the development of which is the subject of the greater part of this paper, came from eggs laid in aquaria by *Ophiura brevispina.* It is not likely that the same species of Ophiuran occurs both at Funchal, where Krohn did his work, and also at North Falmouth, where my material was obtained, but it is very probable that species belonging to the genus *Ophiura* have similar larval forms.

Among Echinoderms, where a direct development from the larva to adult occurs, that is, without the usual highly specialized intermediate pelagic larva, we usually have to do with a species which in some manner takes care of its brood; but in *O. brevispina* the larvæ are free swimming, they being provided with a well developed locomotor apparatus, yet the usual Ophiurid pluteus larva is as completely omitted as it is from the life history of the viviparous *Amphiura squamata.*

From the fact that the usual pluteus skeleton is begun in the larvæ of *O. brevispina* one is led to suspect, however, that at some period in its history the species possessed a larva more nearly like a pluteus than at the present time. On the other hand, on account of the resemblances which exist between the larvæ of *O. brevispina* and *Antedon rosacea* (treated of in another place) we may suppose a close phylogenetic relationship exists between them. If, as many zoologists believe, the crinoids have retained more nearly than any other group the characters of the primitive Echinoderm stock, then in the larva of *O. brevispina* we may have one which has retained unmodified its primitive characteristics.

In this paper, however, the facts only of development are taken up, and the question of the bearing which this larva may have on any theoretical discussion concerning the interrelationships of the Echinoderms is suggested here in order that the reader may keep the subject before him while studying the paper. The points of resemblance between the Ophiuran and Antedon larvæ are enumerated in a chapter further on.

The method used in the preparation of the material for microscopical study, and which gave good results, is as follows: The larvæ were taken up into a pipet with as little water as possible, and squirted into a small bottle containing a solution of sublimate-acetic (98 parts of a sat. sol. $HgCl_2$ being used to 2 parts of glacial acetic acid). After from two to five minutes the sublimate solution was drawn off gently, leaving the larvæ at the bottom where they had settled. Then 50 per cent alcohol was added, which in a few minutes (5) was drawn off and replaced by 70 per cent alcohol, in which a little iodine had been dissolved. In a few hours (3–12) this was changed for clear 75 per cent alcohol, in which the larvæ remained until needed for laboratory study. After staining lightly in acid carmine, so as to facilitate their orientation, the larvæ were dehydrated in the usual way and cleared in oil of cloves. From the clove oil they were oriented by a modification of the Patton method. After an impregnation with 55° paraffin, series of sections three microns in thickness were made in three planes, transverse, longitudinal sagittal, and longitudinal horizontal. The sections were stained on the slide with KLEINENBERG'S hæmatoxylon. Other methods were tried, but none proved so satisfactory as the one just described. The shrinkage in echinoderm tissue, which usually accompanies the unmodified paraffin method, was not to be seen in the tissue of these larvæ, due, no doubt, to its unusual thickness.

It has been thought best to make the following list of terms which are used synonymously in the text of this paper in the description of the larvæ. Those in the same line can, in most cases, be interchangeably used.

Dorsal–aboral–above–over.
Ventral–oral–below–under.
Anterior–forward–before.
Posterior–backward–behind.

In the drawings of the larvæ, when the ventral side is up and the anterior end is nearest the top of the page, then the reader's left is also left in the figure.

For convenience in description, the various stages taken to illustrate the life history of the species have been designated by letters of the alphabet, this method seeming preferable to one in which age is used as a distinguishing character, since the progress of development at any age depends so intimately on the varying conditions of environment.

I take this opportunity to acknowledge my indebtedness to Dr. C. P. SIGERFOOS, at whose suggestion I began the study of Ophiuran development.

I was aided very materially while at the Fish Commission laboratory by Prof. H. C. BUMPUS, who placed at my disposal every facility for work at his command, and to him, also, I am greatly indebted for many suggestions in methods of rearing larvæ at the seashore.

To Professor BROOKS, under whose direction my work has been done, are due my warmest thanks for the interest with which he has followed me in my studies and for the many valuable suggestions he has offered from time to time during the year.

HISTORICAL SKETCH.

The species of Ophiuran, *Ophiura brevispina*, the life history of which is the subject of this dissertation, was first discovered and described by Thomas Say in 1825 (12).

Since this time the species has been rediscovered and renamed as many as three times. It is probably best known at present by one of its synonyms, *Ophiura olivacea*, which was given to it in 1865 by THEODORE LYMAN (8). In his earlier works LYMAN distinguished between *O. olivacea* and *O. brevispina*, but in his *Challenger* report on the *Ophiuridæ* and *Astrophytidæ* (9) he places the two species together as one under its earlier name, which, although less descriptive of the species than that given by Lyman, it is probably best to retain.

In 1852 AYERS described the species under the name *Ophioderma olivaceum* in Vol. IV of the Proc. Bost. Soc. Nat. Hist.

LUTKEN also described it as *Ophioderma serpens* in 1856.

DISTRIBUTION AND HABITS.

Ophiura brevispina is a very widely distributed species, it having been reported from points along the Atlantic coast from Brazil to New England.

It has been taken from the following localities:

1. Bahia, Brazil.
2. Port Antonio, Jamaica.
3. St. Thomas, Bahamas.
4. Cape Florida, Florida.
5. Tortugas.
6. Beaufort, North Carolina.
7. Old Point Comfort, Virginia.
8. Sag Harbor, New York.
9. Dartmouth, Massachusetts.
10. New Bedford, Massachusetts.
11. North Falmouth, Massachusetts.

That part of North Falmouth Harbor which is inhabited by the species is very shallow, its depth at low tide not exceeding 1 fathom.

The bottom is covered with a mat of living and dead grasses and algæ, and in this tangle the ophiurans live, together with a great variety of crustaceans, molusks, and worms.

The usual color of the species is an olive green, with darker bands on the arms and sometimes with a clouded disk.

Through the blending of their colors with the seaweed the ophiurans are greatly protected from their enemies, and it is difficult, even when looking for them, to see them among the seaweed so long as they do not move.

It is quite common to find a small Amphipod crustacean clinging to the arms of dredged specimens, and from the structure of the crustacean it is probable that the two species live together commensally. What benefit either animal can derive from the association it is difficult to see.

One pair of the thoracic legs of the crustacean is so modified as to form a structure beautifully adapted for clinging to the round ophiuran arms. The last segment but one of each of this pair of legs is **Y**-shaped. At the end of one arm of the **Y** is attached a movable segment, the end segment of the leg, which when shut down upon the end of the other arm of the **Y** incloses a triangular space in which the ophiuran arm is held.

The body of the crustacean is colored and banded in such a manner as to simulate closely the color and banding of the ophiuran arms.

When placed in aquaria with their host, the crustaceans cling to the ophiuran arms until the water becomes depleted of oxygen, when they leave the arms and swim about the edge of the dish apparently much alarmed.

In examining the stomachs of the ophiurans one finds bits of other animals, such as crustacean appendages and the skeletons of young horseshoe crabs. From this it is probable that the creatures are scavengers, since an active crustacean would hardly be captured by so slow and poorly armed an animal as an ophiuran. None were ever observed to eat anything when kept in the laboratory, and it is quite out of the question to observe them in their natural habitat, since they are nocturnal animals remaining hidden during the day.

The ophiurans were first examined for sexual elements early in June, and at that time the eggs were very large but adhered closely together in the gonads. The sperm appeared to be fully formed but were nonmotile.

From this time on until the middle of August the species was regularly watched and examined, and on July 16 the first ripe eggs and sperm were obtained. A great number of specimens had that day been dredged and placed in aquaria dishes of fresh, filtered sea water. One week later a great number of adults were again brought in and placed under the same conditions as those which had spawned in the laboratory the week before, but this time very few eggs were obtained, and all subsequent attempts to get the ophiurans to spawn were unsuccessful.

From this it would seem that the breeding season is extremely short.[1]

The time of day at which spawning occurred corresponds well with the time at which I have noted it to take place in *Ophiophilus aculeata* and *Ophiocoma echinata*, that is, between 8 and 10 o'clock p. m.

PHYSIOLOGICAL NOTES.

The locomotor movements of an ophiurid, upon a casual observation, seem to consist of an uncoordinated writhing and twisting not calculated to bring the creature to food or a place of safety except by chance; but a more careful study shows them to be the result of an orderly and nicely coordinated mechanism.

The rapid strides which characterize the movements of a brittle star are in strong contrast

---

[1] During the summer of 1899, after this paper had gone to press, my experience with the species was very different from the above. Specimens brought into the laboratory early in June threw eggs and sperm, but the eggs, after passing through the early segmentation stages, ceased to develop. The eggs were probably immature, and were spawned only because of the bad condition of the water in the aquaria, but spawning always occurred early in the evening at the time when it would have occurred under normal conditions. Why unripe eggs should develop at all, or why eggs mature enough to begin their development should not be mature enough to complete it, is an interesting question.

This phenomenon was repeated every few days until July 26, when about one-fourth the number of eggs spawned developed into normal larvæ. This is ten days *later* than the date when eggs became mature at Woods Holl. From the fact that the water is much warmer at Beaufort than at Woods Holl one would expect to find the spawning season earlier at the latter place.

with the slow creeping movements of a starfish or sea-urchin, the difference being due to the employment of different locomotor mechanisms in the two cases; the starfish and sea-urchin depending entirely upon their tube feet and spines while in the ophiurids, the arms themselves are the efficient locomotor organs, they being used much as we use our arms in swimming.

The arm of an ophiurid consists of a large number of segments, each of which contains a central calcarious ossicle. The calcarious ossicles of adjacent segments articulate with each other like the vertebræ of the spinal column, and are joined together by two pairs of muscles in such a manner that motion is possible in all directions. This mechanism is aided in producing the locomotion of the creature not only by the arm spines, where they are present, but by the foot tentacles. These latter organs, which are the homologues of the tube feet of other echinoderms, have been previously regarded as having given up their locomotor function entirely, but I shall show further on that this is not true in the genus *Ophiura*.

The experiments I carried on last summer on the movements of ophiurans resulted in little that is new, but on account of the confirmation my notes and photographs give to PREYERS' work (11) on the same subject, it has been thought advisable to publish them.

In the usual method of progression one arm precedes, it taking no other part, apparently, than to point out the way; the two arms adjacent to and behind the anterior arm make the stroke; the remaining arms are dragged behind, acting as a rudder.

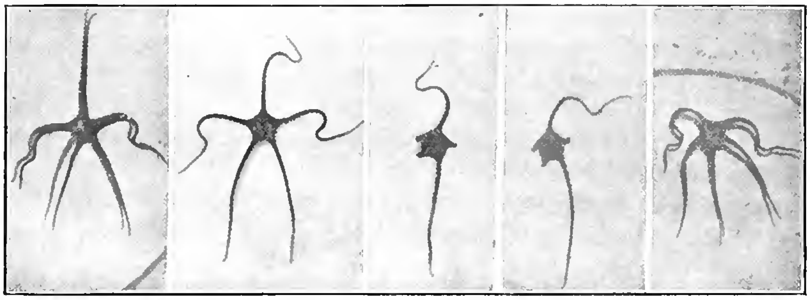


FIG. 1. FIG. 2. FIG. 3. FIG. 4. FIG. 5.

No preference as to which arm should precede could be found in an adult ophiuran, each arm being equally capable of going before, making the stroke, or following behind.

If greater speed is needed, for example, to get away from a strong stimulus, the arm which precedes may also take part in the stroke, its contractions being made simultaneously with those of the side arms. This added force, if produced repeatedly on one side, would soon change the course of progression, but this difficulty is overcome by an alternation of the stroke of the preceding arm, first on one side, then on the other (text fig. 2).

In a third method of normal locomotion the arms are arranged as is seen in text fig. 5, in which only one arm follows, acting as the rudder. This leaves two pairs of arms for the stroke, but the anterior pair is usually most vigorous in its contractions.

Since no physiological differentiation into anterior, posterior, or lateral parts is to be found in ophiurids, the creatures are under no necessity of turning the body when a change in the direction of progression is to be made. The arm which finds itself pointing in the new direction to be traveled takes the lead, although it may have been either lateral or posterior in position in the previous movements.

As has been mentioned before, the foot tentacles aid in making the strokes of the arms efficient in propelling the body. After a stroke has been made, while the arms are being drawn forward and extended for a new stroke, the tentacles can be seen moving actively about, but as the arms come to rest for the backward movement the tentacles are thrust down against the substratum and cease to move. The tentacles thus fit themselves into the inequalities of the surface and afford fixed points for the arms to pull against. The tentacles of the posterior arms act in the same way, and are efficient in preventing the force of the stroke being lost in side motion.

In ophiurans with long arm spines these latter structures may perform the function just described for the foot tentacles, but in the genus *Ophiura* the arm spines are very minute and closely applied to the sides of the arms.

It is interesting to note the wonderful coordination of locomotor movements immediately following the amputation of three of the arms. In this case if the nerve ring has been uninjured one of the remaining arms takes up the part of guiding and balancing, while the other strokes first on one side then on the other (text figs. 3 and 4).

When the central nerve ring is cut at any point the coordination in movement is impaired, and when cut in five places, between the arms, it is lost entirely.

When placed on its aboral surface an ophiuran quickly turns over. The method used is quite definite; two adjacent arms straighten out so that together they form a straight line. On these arms as an axis the body revolves, being pushed over by the three remaining arms, but mostly by the median one of the three.

EARLY STAGES.

The mature eggs are opaque and vary in color from an olive green to an orange yellow. Those of the same individual, however, are constant in their coloration. Until quite well developed the larvæ retain the color which was on the eggs at the time they were laid.

For echinoderms the eggs are very large, being 0.3 millimeter in diameter.

Soon after they are fertilized the eggs throw off two membranes, the first of which is much thicker than the second.

When first laid and during their early development the eggs float, but when their cilia are formed the larvæ are able to swim below the surface.

As I did not know that any special interest would be found in the life history of the species, I did not carefully observe the early stages while living, nor preserve material for future study, and as I have stated elsewhere, all later attempts to get other material were unsuccessful.

This makes it necessary to begin this paper with the description of a late gastrula in which the first pair of enterocœles have already begun to form as lateral pouches from the anterior free end of the archenteron (figs. 1–3).

Larvæ in this stage of development will be designated as "A."

STAGE "A," 36 HOURS OLD.

(Figures 1, 2, and 3.)

At the age of 36 hours the larvæ swim actively, they being uniformly covered with cilia (fig. 1).

The shape of the larvæ is an oval, the length being to the shorter diameter as 2 is to 1.

The animal or anterior pole is slightly more pointed than the posterior vegetative one. The ventral surface is distinguished by the presence of the blastopore, which latter has been pushed from its posterior position to a ventral one by the rapid growth of the ectoderm of the dorsal surface of the larva.

An apical plate of taller cells is present at the anterior end, but I could not see that the cilia at this point were any longer than those which cover the other parts of the larva (fig. 3, ap).

From the blastopore, through which its cavity opens to the exterior, a large archenteron projects forward into the blastocœle.

The remainder of the blastocœle, not taken up by the archenteron or its pouches, is filled with a close network of mesenchyme cells. This mesenchyme tissue is shown in fig. 3, mes, which is a longitudinal sagittal section of "A."

From the anterior free end of the archenteron a large pouch is in process of being cut off. This pouch projects to the right and left as horn-like processes, which latter are to be considered the rudiments of the right and left anterior enterocœles (fig. 2, aer and ael).

As to the method of gastrulation I can not at present speak from observation on larvæ in which it is just taking place, but from a study of the stage now under consideration some idea can be gotten as to how it has proceeded. In figs. 1 and 3 we see a cellular plug (cp) protruding from the blastopore and also extending far into the archenteric cavity. In some cases it extends even into the enterocœle pouch. The contour of this cellular mass is ragged, which is also true of both the outer and inner surfaces of the wall of the archenteron and the inner surface of the ectoderm.

These facts seem to indicate that gastrulation does not take place by invagination, as is usual in echinoderms, but that the larva before gastrulation is a solid, planula-like affair, and later the archenteron is formed by a splitting away of the central core. In the same way the plug of cells is probably formed by the hollowing out of the solid archenteron.

Beside their ragged outline the walls of the larva have another peculiarity in their structure, for, judging by the number and position of the nuclei, they are from two to three cells in thickness (fig. 3).

Cell walls are not distinguishable in any stage of development.

STAGE "B," 42 HOURS OLD.

(Figures 4 and 5.)

According to BURY (2) the hydrocœle does not have the same origin in all the groups of echinoderms. He found that it originates in the crinoids, sea-urchins, and starfishes from the left *anterior* enterocœle, but in the ophiurids it grows out from the anterior end of the left *posterior* enterocœle.

This observation, which BURY records with apparent hesitation, I can completely confirm, as will be seen in the description and figures of "B."

Externally the appearance is the same as in "A," but the internal structures have undergone a great change.

The anterior pouches, the cavities of which in "A" were connected both with each other and with the cavity of the archenteron, are now separate and distinct. The connection between these structures still continues, however, in their fused walls. The left pouch is a little larger than the right and lies behind and to the left of the latter (fig. 4, ael).

Just below the anterior pouches there is to be found a third pouch, which is growing out from the left side and anterior end of the archenteron (fig. 4, hy). It protrudes anteriorly and partially covers the two anterior enterocœles. The cavity of this pouch, which is the rudiment of the hydrocœle, is in wide communication with the archenteron.

From the wall forming the convex sides of the hydrocœle there are, even at this early stage in its formation, five outgrowths which are the beginnings of the radial canals of the adult ophiuran (fig. 4. 1, 2, 3, 4, and 5).

The whole hydrocœle is curving round to the right to encircle the œsophagus, which latter is making its first appearance in this stage as a shallow but definite pit in the central part of the ventral ectodermal wall (fig. 4, oe).

To avoid confusion the hydrocœle was spoken of above as arising from the archenteron, but, as will be seen in the transverse section (fig. 5), taken in a plane posterior to the origin of the hydrocœle, a differentiation is taking place in the archenteron which enables us to distinguish in it the rudiments of two structures, the posterior enterocœles and the stomach. By a longitudinal circular furrow the archenteron is being cut horizontally into a large ventral pouch, the posterior enterocœles (pe) and a smaller dorsal one, the stomach (s). This stomach rudiment bends around the posterior end of the posterior enterocœle and opens to the exterior through the blastopore (fig. 4).

It is from the left side and anterior end of the ventral pouch that the hydrocœle grows out, hence the confirmation of BURY's statement that it arises from the left posterior enterocœle in ophiurids.

In most echinoderms the posterior enterocœles originate as paired structures, and if the statements of BURY and MCBRIDE are correct, that the left posterior enterocœle of the larva forms the hypogastric body cavity of the adult, and the right posterior enterocœle goes to form the epigastric cœlom, then, according to this, the large ventral pouch, which I regard as the fused right and left posterior enterocœles, really represents the left only, because it takes no part in the formation of the epigastric body cavity of the adult ophiurid, but, with the left, does pass directly into the hypogastric.

The origin of the epigastric enterocœle is discussed in the description of Stage "C," in which its rudiment is first found over the stomach.

My reason for regarding the ventral pouch of "B" as the fused right and left posterior enterocœles, is that at the time of its origin it is symmetrically disposed on either side of the plane of larval bilateral symmetry.

Goto (5), too, has shown that the hypogastric enterocœle in the starfishes is not formed from the left alone, but in it are to be found the left and the greater part of the right posterior enterocœles.

The cellular plug of cells, which in "A" fills the archenteric cavity, becomes divided by the furrow which separates the archenteron into enterocœle and stomach and a part of it becomes inclosed in the cavities of each of these structures (fig. 5, cp).

Stage "C," 48 Hours Old.

(Figures 6, 7, and 8.)

The external form of the larva, which in this series of embryos is six hours older than "B," has been changed by the appearance of two lateral thickenings of the ectoderm a little posterior to the median transverse plane (fig. 6).

The blastopore, which in "B" was open to the exterior, has closed, leaving no trace of its former position.

The mouth and œsophagus, which existed in "B" only as a shallow ectodermal pit, now have the form of a deep, hollow tube (figs. 6 and 7, m and oe), which projects vertically inward until it passes through the hydrocœle and beyond the posterior enterocœle, when it curves back under the latter to fuse with the anterior wall of the stomach.

The stomach and posterior enterocœle are still in open communication, as in "B," but the furrow in "C" has deepened, and the process by which the two structures are being separated is almost complete (fig. 7).

Although the walls of the œsophagus and stomach are fused, their cavities are still separate.

This condition renders it easy to see just what part is played by the ectoderm in the formation of the alimentary canal, the entire œsophageal cavity being surrounded by ectoderm.

In "B" the hydrocœle communicates with the posterior enterocœle by a wide opening, and at the same point in "C" the two structures are still in communication, but the connection has been narrowed down to a small tube (fig. 7, hc).

Beside this connection with the posterior enterocœle, a second tube has been formed, joining the left anterior enterocœle with the hydrocœle (fig. 7, st). This new tube, which is the rudiment of the stone canal, enters the hydrocœle at the same point with the tube connecting the latter with the posterior enterocœle.

The left anterior enterocœle lies to the left of the œsophagus, and dorsal to the left half of the hydrocœle (figs. 6 and 7, ael).

It is to be noted that, although we now have a larva possessing both hydrocœle and stone canal, there has been as yet no pore canal formed. This is a marked reversal in the sequence of the formation of these structures from what might be expected from the order of their appearance in other known echinoderms, the pore canal arising usually before the formation of the hydrocœle, while the stone canal appears much later than either.

Returning to the hydrocœle, we find it a horseshoe-shaped structure astride the œsophagus (figs. 6 and 7, hy). The bulging areas which are to form the radial canals of the adult are much longer and more regular in size than in "B." The radial pouch, which lies to the right of the œsophagus and at the end of the right horn of the horseshoe, will hereafter be spoken of as radial canal 1, since it arises from that part of the hydrocœle which was first to bud out from the posterior enterocœle. The other radial canals, passing to the left over the œsophagus, will be designated as 2, 3, 4, and 5. Radial canal 5 lies in this stage over the opening of the stone canal.

The rotation of the hydrocœle around the œsophagus from its original left position, which was begun in "B," has continued to such an extent in "C" that half of it lies to the right of the median sagittal plane of the larva and half to the left. Radial canal 3 lies in this plane and points directly toward the anterior end of the larva (fig. 6).

With its rotation the hydrocœle also moves bodily toward the posterior end of the larva, carrying with it the œsophagus. The œsophagus, coming in contact with the anterior wall of the united posterior enterocœles, causes the latter to be pushed in at the point of contact. As the process continues, those parts of the posterior enterocœles lying on either side of this in-pushing area are forced to flow forward around the œsophagus and under the hydrocœle; thus we have the posterior enterocœles becoming horseshoe-shaped, the two horns of which lie under the horns of the hydrocœle (figs. 6 and 7, he and hy).

Lying dorsal to the stomach we find a small enterocœle which was not present in "B," or if present, not in this position. It is the rudiment of the body cavity, which in the adult lies aboral to the stomach and which has been recently appropriately termed the epigastric enterocœle (figs. 6 and 7, ee).

As to the origin of this structure I have no direct observations to give, but certain facts have led me to believe that it is formed from the right anterior enterocœle. These facts may be summed up as follows: In "B" no epigastric enterocœle exists, but the two anterior enterocœles (fig. 4, aer and ael) lie side by side anterior to the stomach and the posterior enterocœles. In "C" (figs. 6 and 7, ee) an epigastric pouch, equal in size to the right anterior enterocœle of "B" is to be found, but by the side of the œsophagus only the left anterior enterocœle remains (figs. 6 and 7, ael).

During the six hours which intervene between "B" and "C" it seems hardly possible that a complete formation of the epigastric enterocœle should have taken place or that there should have been time for the complete degeneration and disappearance of the right anterior pouch; sufficient time may have elapsed, however, for the migration of the right anterior enterocœle to a position behind the stomach.

Against such an interpretation as the above there is the fact that in no other case has the epigastric enterocœle been observed to take its origin from the right anterior pouch. It has been described as arising from the right *posterior* enterocœle, however, as has been referred to before, in all the groups by BURY, and his observations have been corroborated by both MCBRIDE and GOTO in the starfishes.

STAGE "D," 60 HOURS OLD.

(Figures 9–14.)

The changes which have taken place in "C" to produce "D" are very marked.

The cilia have disappeared, except in four transverse rings or bands, three of which extend entirely around the body of the larva. The third ring, counting from the anterior end, is interrupted by the aboral disk on the ventral surface.

This third ciliated ring first appears on the lateral bulges, which were described in "C," and the fourth ring appears on a second pair of lateral bulges which originate behind the first pair near the posterior end of the larva.

The shape of the larva is no longer oval, but the posterior end has widened laterally and become somewhat dorso ventrally compressed (fig. 9). The anterior end has not changed in shape and may be thought of as forming the handle of the now club-shaped larva.

The enlarged posterior end of the larva contains all its organs and is the part which will enter directly into the formation of the adult ophiurid.

From its homology with the preoral lobe and larval organ of *Asterina gibbosa* I have called the anterior end of the larva the larval organ. It disappears with the metamorphosis into the adult form.

The larval organ is also homologous with the stalk of the Antedon larva, although in the ophiurid larva it never functions as an attachment organ. When swimming, the larval organ precedes. It is filled with a network of mesenchyme cells (fig. 11, mes).

Internally the changes have been even greater than the external ones we have just considered, for it is during this period of development that the rotation and readjustment of organs takes place, which is present in all echinoderms at some stage of their development.

The hydrocœle, which has begun its rotation about the œsophagus as an axis in "C," has completed it in "D" and reached its definite position.

That part of the hydrocœle which in "C" was situated on the left of the plane dividing the larva into bilaterally symmetrical halves, now lies on the right side of the same plane and vice versa. (Compare figs. 6 and 9.)

A revolution of 180° has taken place in the hydrocœle since "C," to which if the 180° of rotation be added, which took place up to the time of "C," we have a total rotation of 360° in the hydrocœle. Radial pouch 1, finally, after having passed around the œsophagus, comes to rest at the point where it originated. Radial pouch 5, it will be noted, is carried only half as far as radial pouch 1, or from its point of origin on the left to a point opposite on the right of the œsophagus. (Compare figs. 6 and 9, (1) and (5).)

This great amount of rotation seemed so peculiar that I hesitated for some time to believe it, and was led to suppose instead that while the hydrocœle moved to the right the other organs lying above it rotated an equal amount to the left.

The early closure of the blastopore and the central position of the mouth in the early stages make such a view as the latter seem possible, and as it may suggest itself to those who study figs. 6 and 7, I will give below the points which seem to me, directly or indirectly, to prove that the hydrocœle revolves under the enterocœles and stomach, rather than that the latter twist over the hydrocœle:

(*a*) The ectodermal bulges, nearer the posterior end in "C" (fig. 6), are the same as those nearer the posterior end of "D" (fig. 9), on which the third ciliated band is situated.

(*b*) If the latter view is the correct one then radial canal 3 points toward the same end of the larva in both "C" and "D" (figs. 6 and 9), but in "C" the end toward which it points is anteriorly directed in swimming and in "D" it points away from the end which precedes. It is hardly thinkable that in any stage in its development the anterior end of a larva should change its physiological function and become the posterior end.

(*c*) By any other view than the one I have adopted the blastopore, or the point where it existed before closing, would be anterior and the larval organ posterior in position. In all known echinoderm larvæ, however, the blastopore marks the posterior end, and in all cases where it occurs the larval organ originates from the anterior end of the larvæ.

(*d*) It may be recalled, also, that in the readjustment of parts which takes place during the metamorphosis of other echinoderm larvæ the rotation is almost entirely confined to the hydrocœle.

As the hydrocœle passes around the œsophagus the tube connecting it with the left horn of the hypogastric enterocœle becomes broken and the left anterior enterocœle, together with the tube connecting it with the left horn of the hydrocœle, are carried anteriorly around the œsophagus (fig. 9, ael and st). In "D," then, we find the stone canal on the right side of a line dividing the larva into symmetrical halves, instead of to the left of the same line as it is in "C." (Compare figs. 6 and 7 with 9.) The anterior enterocœle comes to rest immediately in front of the stomach and œsophagus.

From the point where the stone canal enters the anterior enterocœle the pore canal grows out, passes dorsally to the ectoderm, with which latter its walls fuse, and an opening the water pore (figs. 9 and 11, pc.) breaks through. Thus in this stage the cœlom and hydrocœle are first connected with the exterior.

In "C" the circular water-canal had not closed, but existed in the form of a horseshoe, the concave side of which opened posteriorly, but as the rotation of the hydrocœle takes place its horns grow toward each other until they meet. A fusion of their walls then takes place at the point of contact and a complete ring is thus formed. The part of the ring canal, the formation of which has just been described, lies between radial canals 1 and 5 in fig. 9. The opening of the stone canal into the water ring is situated in "C" at the base of radial canal 5, but by means of the rotation of the hydrocœle about the œsophagus, together with the growth of the ends of the horseshoe, this opening is carried away from its position at the base of radial canal 5 toward radial canal 1. It always remains, however, nearer the former than the latter; in other words, it comes to lie definitively in the *right adradius* between radial canals 5 and 1. (Compare figs. 6 and 9.)

The radial canals, which existed in "C" as simple pouches from the convex side of the hydrocœle, have in "D" each become three-lobed. Near the tip and from the sides of each canal a pair of pouches has budded out, each of which is about equal in size to the end of the canal which lies between and beyond them (fig. 9, et and tl). In these three structures we have the rudiments of the end tentacle and the first pair of foot tentacles of the ophiurid arm.

When we were last considering the hypogastric enterocœle it was in the form of a crescent, the horns of which were very short and its central part very wide. Into its concavity, which was anteriorly directed, the œsophagus fitted. The horns of this enterocœle, beginning in "C" to grow over the hydrocœle, continue the process during the rotation of the latter, the horns of the crescent growing at the expense of the thickness of its central part, and in "D" we have this enterocœle lying directly over the hydrocœle in the form of a perfect horseshoe (fig. 9, he).

Between the ends of the horns of the hypogastric cœlom lies the anterior enterocœle. The walls of these structures come together and fuse in such a way that they together form a hollow circular cœlom surrounding the stomach and lying over the somewhat smaller water vascular ring (fig. 9).

In the four interradii, marked by their positions between radial canals 1 and 2, 2 and 3, 3 and 4, and 4 and 5, four pouches of the hypogastric enterocœle grow downward, outside the water vascular ring, forcing themselves between the radial canals; a fifth pouch, similar to those just described, is formed from the left anterior enterocœle in the remaining interradius between radial canals 5 and 1 (figs. 9, 12, 13, and 14, hip 1–2, 2–3, 3–4, 4–5, and ipax 5–1). These five pouches are the rudiments of the *outer* perihæmal ring, which will be more fully considered in the succeeding stages.

The stomach, after being entirely cut off from the hypogastric enterocœle, was drawn forward during the rotation of the hydrocœle, and the œsophagus was carried in the opposite direction, so that in "D" the stomach lies almost directly over the œsophagus (figs. 8 and 13, oe and s). The partition, which in "C" separated the cavities of these two structures, has disappeared in "D," and the œsophageal cavity opens into that of the stomach. There is present, then, in "D" the definitive alimentary canal of the adult ophiurid.

The "cellular mass," which in "B" and "C" was being divided into two parts by the constriction separating the archenteron into enterocœle and stomach, is to be found, in sections of "D," in the cavities of both the above structures (figs. 11, 12, 13, and 14 cp).

Lying immediately above, or aboral to, the stomach is to be found the epigastric enterocœle. It has enlarged considerably during the interval between "C" and "D," but is not yet of sufficient size for its walls to touch those of the hypogastric cœlom, and hence in this stage no circular aboral mesentery is to be found.

STAGE "E," 66 HOURS OLD.

(Figures 15–21.)

The thickening of the ventral ectoderm which was begun in "D" has continued during the six hours which intervene between "D" and "E" and has spread to the sides of the larva (figs. 15 and 19–21).

Near the edge of this thickened oral disk are to be found five groups of rounded elevations of the ectoderm (fig. 15, I, II, III, IV, and V). The three elevations, of which each group consists, form the angles of an isosceles triangle the apex of which points away from the mouth of the larva (fig. 15). These elevations or evaginated papillæ lie immediately below and inclose the tips of those branches of the radial water canals which form the rudiments of the end tentacle and first pair of foot tentacles of each arm (figs. 19 and 21). In this way each tentacle grows into its ectoderm, the latter closing around it as it pushes out.

The function of these tentacles in the adult being mainly a sensory one, it is interesting to note that they receive their ectoderm from part of the same thickened oral area which gives rise later to the adult nervous system.

The ciliated bands in "E" do not differ in appearance and position from those in "D," but since they were not figured in the earlier stage it may be well to refer to them again in connection with figs. 15 and 16, cb 1, 2, 3, and 4. The first or most anterior band surrounds the larval organ quite near its tip.

Near the first band, and parallel to it, runs the second one also around the larval organ. The third ciliated band is separated from the second by a much wider space than that which separates the first and second bands. Were it not interrupted on the oral disk the third ciliated band would lie in the line separating the bivium and trivium—that is, between arms I and II on the one side and IV and V on the other. The fourth band, passing just posterior to the group of ectodermal elevations lying under the branches of the third radial water tube, surrounds the posterior end of the larva.

In "E" the cavities of the œsophagus and stomach have become obliterated, and the two structures appear in section as one solid mass of cells (fig. 20, st and oe). No degeneration in their size, however, is to be observed, and their outer walls remain well defined, the œsophagus retaining its connection with the ectoderm. As will be seen later, their lumen reappear and they become the definitive alimentary organs of the adult ophiurid.

Returning to the consideration of the water system, we find in "E" instead of one pair of tentacles on each radial canal, as in "D," there are two pairs present (fig. 17, t1 and t2), the second pair having grown out of the radial canal between the first pair and the water ring. The second pair is much smaller than those which were first to be formed, and, contrary to what one would expect, this discrepancy in size does not disappear as time goes on. This is also true in the sea-urchins, in which the primary tube feet in the larva are enormously larger than those which are subsequently formed. The primary tube feet in this case gradually diminish in size after the adult form is reached.

As a rule, among echinoderms the tube feet or tentacles are formed *centrifugally* from the radial canals; that is, between the end tentacle and the last pair of tube feet or tentacles already formed. This process keeps the undifferentiated growing point of each arm at its tip, but in this ophiuran, and the same is true of Antedon, the formation of the tentacles *begins* in a centripetal manner; that is, the second pair of tentacles appears, not between the end tentacle and the first pair, but between the first pair and the ring canal.

This second pair of tentacles is the rudiment of the buccal tentacles, and although differing in both function and position in the adult from that of the foot tentacles, is nevertheless entirely homologous with the latter. This homology is shown by their origin and the fact that for a time after forming they are directed away from the mouth toward the end of the arm just as is the case with the foot tentacles. After a time, however, as will be seen later, they turn back and point toward the mouth, thus showing that in this second pair of outgrowths from the radial canals we have to do with the first pair of buccal tentacles of the adult. After budding, as we see, from the radial canals, they migrate to a position on the ring canal, with which we find them connected in the adult.

In "E" the buccal tentacles have no ectoderm nor rudiment of such, the ectoderm under their tips being as yet undifferentiated from the oral disk.

The hypogastric enterocœle has assumed a more pentagonal shape than in "D," it having grown out over the radial water canals (fig. 17, he). These projections of the hypogastric enterocœle will continue to grow with the growth of the arms and become the brachial extensions of the body cœlom.

The interradial pouches of the hypogastric enterocœle, which were beginning to form in "D," have pushed down further and further between the radial canals until, coming in contact with the ventral ectoderm, they bend over, inserting themselves between the ring canal and the oral disk (figs. 17–21, hip 1–2, 2–3, 3–4, and 4–5). In the same way the pouch from the anterior enterocœle in the stone canal interradius has grown under the water ring. In these five interradial enterocœlic outgrowths, as has been mentioned before, we have the rudiments of the outer perihæmal sinus of the adult. The process by which this perihæmal sinus is formed in *Ophiura brevispina* agrees in every detail with its method of origin in *Asterina gibbosa* as described by McBride (10).

The epigastric enterocœle is in much the same condition as that in which we left it in "D," it being as yet too small to meet and form a mesentery with the dorsal edges of the hypogastric cœlom (fig. 19, ee).

The stone and pore canals, too, have changed very little during the interval between "D" and "E." From the ring canal at a point to the left of the origin of radial canal 1 the stone canal passes upward and opens into the right postero-dorsal part of the anterior enterocœle. The pore canal begins at the same point where the stone canal ends, the two canals thus having a common opening into the anterior enterocœle or ampullæ. The pore canal extends from the enterocœle to the dorsal surface of the larva, where it empties through the dorsal pore at a point a little to the right of the median sagittal plane. These two canals, although extending in the same direction, do not lie in the same straight line, the pore canal being set a little anterior to and to the right of the stone canal (figs. 17, 18, and 21, st and pc; also fig. 11).

STAGE "F," 5 DAYS OLD.

(Figures 22–30.)

Although "F" is separated from the stage last described by a considerable space of time, the changes in the larva which have been brought about are easy to follow.

The larva is considerably larger than in "E," and has reached its full development. From this time on the larval organ gradually degenerates and is finally completely absorbed by the developing star (Compare figs. 22 and 31 lo.)

The external form of the larva has been changed by the appearance of a number of elevations and depressions in its outer surface, the ciliated bands being elevated upon circular ridges (fig. 22, cb 1, 2, 3, and 4), while at points on the sides of the disk beyond the end tentacles projections in the ectoderm have made their appearance, these being the rudiments of the ophiuran arms (fig. 22, I, II, III, IV, and V).

The larval organ is cylindrical, but the disk has continued its dorso-ventral flattening. (Compare figs. 22 and 26.)

The first and second ciliated bands are situated in the same places as in "E." The third, while retaining its old position, has grown in upon the ventral disk toward the mouth (fig. 22, cb 3). On the ventral side of the larva the fourth band has shifted from its old position behind the third radial canal to one on the interradii between arms II and III and III and IV. It has also become interrupted on the oral disk in a manner similar to the third ciliated band (fig. 22, cb 4).

The depressions before referred to are caused by the invagination of the nervous system, which structure has been forming since "D" in the thickened oral disk of ectoderm. Immediately below the water ring and radial water canals the thickening has increased more rapidly than at other points, thus producing a ring-shaped internal ridge, from which extend five radial thickened ridges. These rudiments of the nerve ring and radial nerves bulge inwardly, no evidence of their presence being apparent on the outside. When the thickening process has been completed the whole nervous system gradually sinks in, leaving a circular groove from which five radial grooves pass out. This is the stage in the formation of the nervous system which has been reached in "F" (fig. 22, eg and rg). The invagination process begins at the ends of the radial nerves, just inside of the curved tips of the end tentacles, the nerve ring being invaginated last of all. (Compare figs. 23–27.) As development goes on the edges of the grooves gradually close over the nerves, the closure taking place in the same order as the invagination proceeded—that is, first over the ends of the radial nerves, then finally, after gradually traveling up the radial nerves, closing over the nerve ring.

By the meeting and subsequent fusion of the edges of the grooves, part of their cavity becomes cut off from the exterior and is left below the nervous system as the subneural space. But this will be referred to again in an older larva, in which the process of its formation is more nearly completed, it having begun in a few only of the most advanced larvæ of Stage "F."

The nervous system shows a differentiation into two distinct layers, a fibrous one nearest the water system and a cellular layer lying below the fibers (figs. 23–29). The nuclei of the cellular layer are oval, with their long diameter perpendicular to the fibrous layer.

Above the nervous system, separating it from the water system, is to be found the outer perihæmal space (figs. 23–30, opr). Recalling the condition of the perihæmal system in Stage "E," we see that the ends of the interradial projections from the hypogastric and anterior enterocœles have grown out over the nervous system, spreading in both directions until the outgrowths of each interradial pouch meet those of its adjacent fellows in the radii over the origins of the radial nerves; here the ends of the pouches fuse, and together they grow out over the radial nerves as the radial perihæmal sinuses.

In the starfishes, where the formation of this perihæmal system has been observed, it is said that no fusion takes place between the diverticula of the interradial pouches of the hypogastric and anterior enterocœles when they meet in the radii, but that a mesentery is formed at the points where the diverticula come in contact. This mesentery is described as continuing to the end of the arms, separating the radial spaces into two parallel cavities.

Nowhere could I find such a mesentery in sections of the larvæ of *O. brevispina*, nor could I feel sure that it exists in the adult ophiuran.

McBride (10) and Goto (5) both agree that in starfishes the *inner* perihæmal ring sinus arises from the anterior enterocœle, although they differ as to the method of its formation. In none of the larvæ I have is the structure in question fully formed, but in Stage "F" a cavity is arising, as an outgrowth from the anterior enterocœle in the stone canal interradius, which I take to be the rudiment of the inner perihæmal ring space. It lies to the left of the stone canal near the median sagittal plane of the larva. From the posterior side of the ventral end of the anterior enterocœle the outgrowth takes its origin, then extending posteriorly until past the water ring it bends over and grows down until its end reaches the nerve ring at a point inside the outer perihæmal sinus. Here the end of the pouch in question begins to spread under the nerve ring in both directions, parallel to the outer perihæmal ring (figs. 24 and 26, ips). This coincides exactly with its method of origin in *Asterina gibbosa* as described by McBride.

Although the outer perihæmal ring is entirely cut off from the body cavities at this stage, there still remain traces of the interradial pouches which gave rise to it (fig. 29, hip 1-2 and 4-5).

The hypogastric enterocœle itself has changed very little since Stage "E," but the epigastric has enlarged to such an extent that its edges now meet the edges of the hypogastric and a circular aboral mesentery is formed (figs. 23-29, cm).

In the water system considerable growth is to be noted in the tentacles, the end and first pair of foot tentacles being capable of protrusion considerably beyond the disk. By means of these tentacles the larvæ are able to cling tenaciously to the surfaces of foreign bodies, it requiring a strong jet of water from a pipette to detach them. Special notice was taken to be sure that it was the tentacles and not the larval organ which was used as a means of attachment.

The second pair of tentacles (buccal tentacles) have acquired their ectoderm in this stage and they protrude, like the other tentacles, over the radial nerves into the radial grooves (figs. 22 and 26, t 2).

The axial sinus or ampulla is present in "F," it being that part of the anterior enterocœle which remains after the pouches have been cut off, which will form the inner perihæmal and part of the outer perihæmal systems (figs. 24, 25, and 26, ax sin).

It will be noted that beside the ampulla, which is situated anteriorly to the stone canal, there are two other cavities near the stone canal to be accounted for (fig. 26, sin a and sin b). I can not be sure of their origin, but I believe that they also come from the anterior enterocœle. I have distinguished them by the letters a and b, as they are probably the same cavities as those so lettered by McBride (10) in his figures of Amphiura.

The cavity McBride has lettered b′, and which he thinks represents the degenerated *right* hydrocœle, I have been unable to find in any of my sections.

The stomach and œsophagus are in a condition the same as we found them in "E;" that is, without lumen.

Stage "G," 5½ Days Old.

(Figures 31 and 32.)

Larvæ a few hours older than "F" show a decided degeneration in the larval organ (fig. 31, lo), but otherwise the external appearance of the two stages is about the same.

The grooves caused by the invagination of the nervous system have begun to disappear by the growing together of their edges, and instead of the deep furrows we find a slightly depressed line where the edges of the grooves have met (fig. 28, rg).

In the nervous system a pair of tentacle nerves has been formed from each radial nerve (fig. 31, nl). They grow out laterally from the radial nerves at points proximal to the first pair of foot tentacles, around which latter they grow and to which they belong. No nerves as yet have appeared to supply the buccal tentacles.

In "F" the buccal tentacles had only begun to curve away from the end of the arm; but in "G" this proximal bending has continued until they curve over the nerve ring and point toward the mouth.

Beside this change in the water vascular system we find in "G" the first appearance of the rudiments of the polian vesicles. They are four in number and are in the form of small interradial pouches growing distally from the convex wall of the water ring (figs. 31 and 32, pv). There is no polian vesicle present in this species in the stone canal interradius.

As no perceptible change has taken place since "F" in the organs not referred to above, the description of them given in the previous chapter will serve equally as well for "G" as for "F," and the figures of these organs in "G" may be examined in connection with their description in "F."

STAGE "H," 8 DAYS OLD.

(Figures 33 and 34.)

In the oldest larvæ I have, the metamorphosis has been almost completed. The larval organ has nearly disappeared, that part of it which yet remains being found sticking to the edge of the aboral disk of the young pentagonal star.

When living the little ophiurids clung to the bottom and sides of the aquaria dishes. Although the ciliated bands were still evident on the disk their free swimming habits had been wholly given up.

The pore canal still opens on the aboral surface, but with the growth of the latter it is traveling toward the edge of the disk, and by a continuation of this process the oral surface will ultimately be reached.

As the closure of the grooves over the nervous system took place, circular areas below the tips of the tentacles were left open, the tentacle pores, and through these the tentacles, were able to protrude and withdraw themselves.

The subneural sinuses which had begun to be formed in "F" have been completed in the eight-day larva (figs. 31 and 34 ss). In "H," then, the nervous system is cushioned below by the subneural sinus and above by the outer perihæmal ring.

The stomach, which for so long a period has been at a standstill in its development, has begun to grow, its sides pushing out between the epigastric and hypogastric body cavities. The lumen of both stomach and œsophagus have reappeared (fig. 34 s). The glandular structure which makes the walls of the stomach so complicated in the adult has not begun to form in "H," the walls being simple and one cell in thickness.

No figure of "H" as a whole object has been made for the reason that the skeletal plates should be included, and material adequate to a complete study of them is at present not in my possession.

RELATION OF LARVA TO ADULT.

The hydrocœle is the first organ to show radial symmetry in the developing larva of *Ophiura brevispina*, and from the time when this organ has completed its rotation about the œsophagus it shows a definite relation to the plane of bilateral symmetry of the larva.

The hydrocœle is not only radially symmetrical, but bilaterally symmetrical, since it is divided into symmetrical halves by the plane which passes through radial canal 3 and through the interradius of the stone canal. This plane coincides with the plane of bilateral symmetry of the larva. The other parts of the star are built about the water vascular system; hence it, as a whole, bears a similar relation to the larva as was initiated by the hydrocœle.

No secondary twisting of the various parts of the star occurs, and its relation to the larva remains constant as it began, and throughout the life history of the species the following statements hold true: Ventral and dorsal in the larva are equivalent to oral and aboral in the adult. Although no physiological differentiation exists, if we regard that part of the adult as anterior which was anteriorly directed in the free swimming larva, the trivium is anterior, the bivium is posterior.

In the foregoing I have confirmed, in an ophiurid, the conclusions drawn by GOTO from his studies on a starfish. In his work on the development of *Asterias pallida* GOTO (5) thought he was able to prove the coincidence of bilateral symmetry, which obtains in the adult starfish, with the plane of bilateral symmetry of the bipinnarian and brachiolarian larvæ.

The study of the relation of larva to adult in the starfishes is made most difficult, however, by the independent origin and subsequent twisting of the parts of the star. At the time of their origin no two parts of the star bear the same relation to the larva. The relation of each part to the larva also changes as metamorphosis proceeds.

The facts just enumerated admit of other conclusions than those deduced by GOTO, and no two investigators have reached the same conclusion. The point of view from which the subject has been approached is not the same in all cases, but the results obtained by those who have studied the question admit of being reduced to the same basis; that is, the relation of the planes of bilateral symmetry in larva and adult.

Cuénot (4) in his latest work denies the existence of any known relation between them.

Semon (13), working on a holothurian, found the two planes in question to coincide, but his conclusion is based on the supposition that the dorsal mesentery of the adult is the same as that of the auricularia larva, which supposition Bury has since shown to be incorrect.

Bury (3), after working on members of all the groups of echinoderms, concluded that the plane of bilateral symmetry of the larval form coincides not with the plane dividing the adult form into two symmetrical halves, but with the plane of radial symmetry.

McBride's (10) observation on a starfish, *Asterina gibbosa*, led him to adopt about the same view as that of Bury. He found that the plane of radial symmetry of the star makes an angle of 70° plus with the frontal plane of the larva, but may, without error, be considered as 90°. This is equivalent to saying that the plane of radial symmetry of the star is parallel with the sagittal plane or the plane of bilateral symmetry of the larva, and is also reducible to the statement that the planes of bilateral symmetry of the larva and adult are at right angles to one another. Thus right and left in the larva become aboral and oral in the adult.

The difference in results arrived at by Goto and McBride are due almost wholly to the stages in the metamorphosis selected in each case for the study of the question, Goto selecting a very late stage, when the larval body had all but disappeared, while the stage chosen by McBride is an early one, in which the rudiments of the star are just appearing.

If the five groups of echinoderms have sprung from a common stem after radial symmetry had been established, then in the metamorphosis which is found in all the groups there should be discoverable a unity of relation between larva and adult. It is hard to conceive of the radial symmetry of echinoderms as having been independently acquired by each group, although it is easy to see how secondary changes may have arisen in the metamorphosis since the groups separated.

The five groups of echinoderms stand isolated from one another almost as completely as does the echinoderm phylum from the other phyla of the animal kingdom, and it is not my intention at this time to enter into a discussion of the interrelationships of echinoderms. I wish, however, to point out an interesting series of facts presented by members of the Asterid, Crinoid, and Ophiurid groups which may have a bearing upon the subject, and in the same connection I wish to call attention to how well McBride's hypothetical ancestor of the Asterids and Crinoids (10, fig. —), when details are not too closely compared, fits into the facts of the larva of *Ophiura brevispina*.

In one of the Asterids Goto has shown that toward the end of metamorphosis the almost complete star sits as a cap at the posterior end of the larva, with its aboral end posterior, its oral surface anterior, the bivium dorsal, and the trivium ventral.

In Antedon, like the starfish, the rotation brings the developing crinoid head to the posterior end of the larva, but differing diametrically from the starfish in that the oral instead of the aboral surface of the crinoid is posterior; but this difference does not in any way affect the homologies between the two groups as has been supposed.

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COMPARISON OF THE LARVA OF ANTEDON ROSACEA WITH THAT OF OPHIURA BREVISPINA.

While I was studying the larva of *Ophiura brevispina*, characters were constantly being found which reminded me of the larva of Antedon as described by Bury (1). Some of these points of resemblance are no doubt only superficial, but others are such as to make it worth the while to devote a short chapter to the similarities of the two larvæ.

The entire ciliation of the very young larvæ gives place in both to a series of transverse ciliated bands, five in Antedon, four in Ophiura. The band nearest the anterior end of the Antedon larva, however, is small and incomplete. Two bands only in each case surround that part of the larva from which the disk is formed.

The blastopore in both larvæ, after shifting from a posterior position to one on the ventral surface, closes and the archenteron loses its connection with the ectoderm and lies free in the body cavity.

In the seven-day embryo of Antedon and Stage "C" of Ophiura the hydrocœle is a horseshoe-shaped structure lying in the posterior ventral part of the larvæ with the open end directed anteriorly, and in each case the plane of radial symmetry of the hydrocœle is at right angles to the plane of bilateral symmetry of the larvæ.

In the formation of the paired tentacles from the radial water canals the process is *begun* centripetally in both larvæ, the second pair of tentacles appearing between the first pair and the water ring instead of between the first pair and the end tentacle, as is the case in the other groups of echinoderms.

In the five-day Antedon larva and those stages represented by "D" to "F" in Ophiura the stalk and larval organ are strikingly similar, both in shape and position, the two structures being anteriorly directed in swimming.

The stem of the Antedon larva, as a result of metamorphosis, comes to be an aboral structure, and just before the disappearance of the larval organ from the ophiuran larva it is to be found as a small knob, not in the *center* of the aboral disk, it is true, but on its edge. In the starfishes it may be recalled that the preoral lobe disappears on the *oral* surface of the metamorphosing star.

To the above larval characteristics may be added the similarity which exists in the disposition of the alimentary and cœlomic systems in the adult forms.

In both Crinoids and Ophiurans the digestive apparatus is confined to the disk.

The body cavity is continued into and to the ends of the arms. When a transverse section of a pinnule of Antedon is compared with a transverse section of an ophiurid arm, the following striking correspondence is found in the parts: Aborally, segmentally arranged calcarious ossicles and muscles are present; a continuation of the body cœlom runs between and oral to the muscles; connected with and on each side of this central brachial body cavity are two other cavities, the subtentacular canals of Antedon. These latter in the Ophiurans are connected with perihæmal space in each vertebral segment.

The radial water tube lies between the subtentacular canals, and in each segment sends out a pair of tentacles. The tentacles in both the Crinoids and Ophiurids are devoid of the terminal suckers, which are so characteristic of the other echinoderms.

Separating the radial water tube from the nerve cord is to be found the radial perihæmal sinus.

In ophiurans a subneural space is present which is not represented in the crinoid arm. This is due to the fact that in Antedon the nervous system is superficial, while in Ophiura it has been invaginated, and with its invagination a space has also been carried in below it.

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EXPLANATION OF PLATES.

The figures illustrating this paper were drawn to the same scale of magnification, 330 diameters, and were reduced one-half in reproduction.

Figs. 1, 2, 4, 6, 7, 9, 17, 31, and 32 were reconstructed from series of transverse and sagittal sections.

In all cases the part of the figure which is nearest the top of the plate is either anterior or else ventral in the larva.

ABBREVIATIONS USED.

ael	Left anterior enterocœle.
aer	Right anterior enterocœle.
ap	Apical plate.
ax sin	Axial Sinus.
b	Blastopore.
cb 1, 2, 3, and 4	Ciliated bands.
cg	Circular groove.
cm	Circular mesentery.
cp	Cellular plug.
d	Dorsal pore.
ee	Epigastric enterocœle.
et	End tentacle.
hc	Canal connecting posterior enterocœle and hydrocœle.
he	Hypogastric enterocœle.
hip 1–2, 2–3, 3–4, 4–5	Interradial pouches of the hypogastric enterocœle.
hy	Hydrocœle.
ips	Inner perihæmal sinus.
ipax 5 1	Interradial pouch of axial sinus.
lo	Larval organ.
m	Mouth.
mes	Mesenchyme.
n1	First pair tentacle nerves.
nr	Nerve ring.
oe	Œsophagus.
od	Oral disk.
opr	Outer perihæmal ring.
pc	Pore canal.
pe	Posterior enterocœles.
pv	Polian vesicle.
rad n	Radial nerves.
rg	Radial grooves.
rps	Radial perihæmal space.
sin a	Sinus "a".
sin b	Sinus "b".
st	Stone canal.
ss	Subneural sinus.
s	Stomach.
t1	First pair foot tentacles.
t2	Buccal tentacles.
wvr	Water vascular ring.
I, II, III, IV, V	Arm rudiments.
1, 2, 3, 4, 5	Radial water canals.

PLATE I.

FIG. 1. Larva in Stage "A," seen from the right side, the right half of the ectoderm removed and the mesenchyme omitted.
FIG. 2. The same larva, seen from the ventral side as a transparent object.
FIG. 3. Median longitudinal section of a larva in Stage "A."
FIG. 4. A larva in Stage "B," viewed from the ventral side as a transparent object.
FIG. 5. Transverse section of a larva in Stage "B" in a plane halfway between the blastopore and the point where the hydrocœle is connected with the archenteron.
FIG. 6. Larva in Stage "C," seen from the ventral side, the ventral half of the ectoderm, the mesenchyme, and part of the œsophagus removed.
FIG. 7. The left half of the same larva.
FIG. 8. Transverse section through Stage "C" in a plane indicated on fig. 6 by the letters *a–b*.
FIG. 9. The reconstructed internal anatomy of a larva in Stage "D," the ventral ectoderm removed and with it part of the œsophagus.
FIG. 10. An outline drawing of fig. 9, on which are indicated by lines the planes of the sections which follow in figures 11, 12, 13, and 14.
FIG. 11. Longitudinal section taken through a larva in Stage "D" in the plane indicated on fig. 10 by the line *m–n*.
FIGS. 12, 13, and fig. 14 of Plate II. Transverse sections taken through Stage "D" in planes indicated on fig. 10 by the lines *a–b*, *c–d*, and *e–f*.

PLATE II.

FIG. 15. Ventral view of a larva in Stage "E," to show ciliated bands and first appearance of the arm rudiments.
FIG. 16. Dorsal view of Stage "E," showing the ciliated bands.
FIG. 17. A reconstruction of the anatomy of a larva in stage "E," the ventral ectoderm removed.
FIG. 18. An outline drawing of fig. 17, on which are indicated by lines the planes of the sections shown in figs. 19, 20, and 21.
FIGS. 19, 20, and 21. Transverse sections taken through larva in Stage "E" in planes indicated on fig. 18 by the lines *r–s*, *t–u*, and *v–w*.
FIG. 31. Reconstruction of the anatomy of a larva in Stage "G." In this case as in all the other reconstructions the ventral surface is up and the ventral ectoderm removed.
FIG. 32. An outline drawing of the water vascular system of a larva in Stage "G," seen from the ventral surface.
FIG. 33. Transverse section of Stage "H," taken through the region of the stone canal.
FIG. 34. Transverse section of a larva in Stage "H," taken through the stomach.

PLATE III.

FIG. 22. Ventral view of the fully developed larva before metamorphosis has begun. Stage "F."
FIG. 23. Outline drawing of fig. 22. The lines indicate the planes of the sections, which have been drawn to show the anatomy of a larva in Stage "F."
FIGS. 24, 25, 26, and 27. Longitudinal sections of a larva in Stage "F," the planes of which are indicated on fig. 23 by the lines *a–b*, *c–d*, *m–n*, and *x–y*.
FIGS. 28, 29, and 30. Transverse sections of a larva in Stage "F," the planes of which are indicated on fig. 23 by the lines *c–o*, *d–o* and *e–o*.

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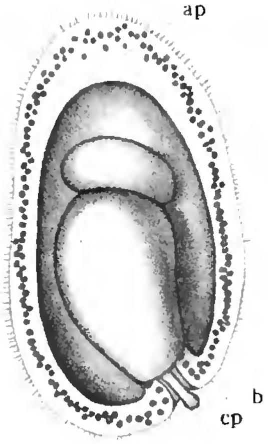


Fig. 1.

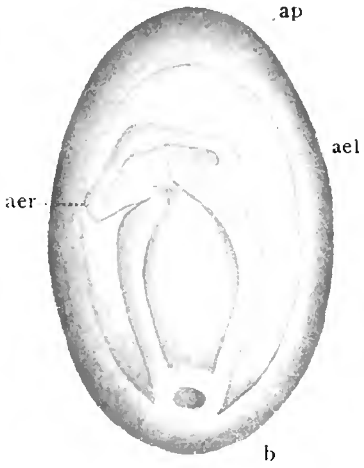


Fig. 2.

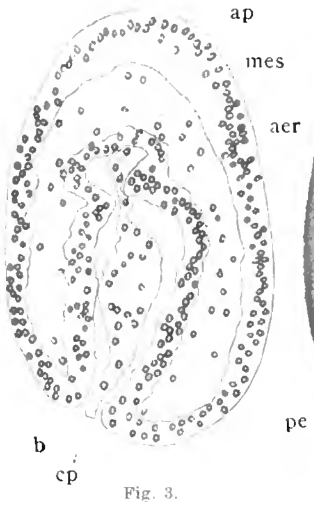
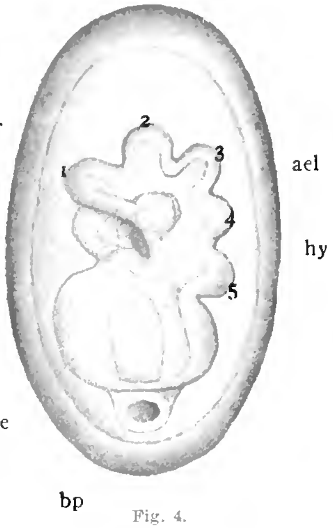


Fig. 3.



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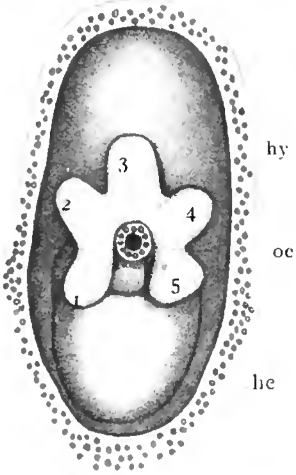


Fig. 6.

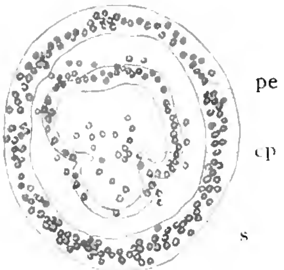
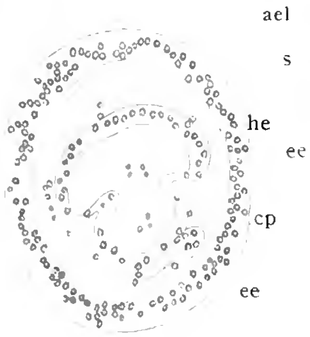


Fig. 5.



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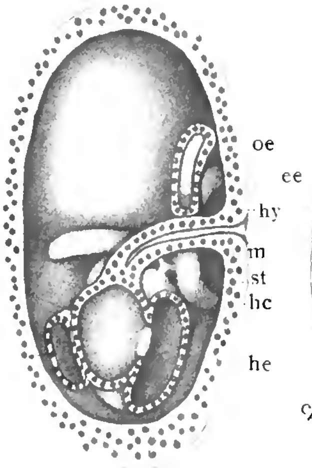

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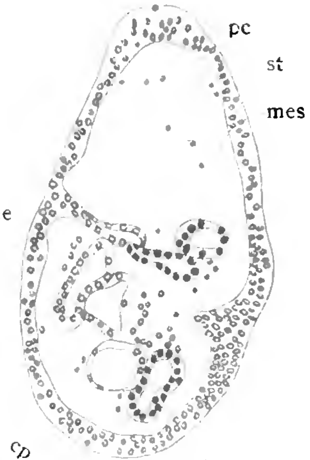

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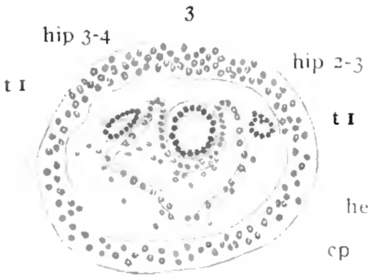

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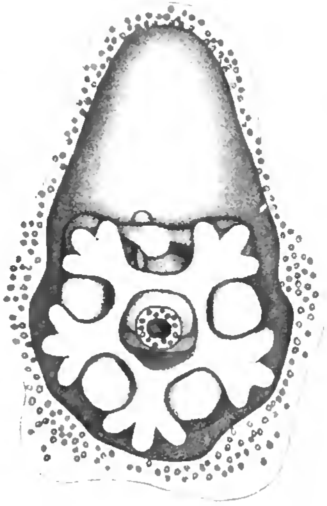


Fig. 9.

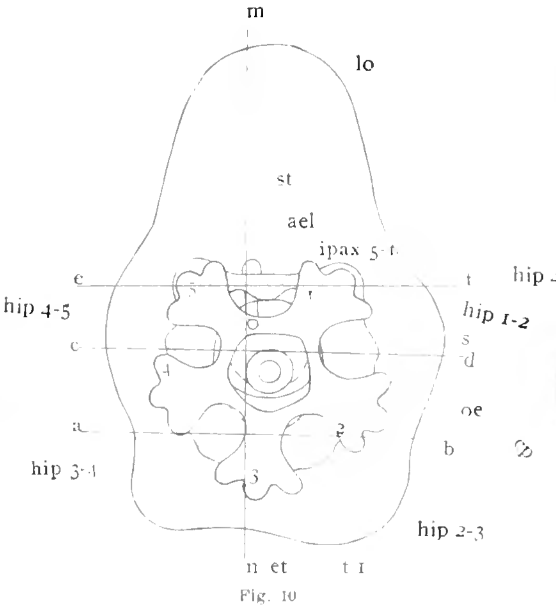


Fig. 10

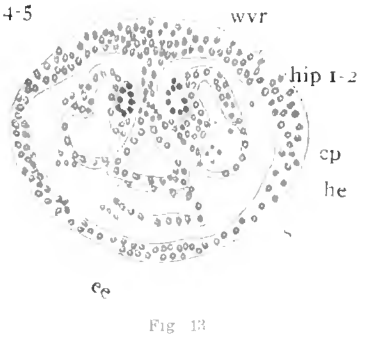


Fig. 13

CASWELL GRAVE DEL.

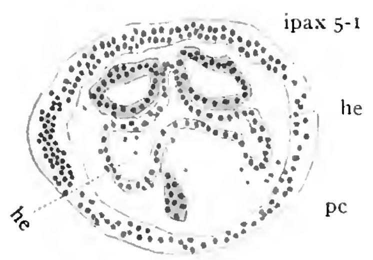


Fig. 14.

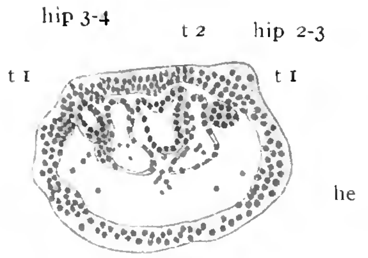


Fig. 19.

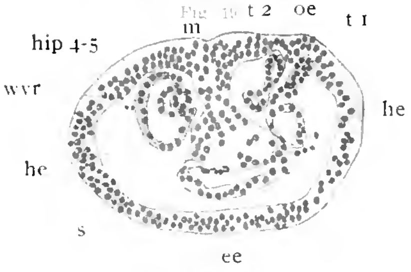


Fig. 20.

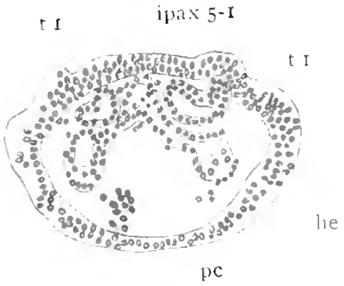


Fig. 21.

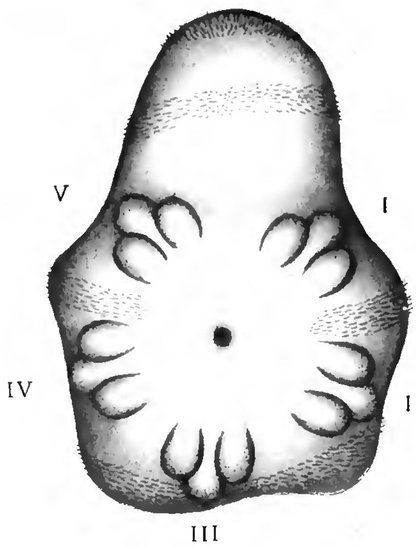


Fig. 15.

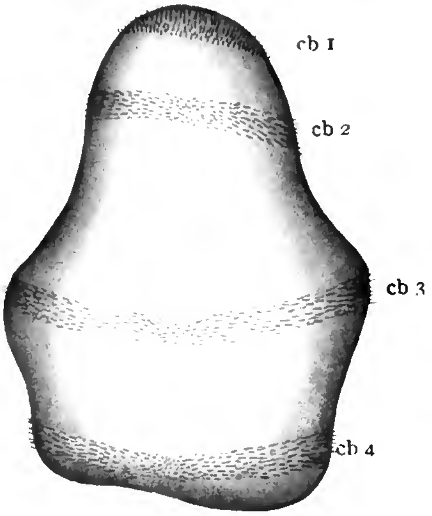


Fig. 16.

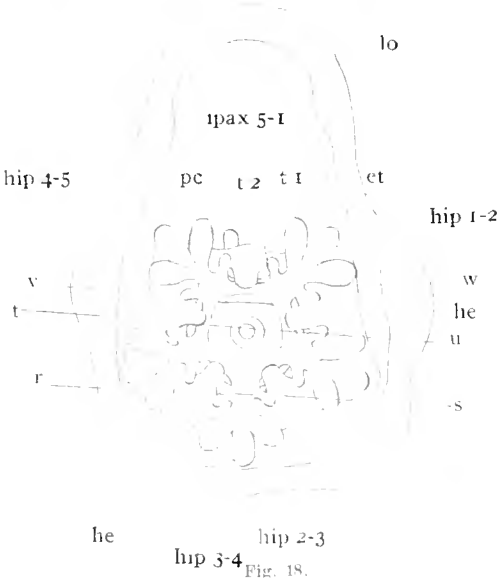


Fig. 18.

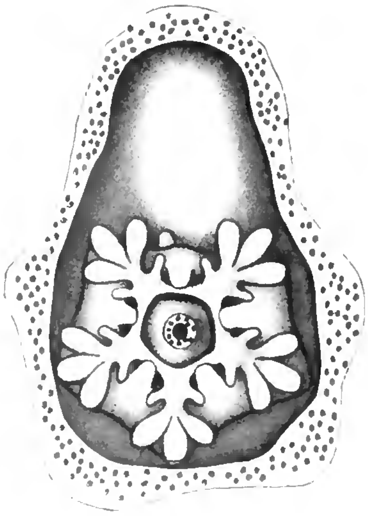
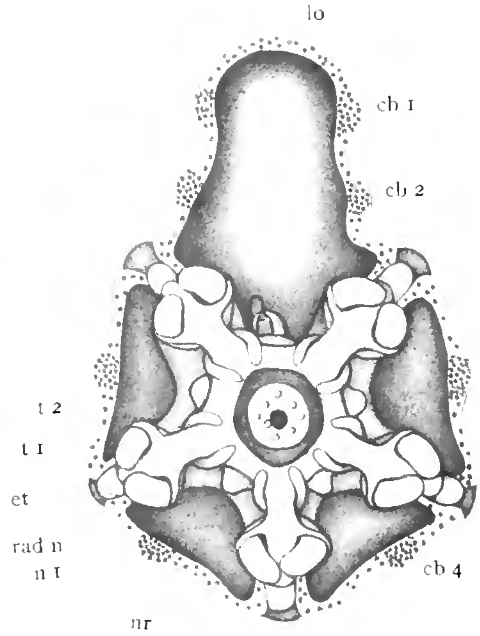


Fig. 17.



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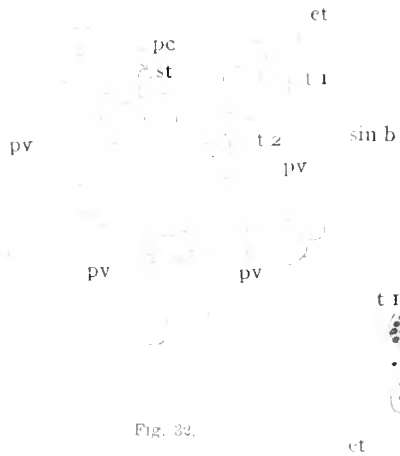


Fig. 32.

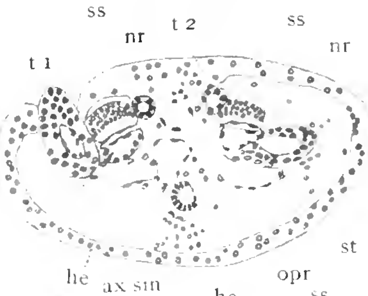


Fig. 33.

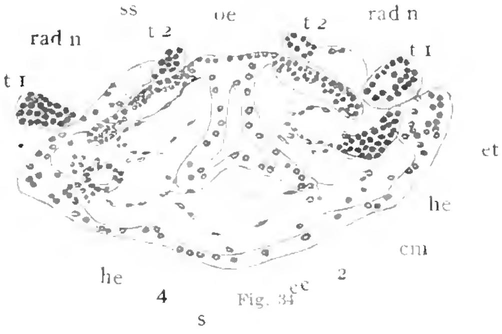
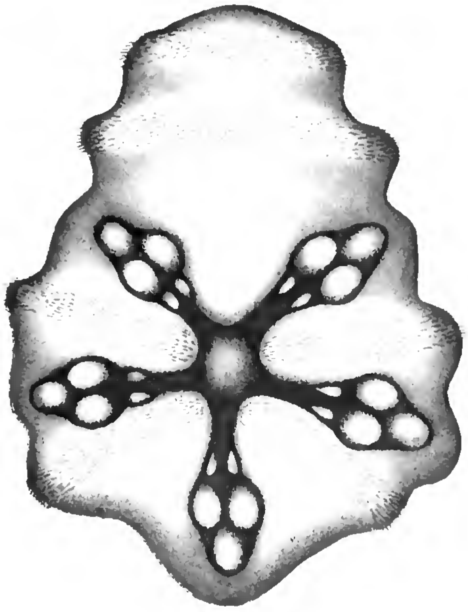


Fig. 34.

CASWELL GRAVE DEL.



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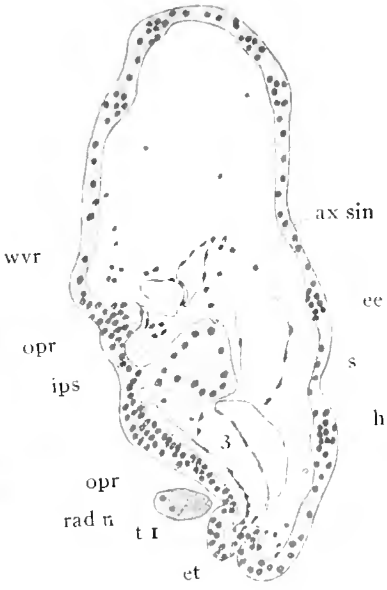

Fig. 24.

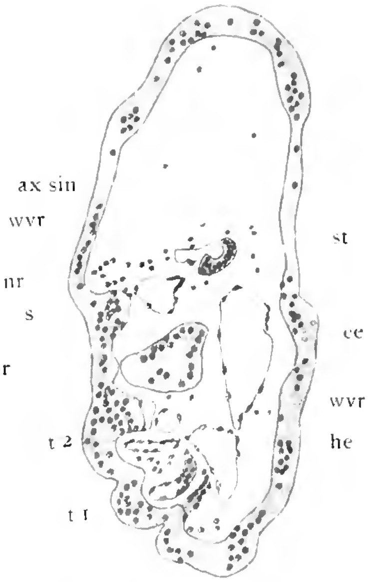

Fig. 25.

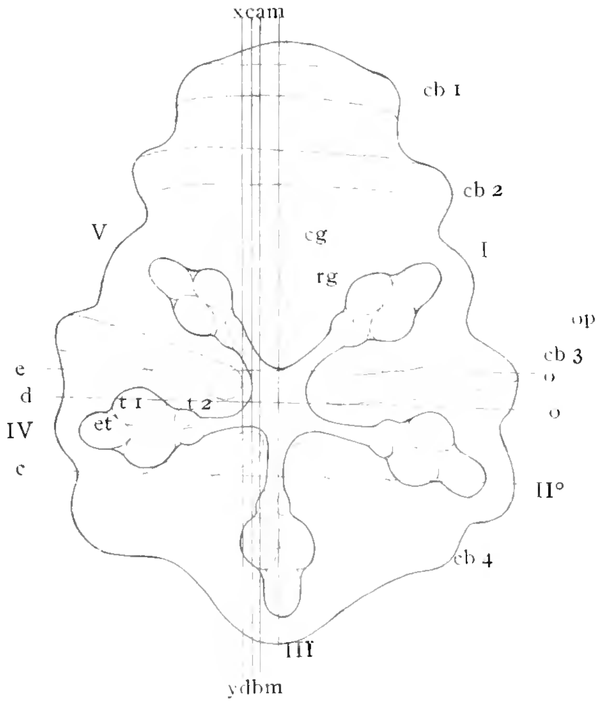

Fig. 23.

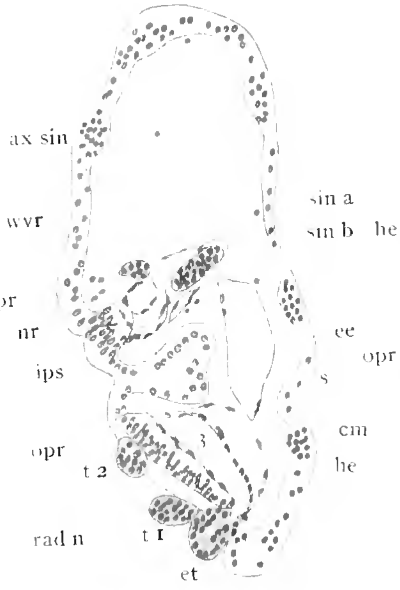

Fig. 26.

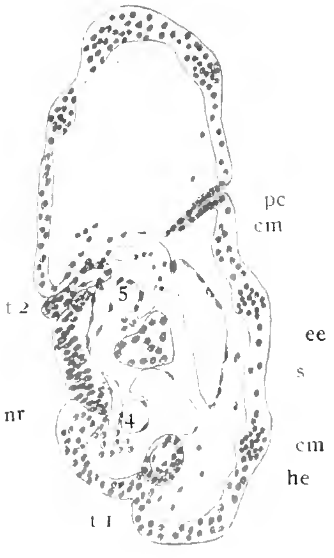

Fig. 27.

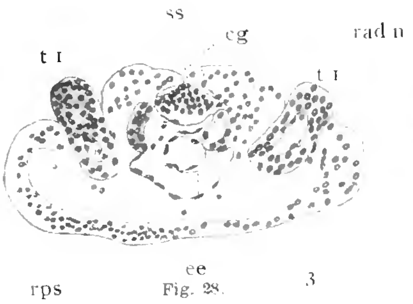

Fig. 28.

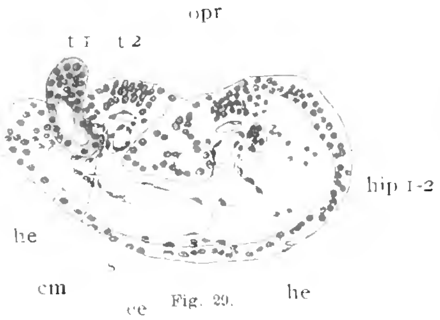

Fig. 29.

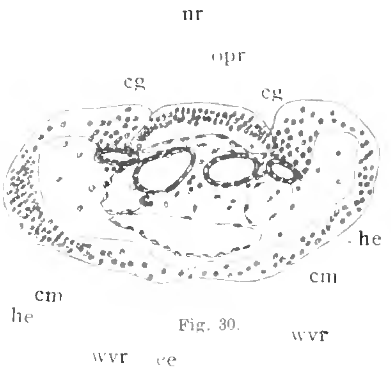

Fig. 30.

CASWELL GRAVE DEL.

6. THE ANATOMY AND DEVELOPMENT OF CASSIOPEA XAMACHANA.[1]

BY ROBERT PAYNE BIGELOW.

INTRODUCTION.

During the summer of 1891 the Marine Laboratory of the Johns Hopkins University was stationed in the Island of Jamaica. It was at Port Henderson, — a little hamlet situated at the west side of the mouth of Kingston Harbor, at the point where the Salt Pond Hill, eight hundred feet high, descends to the salinas and mangrove swamps surrounding the mouth of the Rio Cobre. On the other side of the hill, and to the south of it, there is a considerable body of salt water, known as the Great Salt Pond. It is completely separated from the sea, but only by a beach of sand, which at its narrowest part is not more than a few rods in width; and it is said by those who live near that in times of storm or freshet this barrier may be broken through.

One morning in June Dr. G. W. Field was hunting birds along the seaward shore of this pond, and came upon a little bay that forms a deep indentation in the barrier and is connected with the pond by a narrow inlet. The bay is overhung by low cashaw and mangrove trees. At one side is a sunny sandy spot where a crocodile had made its bed, and a fresh zigzag mark showed where it had recently slid into the water. A school of fish was circling about in the clear water, and barnacles and sea-anemones spread their tentacles from the submerged roots of the mangroves, while the bottom at the inner end of the bay was completely carpeted by a colony of beautiful rhizostomatous medusae.

A few very small specimens might be seen swimming about, but most of the medusae, especially the larger ones, would not ordinarily leave the bottom. They lay there upon their backs, with their voluminous, branching mouth parts spread out over their discs, which were motionless, except for occasional flaps of their margins. If any of these animals were disturbed, they would, however, swim about like ordinary medusae; but before long they would settle down again and assume their usual attitude upon the bottom.

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[1] An earlier draft of this paper was accepted in May, 1892, by the Board of University Studies in the Johns Hopkins University as a thesis for the Degree of Doctor of Philosophy. During the years 1891–92 and 1892–93 I held the Adam T. Bruce Fellowship in the Johns Hopkins University, and was thus enabled to make a second journey to Jamaica. Publication has been delayed in order that the results of this journey might be incorporated in the paper, and it is hoped that the greater accuracy and completeness thus obtained have added materially to its value.

Within this limited area there were countless numbers of them, and in many places they were so thickly spread that their margins touched upon all sides, or even overlapped.

The spectacle presented by this collection of medusae was truly marvelous; and in order to show something of it to the rest of us, Dr. Field gathered a pailful of specimens and brought them to the laboratory. Upon examination they were all found to belong to a single new species of Cassiopea, — a genus of which only one species was known to occur outside of the Red Sea, Indian Ocean, and southwest Pacific;[1] and this pailful, taken up at random, contained both adults and young in various stages of growth.

Professor Brooks made drawings of some of these, and then I made a visit to the Salt Pond to obtain more of the young medusae, and at the same time I collected submerged bits of wood and stems of plants. My hopes were more than realized when, upon examining these objects in the laboratory, I found them thickly studded in places with scyphistomas in various stages of development. I was particularly delighted when I noticed in one of the largest larvae certain glistening spots in the bases of the tentacles and found, on putting them under the microscope, that they were unmistakably masses of calcareous bodies that would form part of the marginal sense organs of the adult. They excited my interest, especially as I had been studying the development of these structures in Discomedusae (**'90**), and had been unable hitherto to obtain the early stages.

After this discovery I began, with the advice of Professor Brooks, to make a careful study of this species, with the intention of carrying the investigation of its anatomy and development as far as the limited amount of time at my command would allow. Preliminary accounts of my results were published in 1892 (Bigelow, **'92**, *a*, *b* and *c*). In the spring of 1893 I had another opportunity to visit Port Henderson with a party from the Johns Hopkins University, and was able to make important additions to my earlier observations.

During the first visit to Jamaica I was unable to find Cassiopea outside of the one locality that I have described, and, although both the adults and the young in nearly all stages were present at this place in such great numbers, searches for males and for females with ripe eggs were equally fruitless. The great abundance of young and the range in their apparent ages was, therefore, surprising, until I found that the scyphistomas were multiplying freely by budding, in a manner to be described later on. During my second visit I found this species as abundant as ever in this locality, and I also found a number of adult specimens in several of the small shallow lagoons among the mangroves in the rear of Port Royal. But these were all females, and it was still impossible to obtain males or eggs that would develop.

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[1] Although Fewkes (**'82**) identifies his *Cassiopea frondosa* Lamarck, of Key West and the Tortugas, with *Polyclonia frondosa* Ag., it is nevertheless a true Cassiopea, not a Polyclonia.

Full-grown medusae could be kept in good condition in aquaria for a number of days, and could be kept alive for weeks; while the young medusae and scyphistomas would thrive there an indefinite time, if there were a little pond ooze at the bottom of the aquarium and the water were changed twice a day. Indeed the growth and multiplication of the scyphistomas would proceed actively under these conditions. By keeping the larvae in shallow dishes I was able to watch the whole course of non-sexual development; but the development from eggs remains unknown to me because of the impossibility of finding any that would develop. It was not until a few days before we left Jamaica in 1891 that I discovered the habit that the very young free-swimming larvae have of hiding beneath the bits of bark and the like to which the scyphistomas in the aquarium were attached, and therefore the greater part of my work on the early stages of development was done during the second expedition.

After a few words concerning technique I shall begin with a systematic description of the species, followed by an account of the anatomy of the adult, and the remaining part of the paper will contain what I have learned of the development from the observation of the living animals while in Jamaica, and by the study of sections of preserved material, carried on chiefly at the Biological Laboratory of the Johns Hopkins University, but in part also at the Marine Biological Laboratory of Woods Hole and at the Biological Laboratory of the U. S. Fish Commission in the same place.

I wish to express my thanks to Professor W. K. Brooks for the advice and encouragement that he gave me while I was doing this work as one of his students, and I am also indebted to Professor C. O. Whitman, to the Hon. George M. Bowers, and to Professor H. C. Bumpus for the many courtesies received while at Woods Hole.

TECHNIQUE.

For the preservation of the very young larvae a one quarter saturated solution of picric acid, with 2% of sodium chloride added, gave good results. Erlicki's fluid with the same addition, and $\frac{1}{2}$% osmic acid followed by Erlicki's fluid, did fairly well for scyphistomas, but the best specimens obtained were those killed in the following mixture:

10% solution copper sulphate	100 c. c.
saturated solution corrosive sublimate	10 c. c.

As soon as they were killed, the specimens were placed in 5% bichromate of potassium and left there until hardened, after which they were washed in 35% alcohol containing a trace of hydrochloric acid and preserved in 70% alcohol. Excellent preparations of the medusae were obtained by this same method, and Flemming's fluid also gave good results.

Systematic part.

Genus **Cassiopea** Péron and Lesueur (*1809*). — This genus, as limited by Haeckel ('80), may be defined as follows: Discomedusae without tentacles and without a central mouth opening; provided, instead of the latter, with numerous oral funnels attached to the ventral, or axial, side of the *eight oral arms*, which are *pinnately or trichotomously branched*, have a *subcylindrical*, or *subconical, gelatinous support continuous to the tips of the principal branches*, are provided with *numerous club-shaped vesicles* among the oral funnels, and are without appendages on the dorsal, or abaxial, side; also with four interradial gonads in the aboral wall of the four separate subgenital cavities; *sixteen marginal sense organs* (*rhopalia*); and *thirty-two radial canals* connected by a network of anastomosing branches.

For the sake of clearness this definition is made to include the characters of the family Toreumidae Haeckel, to which this genus belongs, and the purely generic characters are italicized.

Cassiopea xamachana.[1]

Cassiopea xamachana Bigelow, Zool. Anzeiger, no. 393, 1892, pp. 212–214.

(?) *C. frondosa* Fewkes, Bull. mus. comp. zool., vol. 9, no. 7, 1882, pp. 254–259.

Diagnosis. — A Cassiopea with a disc-like umbrella, concave on the aboral side; when regular, with eighty short and obtuse marginal lobes separated by deep grooves on the surface of the exumbrella (in each of the sixteen parameres three velar lobes between two ocular ones); white markings on the exumbrella, consisting of a circular band with a diameter somewhat greater than that of the concavity, within this sixteen oval or eliptical spots lying in the radii of the rhopalia, and on the outer side eighty marginal spots, one for each marginal lobe; oral arms rounded and slender, never angular, exceeding the radius of the umbrella by at least one half of its length, and bearing nine to fifteen primary branches which are, in turn, copiously branched, giving the whole appendage a spatulate outline; very numerous small oval vesicles attached at the axils of the small branches and thickly massed upon the oral disc of adult females, and many small and a few large, flattened, linear vesicles attached one at the axil of each of the larger branches

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[1] This name, suggested by Professor Brooks, must stand as printed in the preliminary description of the species, according to the current rules of nomenclature, followed by the Boston Society of Natural History. But it should have been written *xamaycana*, from *Xamayca* (the *x* is pronounced like *ch* in the German *ach*), the Indian name for the island of Jamaica, as written by the early Spanish historians (see Herrera, Novi orbis pars duodecima, sive descriptio Indiæ occidentalis, 1624; also Encycl. Brit., 9th ed., article, Jamaica). The form *Xaymaca* given by Bridges, Annals of Jamaica, 1827, and followed by several subsequent authors, is probably a misprint.

and to the canals on the oral disc, the thirteen largest vesicles being one at the axil of the largest branch on each arm and one at each junction of the canals on the oral disc; oral funnels entirely wanting on the oral disc in adult females, but present in immature specimens.

Special description. — A detailed account of the anatomy of this species will be given in the anatomical portion of this paper. It is intended here to call attention merely to the features that distinguish our species from its nearest allies. *Cassiopea xamachana* resembles very closely two medusae that inhabit the Red Sea and Indian Ocean, *Cassiopea andromeda* Eschscholtz and *C. polypoides* Keller (**'83**), but it seems, nevertheless, to be distinct from either.

Upon comparison with the descriptions of *Cassiopea andromeda* given by Tilesius (**'29**), Haeckel (**'79**), and Vanhöffen (**'88**), and with the figures of Tilesius (**'29**) and Forskål (**1776**), *C. xamachana* appears to differ from this species in the following particulars: The exumbrella is not merely flat, but is concave; besides the ninety-six white spots on the exumbrella, there is a broad circular band of white more or less connected with all of the marginal spots (Fig. 35), the oral arms are more thickly branched and are longer, exceeding by one half to two fifths the radius of the umbrella, instead of being only one third longer; moreover the arms have none of the flattened appearance figured by Tilesius and mentioned by Haeckel.

C. xamachana differs from *C. polypoides* in having more slender oral arms, with five to seven pairs of branches instead of three, and with fewer very large vesicles, and these apparently not so large and always flattened. The color pattern in the two species is nearly the same, except that in *C. xamachana* the three white spots on the three velar lobes of each paramere are seldom widely separated from the circular band of white. The colors in the pattern, however, differ considerably in the two species. The ground color in *C. xamachana* is never light brown, but is always much darker, a greenish brown, usually with a distinct shade of blue on the subumbrella. The large oral vesicles are never sky-blue, rose-colored nor white, but are yellowish green, often with a bluish green stripe; and, while the margins of the oral funnels are deep brown, they are always fringed with the white digitella.

C. xamachana is easily distinguished from *C. ornata* Haeckel by the presence of large oral vesicles and by the more extensive branching of the arms; and it differs from *C. mertensii* Brandt (**'38**), *C. depressa* Haeckel (**'80**), and *C. picta* Vanhöffen (**'88**), in the number of marginal lobes on the umbrella. *C. ndrosia* Agassiz and Mayer (**'99**) differs also in number of marginal lobes and in coloring. Fewkes (**'82**) has described a medusa from Key West and the Tortugas under the name "*Cassiopea frondosa* Lamarck," which he regards as identical with *Polyclonia frondosa* Agassiz. From the description given by

Fewkes it is impossible to identify his species positively. But a comparison of his figures with living specimens of both sexes of *P. frondosa* shows at once that the two species are distinct; while a comparison with *C. xamachana* shows so close a resemblance that I am inclined to think that Fewkes has discovered one of the varieties of our species, described in the next section. Not only is *P. frondosa* perfectly distinct from *C. xamachana*, but I think we are justified in retaining the former, for the present at least, in a separate genus; and there can be little doubt that Lamarck's *Cassiopea frondosa* dwelling in the "Ocean of the Antilles" with its "*margine decem-lobata*" is none other than Agassiz's *Polyclonia frondosa*. Therefore, even if it should be proved that the form described by Fewkes is the same as the subject of the present memoir, the name that I have given to it will hold, nevertheless, as the designation of the species.

Variations. — If we compare the average dimensions of various organs, expressed in thousandths of the diameter, with the maxima and minima, as may be done by examining the third, fourth, and fifth columns in Table 1, p. 201, it becomes evident that there is a very considerable amount of variation in the relative size of parts of *C. xamachana*.

In the oral arms, not only does the relative size vary, but the number and the arrangement of the branches are both variable. Moreover this variability exists between the different individuals. In nineteen specimens examined the maximum number of branches found on one arm was sixteen, the minimum nine, and the greatest difference on any one individual was four.

The most striking variations in *C. xamachana*, however, are to be found in the structures at the margin of the umbrella. These are highly variable in this species, and have been found to be variable, although to a less extent, in other medusae. It is unfortunate, therefore, that in his beautiful systematic work on the medusae Haeckel should have found himself forced to distinguish the genera chiefly by differences in the marginal structures. He himself notes the variability in the number of parameres of *Polyclonia frondosa*. Agassiz and Mayer ('99) found in one specimen of *C. ndrosia* eighteen rhopalia, and in another twenty-two.

The number of rhopalia was counted in twenty-seven specimens of *C. xamachana*. Of these ten were found to have sixteen, the typical number for the genus, and twelve had more than sixteen, three having seventeen, and three more, eighteen. The largest number on one individual was twenty-three. There were five specimens with fewer than sixteen rhopalia, but only two had less than fifteen, and both of these showed correlated abnormalities in the mouth parts and subgenital cavities. One had fourteen rhopalia, four oral arms, and two subgenital cavities and gonads. The other had ten rhopalia, only five oral arms, with three oesophageal canals leading from the stomach to the canal system of the arms, and three normal subgenital cavities and one very small vestigial one (Fig. A.).

Redundancy of mouth parts is not nearly as common as of the marginal structures. Only two cases were observed. One specimen with an additional pair of oral arms in one interradius had seventeen rhopalia. The other had eleven arms, with five subgenital spaces and gonads, and this one had twenty-two rhopalia. On the other hand, five specimens were found with twenty or more rhopalia, and perfectly normal mouth parts.

It will be seen, then, that the number of rhopalia, which has been taken as the principal generic character in the group, is a highly variable one. The number of marginal lobes in each paramere has been taken as one of the principal specific characters, and this is, likewise, highly variable. The variation consists principally in the interpolation of a small secondary lobe between two typical ones. Even in a regular and typical specimen, such as is shown in Fig. 35, the position that would be taken by these secondary lobes is indicated by small ridges on the dorsal surface. A specimen with a large number of rhopalia is as likely to have the marginal lobes in each paramere arranged typically as one having a smaller number. Conversely, a specimen with fifteen to seventeen parameres is as likely as not to vary from the typical form. The variation may consist in the addition of two secondary lobes in the paramere, the addition of four lobes, or in a quite irregular arrangement; and this modification may affect all of the parameres alike or only a portion of them.

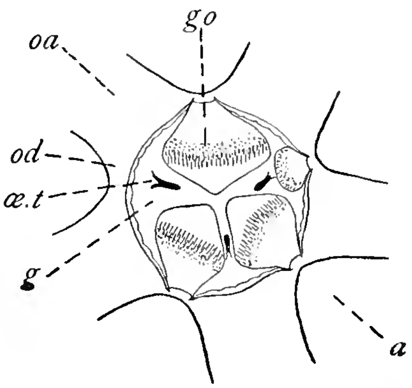

Fig. A. Section through the stomach of a specimen with only 10 rhopalia and 5 oral arms, to show the abnormal arrangement of gonadia and oesophageal canals. In the region marked *a* the margin of the umbrella presents a wide space in which there are no rhopalia. *go* = gonad. For explanation of the other lettering see Explanation of Plates.

Throughout all of these modifications of the margins there is manifested a constant regard, as it were, for the symmetry of the parts. It is very seldom that an additional rhopalium appears as if attached fortuitously in some irregular way. Almost always either it is in the midst of an entirely new paramere or else there is a distinct line of symmetry running between two adjacent rhopalia that evidently correspond to an originally single one. In other words, a paramere has been incompletely doubled, and the two parts are bilaterally symmetrical to one another. We find all degrees of this doubling in the adult from a double-headed rhopalium[1] to two complete parameres, and the same process may be seen in the forked tentacles frequently found in the larvae (Figs. 14 and 21, *x*). With the exception of the forked tentacle and the double-headed rhopalium, these stages of duplication are well represented at *u*, *w*, *x*, *y* and *z* in Fig. 30.

The radially arranged stripes and spots on the exumbrella, which, with a circular band, form the color pattern described in the next section, vary in number with the rhopalia and marginal lobes. But when two rhopalia are close together there may be only one corresponding rhopalial stripe, and it will then occupy a position intermediate between the two. For example, in the specimen mentioned before as having only ten rhopalia, two of the rhopalia were very close together and there was but one rhopalial stripe corresponding to them. The other rhopalia were evenly spread, except that they were absent from one rather wide section of the circle. The rhopalial stripes, nine in all, were placed in a corresponding manner, and were absent from the corresponding area.

There is also a wide degree of variation in the extent of fusion between the circular band and the marginal spots. The spots on the velar lobes are usually not fused to the circular band in young specimens, and they frequently remain distinct in adults. It was found, however, that this is more usually true of specimens from the Salt Pond than of those from Port Royal. I thought that I could see, also, correlated differences in the sizes of certain of the mouth parts, and I was thus led to inquire if there were a division here of the species into two races. For this purpose Table 2, p. 201, was constructed. From this it will be seen that the specimens from the Salt Pond (var. *A*) have on the average longer oral arms and shorter vesicles than the ordinary specimens from Port Royal (var. *B*), while the stomach is of the same size in the two groups. Whether these slight differences are in any way connected with the probable difference in density of the water in the two localities, experiment alone can determine.

In the third column of this table dimensions are given of some specimens from Port Royal (var. *C*) that are so different from the rest that they might be regarded as of a distinct species.[2] Suspicion of their being merely sports is aroused, however, by the fact that only two specimens (female) were found living among a large number of the usual form.

The most striking peculiarity of these two specimens was the great number (forty to fifty) of uniformly large oral vesicles, two to four centimeters in length, scattered over

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[1] Fewkes, ('82) has observed similar double-headed rhopalia, and it is on account of the variability of the marginal structures that he regards Polyclonia as merely an abnormal Cassiopea.

[2] It is possible that this variety may be the same as *Cassiopea frondosa* Lamarck of Fewkes, although his figures do not show any large vesicles on the proximal parts of the oral arms.

the whole extent of the mouth parts. Among them the central, radial, and primary vesicles were hardly distinguishable, although so easily recognized by their greater size in the typical form of the species.

Another peculiarity was a projection of the mesogloea on the oral side of each subgenital osteum, so that the interradial diameter of the oral disc was considerably longer than the radial diameter, as shown in the table. These specimens presented also some peculiarities of coloring, which will be noted in the next section.

Color.—The coloring of this semi-transparent animal consists of certain white markings, together with shadings of subdued tints of brown, green and blue, that are often very beautiful.

If we turn the aboral side (Fig. 35) of the medusa toward us we find often a brownish band encircling the disc at the periphery of the concavity and shading off gradually on both sides. Deeper within the mesogloea there is a much wider white circular band extending under the brownish one; and white bands, or spots, extend in a radial direction outward from this along the marginal ridges. There is one spot to each ridge, and it reaches nearly to the tip of the marginal lobe. The bands on the rhopalial lobes are interrupted, however, by a roughly circular, transparent area over each rhopalium; and in many specimens, especially young ones, the interrhopalial (velar) spots are not fused with the circle. On the inner side of the circular band of white there is a circle of large white spots, "rhopalial spots," or stripes, that lie deep in the substance of the exumbrella and are visible through the mesogloea, one in the radius of each rhopalium. The spot is elliptical in outline, and extends from the white band to a point about two fifths of the distance between the periphery of the concavity and the edge of the stomach. These spots, while usually continuous with the band, like the marginal spots, are not always so.

At the centre of the umbrella the stomach and subgenital cavities may be seen through the mesogloea as a reddish brown circular area with a diameter of about one fourth of the total diameter of the disc; while surrounding the stomach there is a deep blue halo with points that extend outward between the last-mentioned bands of white.

Now if the animal be allowed to return to its usual position, the subumbrellar surface will be found to be pretty evenly stippled by the greenish brown cells in the mesogloea. Apparently beneath this stippling there is a blue pigment forming a circle around the margin of the stomach and extending outward in broad bands, one along each interrhopalial radius, nearly or quite to a large, more or less distinct patch of blue, that lies close to the margin between every two rhopalia. The radial canals, and the fine, connecting network of tubes, appear as rather indistinct, opaque, white lines.

The mesogloea of the oral arms is transparent and colorless, except for an opaque white stripe beneath the dorsal surface of each arm, of the same character as the white markings of the umbrella. There is a similar stripe on the dorsal side of each of the larger branches which may, or may not, be continuous with the stripe on the main stem. The bases of the oral funnels are of a delicate blue color, which often extends to the brachial canal. The margin of each funnel is a deep brown, that shades off over the blue; while the small tentacles, or digitella, that spring from this margin are pure white. The larger tongue-shaped vesicles on the arms and oral disc have a greenish yellow color with a bluish green longitudinal stripe. The smaller vesicles on the arms are colored in a similar way and are inconspicuous, but the cluster of very small vesicles that occupy the greater part of the oral disc has a very different appearance, being lightly tinted by fine reddish brown pigment spots.

The two specimens that I have called variety *C*, are somewhat differently colored. The markings are yellowish white. The circular white band is indistinct. The rhopalial bands are interrupted at the margin of the concavity of the exumbrella, and stop short about half a centimeter from the rhopalial hood. At the margin of the umbrella there is a white spot on each rhopalial lobe and a strap-shaped spot on each velar lobe. The centre of the umbrella is whitish and opaque, so that the stomach does not show through. The oral arms are translucent, milky white tinged with brown, and without distinct white markings, except on the dorsal side of the principal branches. The large oral vesicles are yellow and greenish yellow, with a brown centre.

Size. — The diameter of the largest specimen found is 24 cm., while the smallest specimen that contained eggs measured 6.5 cm. The average diameter of twenty-three adult specimens was 13.7 cm. The relative sizes of the parts are exhibited in the following tables. Table 1 shows what may be regarded as the normal proportion for the species, though, to be sure, some of the measurements were made only on Port Royal specimens. Some of the dimensions were measured on a smaller number of specimens, and for these the average diameter of the umbrella of the specimens on which these measurements were made is given separately to show the correct proportions. Table 2 furnishes a means of comparing the proportions in the three varieties.

TABLE 1. DIMENSIONS OF SPECIMENS FROM BOTH SALT POND AND PORT ROYAL (VARIETIES *A* AND *B*.)

	Number of specimens measured	Average dimensions in centimeters	Average dimensions in thousandths of average diameter	Maximum	Minimum	Remarks
				(In thousandths of diameter unless otherwise noted)		
Diameter of umbrella	21	14.33	1000	24 cm.	9 cm.	Salt Pond and Port Royal specimens taken together.
Length of arms measured from centre of oral disc	21	11.21	782	888	642	
Length of central vesicle	21	2.71	189	287	103	
Length of primary vesicle	21	1.82	126	190	71	
Diameter of umbrella	10	15.79	1000	24 cm.	12 cm.	Port Royal only.
Length of radial vesicle	10	3.01	190	250	117	
Diameter of umbrella	11	13.62	1000	16.3 cm.	6.3 cm.	Salt Pond and Port Royal.
Diameter of stomach	11	4.22	311	333	292	
Diameter of umbrella	3	18.66	1000	24 cm.	15 cm.	Port Royal.
Thickness of umbrella	3	1.33	71	73	70	
Total depth	3	3.59	191	212	173	
Diameter of umbrella	2	20.50	1000	24 cm.	17 cm.	Port Royal.
Diameter of oral disc	2	8.00	390	441	354	

TABLE 2. AVERAGE DIMENSIONS OF THE THREE VARIETIES, GIVEN IN THOUSANDTHS OF THE AVERAGE DIAMETER OF THE UMBRELLA.

	Variety *A*—Salt Pond	Variety *B*—Port Royal	Variety *C*—Port Royal
Length of arms	850	715	818
Length of central vesicle	157	217	—
Radial vesicle	—	190	163
Primary vesicle	112	138	167
Diameter of stomach	298	311	322
Thickness of umbrella	—	71	80
Total depth	—	191	213
Radial diameter of oral disc	—	390	394
Interradial diameter of oral disc	—	390	470

Locality. — Great Salt Pond, and mangrove swamps ("The Lakes") in the rear of Port Royal, Jamaica.— BIGELOW.

(?) Moat outside Fort Jefferson on Garden Key, Tortugas Islands, and Mangrove Keys, near Key West, Florida. — FEWKES.

ANATOMY.

Form of the Body. — To one who is familiar with the cyaneas, aurelias, and the like, of our northern coast, the shape of this medusa appears very strange. The aboral, or exumbrellar surface (Fig. 35), instead of being convex in *Cassiopea xamachana*, as it is in the great majority of medusae, is concave when the animal is at rest, except for a slight convexity over the stomach, and except in the region of the thinner marginal part of the umbrella, where also it is convex. The surface of the subumbrella, on the other hand, is convex, except in this same thinner marginal area, where it is in turn concave. The umbrella thickens very gradually from its margin to the centre, and the elevations and depressions of its surface have very gentle slopes, so that its general shape is much nearer that of a flat disc than the dome-like form of most medusae (Fig. 35).

A circular column arises from the centre of the oral surface of the umbrella. It is broad, but very short; and a few millimeters from the umbrella it loses its circular outline, owing to eight stout arms that spring from it at regular intervals (Fig. 34). These are smooth and rounded, except along a line on the oral side, where they bear the fringe of oral appendages, and they are long and much branched. This column is the *oral disc*, and its arms the *oral arms*.

The Structure of the Mesogloea. — By far the greater part of the mass of the oral arms and disc, as well as the umbrella, is composed of a firm, elastic, gelatinous substance, the *mesogloea*, and it is to this that the shape of the body is due.

The description given by Keller (**'83**), of the structure of the mesogloea in *C. polypoides* would apply almost equally well to our species. The mesogloea consists of a hyaline matrix, in which are imbedded certain fibres and three kinds of cellular elements. Most of the fibres appear to be analogous to connective tissue fibres, and take a general course through the mesogloea at right angles to the surface. Others seem to be protoplasmic. At any rate, they may be observed to proceed from the star-shaped cells that are scattered throughout the jelly.

The cellular elements are: the star-shaped cells, just mentioned; vesicular bodies, found in certain restricted localities; and the green cells, which, as it will be shown later, are symbiotic plants.

The star-shaped cells remind one of osteoblasts, and are probably analogous to them, in that they are concerned in the formation of the jelly. Hamann (**'81**) has called them *colloblasts*. They are small, often somewhat elongated, and have a well-marked nucleus.

The vesicular bodies give rise to the white markings that were mentioned in the description of the species. These vesicles are much larger than the colloblasts. Each one seems to be made up of a wall of exceedingly minute refractile granules, surrounding a clear space. That this body is a cell, however, is shown by the presence of a nucleus pressed closely against one side.

The green cells, or *zoanthelae*, are widely distributed throughout the mesogloea, but are most abundant in the umbrella. They are not infrequently found imbedded in the endodermal epithelium. The living cells have a greenish brown color, which they impart to the animal as a whole. They are of considerable size, are globular, without projections of any kind, and are generally to be found in clusters of two or more (*za*, Figs. 52, 56, and 63). Each one contains a nucleus and numerous granular bodies, and apparently is surrounded by a cell wall; but the latter is hard to distinguish from the edge of the adjacent matrix.

Keller thought that similar bodies in *C. polypoides* could not be algae, because he failed to find any evidence of a cellulose cell wall. He regarded them, therefore, as essential elements of the "mesoderm."

In those of my specimens, however, which have been killed in Erlicki's fluid and stained with borax carmine, the nucleus of these cells is found to be red, while the granular contents of the cell are bright green, and there are often one or two green bodies present that are as large or larger than the nucleus. They have all the appearance of chlorophyl bodies, and it is well known that the chlorophyl of some algae is not readily removed by alcohol. Moreover, in teased preparations treated with iodine solution these cells are found to be filled with granules that quickly turn deep blue, — evidently starch. The test for cellulose with iodine followed by sulphuric acid, gave, however, unsatisfactory results. The outline of the cell would become distinctly darker, but not recognizably blue. In the same way with chloriodide of zinc, a very marked reaction for starch was obtained, the granules becoming almost black; but so long as the object was viewed by direct transmitted light, no reaction for cellulose could be detected with certainty. On the other hand, when the light was thrown upon the object obliquely by means of a condenser with a central diaphragm, the effect was quite different. The starch granules became a deep ultramarine, and the parts of the cell not occupied by the starch appeared distinctly violet, showing without doubt the presence of cellulose.

Both starch and cellulose, as well as some form of chlorophyl, having been demonstrated in them, there can be no further question that the green cells in Cassiopea are symbiotic algae.

The Oral Arms and their Branches. — The eight oral arms (Fig. 34) arise from the central oral disc at about equal intervals; and when an arm is extended, the distance from the centre of the oral disc to the tip of the arm about equals three quarters of the diameter of the umbrella. But the arms are very contractile, and may be shortened to half this length. The arms are slender and graceful in shape, the mesogloea tapering very gradually to the tips of the finest branches. The branches are arranged alternately. The largest one, which is the first formed, is at a point about two thirds the length of the arm from its base. From this point the branches decrease in size gradually toward the base of the arm, and more rapidly toward the apex. The general outline of the arm, therefore, including its branches, is roughly spatulate.

The Oral Funnels and Brachial Appendages. — Just below the surface of the oral side of each arm there is a longitudinal tube, the *brachial canal,* that ramifies to each branch, and finally opens to the exterior by funnel-shaped *oscula* (*os.*, Fig. 34) at the tips of the numerous ultimate branches, and at many places along the course of the tube. The margins of these oscula, or oral funnels, are provided with short tentacle-like projections, the *digitella.* These are covered by an epithelium containing nettle cells, and each has a gelatinous axis in which there are transverse plates of greater density than the rest of the jelly, and these give the structure the cellular appearance first described by Hamann (**'81**). The epithelium lining the tubes and funnels is ciliated.

There open also into the brachial canals the lumina of the oral vesicles (*v.*, Fig. 34). These structures, as already stated in the diagnosis, have their points of attachment in the axils of the branches. All except the smallest are flattened laterally. The smaller ones are oval in outline, the larger ones linear. At one side near the apex there is a cluster of short processes that Hamann has homologized with digitella.

The Oral Disc. — Although the eight oral arms seem to be placed at equal distances and to be alike, they are morphologically in pairs, each pair being homologous to one of the four lips of a semostomous medusa, — an aurelia, for example. The line that separates two members of a pair is therefore, according to Haeckel's nomenclature a perradius. The brachial canals from each pair of arms, on entering the oral disc, converge and unite into a single radial tube that is continued to the centre of the disc, where it unites with the other three. In this way the course of the tubes on the oral disc forms a pattern that resembles a Maltese cross. The larger *central vesicle* is attached at the centre of the cross. In a living specimen 11 cm. in diameter this measured 3 cm. in length. There are four other vesicles that most nearly approach the central one in size, and these arise from the radial canals near the junction of the brachial canals, and I have called them, therefore, the *radial vesicles.* In full-grown individuals there are eight more vesicles upon the oral disc, a little smaller than the last, one on each brachial canal distal to the junction. It is only near the periphery of the disc that the canals are provided with oral funnels. For most of their course on the disc the canals give rise to the very small vesicles, finely speckled with a reddish brown pigment, that already have been mentioned. These have nettle batteries at their tips, and are so numerous as to cover completely the greater part of the disc and to hide the course of the canals. This mass of small vesicles, however, is not acquired until late. Specimens as much as 6 cm. in diameter will be found to be without them. In such specimens we have the five largest vesicles, and a number of oral funnels are scattered along the canals, just as they are upon the arms. This replacement of the oscula on the oral disc by small vesicles has been observed to occur also on adult females of *Polyclonia frondosa*, but not in the males (Bigelow, **'93**). It is not improbable therefore that a similar difference between the sexes may be discovered in our species of Cassiopea.

The Subgenital Cavities and the Digestive Tract. — At each of the four points of junction of the brachial canals there is a slit-like passage, oesophageal canal, dipping vertically into the mesogloea of the disc, and opening into the stomach. The latter is a lens-shaped cavity, with a gently arched roof. Its floor consists chiefly of four lozenge-shaped areas, where the body wall is very thin and plaited in radial folds (Fig. 34). These thin parts of the body wall form the roofs of the subgenital cavities, which open to the exterior, each by an elliptical orifice, *osteum*, (*x*, Fig. 34) in the side of the oral disc near the subumbrella and in the angle between two pairs of arms (interradial). The gonad appears as a band which crosses this membrane tangentially at its greatest width. Just central to each gonad there is a multiple series of very many small gastric filaments forming a narrow band parallel to the ovary. These are ciliated, and provided with nettle and gland cells. The portion of the floor of the stomach not made up of these lozenge-shaped membranes is bounded by the firm mesogloea of the oral disc. This area has the shape of a Maltese cross, and it is in the arms of this cross, between the subgenital cavities, that the passages from the oral canals open into the stomach.

Near its periphery the floor of the stomach is marked by radial grooves. These are continued, each into one of the radial canals that extend outward from the edge of the circular stomach to the marginal region of the umbrella. There are regularly thirty-two of these, sixteen in the radii of the rhopalia, and sixteen interrhopalial. When the number of rhopalia is increased, the number of radial canals may or may not increase in proportion. There are often thirty-four or thirty-six of them. The canals in the radii of the rhopalia are larger and more nearly straight than the interrhopalial ones, and all are connected by a fine network of anastomosing branches, among which no distinct circular canal can be recognized. The meshes in the network of canals are connected by a plate of endodermal cells, the *endodermal lamella*. This lamella is also in contact with the subumbrellar ectoderm along a line encircling the umbrella a short distance from its margin, so that there is a complete sheet of endoderm separating the subumbrellar from the exumbrellar mesogloea.

Musculature. — The exumbrella is devoid of muscles, but on the opposite side there is a continuous sheet of muscle fibres, which is spread over the subumbrella, except a narrow zone at its margin, and is continued over the oral arms to their finest ramifications, and also into the subgenital cavities.

Most of the fibres on the subumbrella do not take an evenly circular course, but are undulating. They form in this way a series of double "arcades" like those found by Haeckel in other species of Cassiopea. There is one of these double arcades for each interrhopalial space. The surface of the mesogloea in this region is grooved. The sheet of muscle fibres lies directly upon it, and is therefore corrugated, the grooves being parallel with the fibres.

The muscular layer upon the oral arms is smooth, and its fibres take a longitudinal course, extending to the digitella and oral vesicles.

In the subgenital cavities the arrangement of the muscle fibres could not be made out; but their presence was revealed by the squirming movements of the thin membrane that separates the subgenital cavity and bears the gonads and gastric filaments.

Structure of the Marginal Sense Organs. — Each rhopalium has a pigment spot on the aboral side near the extremity, and each one lies in a deep sensory niche. The dorsal sensory groove, common in the Pelagidae, Aurelia, etc., is entirely lacking; although Keller found in *C. polypoides* a slightly depressed thickening of the ectoderm that corresponds to it. The sensory niche and rhopalium are, with the exception of the pigment spot, similar in all essential particulars to those found in Pelagia. The rhopalium is the only organ in the sensory niche (Fig. 56). It is a hollow, finger-like projection attached by its base to a low ridge that runs along the roof to the central wall of the niche. This ridge is penetrated longitudinally by the continuation of a radial canal from the stomach, and the lumen of the rhopalium opens into the distal end of this canal. In the distal half of the rhopalium the lumen is nearly obliterated by the increase in thickness of its endodermal lining. Here the endoderm, instead of being a columnar epithelium as elsewhere, is a mass of parenchyma-like cells, each of which contains a large calcareous concretion, a so-called otolith. A thin, supporting membrane separates the endoderm from the ectoderm. At the distal extremity of the rhopalium the ectoderm is a thin, cuboidal epithelium, while over the rest of the surface it is a thick, sensory epithelium resting on a thick network of fine nerve fibres. This, in turn, rests on the supporting membrane. I have observed no ganglion cells in this layer of nerve fibres, which is continued under the epithelium of the rhopalial ridge to the central wall of the niche, where it becomes imperceptible. There are no thickened bands of these fibres running to ciliated pockets, such as are found in Dactylometra (Bigelow, '**90**), and the fibres probably spread out finally into a thin network underlying the general epithelium of the subumbrella.

The one feature in which this rhopalium differs from what is found in Pelagia is the presence of the pigment spot, already mentioned, lying on the aboral side of the rhopalium immediately above the centre of the mass of concretions. This area is probably sensitive to light, but it only differs from the rest of the sensory epithelium in that here the superficial cells are deeply colored by a yellowish brown pigment. A more careful examination would undoubtedly show the histology of this structure to be similar to what Schewakoff ('**89**) has found in Aurelia.

HABITS.

The species of Cassiopea and the closely related genus Polyclonia find their habitat usually in quiet lagoons among the mangroves along the shores of the tropical seas. The mode of life of several species has been described by Brandt ('**38**) on the authority of Mertens, L. Agassiz ('**62**), Gray ('**69**), A. Agassiz ('**81**), Archer ('**81**), Fewkes ('**82**), Guppy ('**82**), and Agassiz and Mayer ('**99**). *Cassiopea xamachana* is no exception to the rule either in its habitat or its sedentary mode of life.

When the young medusa is set free from the strobila it is an active swimmer. It gradually becomes less active as the mouth parts acquire their adult structure, and by the time the animal has reached a diameter of two centimeters it has definitely taken up its abode upon the bottom. It lies there, as described in the Introduction, with the oral appendages upward, and seldom changes its position unless disturbed. The concavity of the exumbrella is an important aid in maintaining this posture against the action of waves and currents. The gelatinous tissue is firm and elastic, and causes the umbrella to assume its normal shape when the subumbrellar muscles are relaxed. The slight suction thus produced when the medusa comes to rest on a flat surface gives it such a hold that a certain amount of force is required to remove it.

Usually, however, the water in the lagoons is very quiet, and there is more danger from its stagnation than from its motion. A Cassiopea is enabled to avert this danger by the slight swimming movements of the thinner marginal part of the umbrella. By means of these rhythmic contractions the water is drawn in on all sides, and then is driven upward and away. A healthy specimen lying undisturbed on the bottom of an aquarium was observed during seven minutes to make on the average 19.7 contractions of the umbrella per minute. In this way the animal is enabled to draw to itself a fresh supply of oxygen and of its minute food material.

The oral arms and their branches are usually spread out so as to cover the subumbrella completely, but they are almost always in motion, bending to one side or the other, and they may be flexed aborally until the tips come within the umbrellar margin, or extended until they reach far beyond. Besides these general movements, the various appendages of the oral arms have movements of their own. Muscular contractions may be observed also in the thin membrane that separates the stomach from the subgenital cavities, and they probably serve to renew the water that bathes the gonads.

When the oral disc has been severed from the umbrella, both parts may remain alive for several days, and both retain their powers of spontaneous movement. The first effect of the operation is often to throw all of the parts into a strong tetanus, but shortly afterwards the pulsations of the umbrella may be renewed at a rate considerably more rapid than normal, — 32 to 34 per minute in one case. When the medusae have been for some time under unfavorable conditions, it frequently happens that the part of the body-wall surrounding the periphery of the stomach is ruptured, and thus the mouth parts as a whole become separated automatically from the umbrella.[1]

While at Bimini, Bahamas, in 1892, I observed that the food of *Polyclonia frondosa* consists chiefly of copepods and other small crustacea, and that these are caught by the combined action of the oral vesicles and the oscula (**'93**, p. 106). If a copepod strikes a vesicle, the vesicle bends quickly so as to cover the mouth of the adjoining osculum, and the copepod is thus enclosed in a trap. Artificial stimulation would cause the same reaction.

Experiments on *Cassiopea xamachana* made to determine whether or not this species obtains its food in the same way gave negative results. Stimulation of an oral vesicle causes only a slight bending on the side stimulated. Although these vesicles are provided with batteries of nettle cells near the tip, I was unable to see that they played any part in the taking of food. It may be that they are protective, but the sting is very feeble.

Examinations of the contents of the stomach were almost equally unsatisfactory. The contents of twenty-two stomachs were examined, and of these fourteen contained only a clear, very viscous fluid and, in some cases, a few apparently ripe eggs, more or less distorted, some small, colorless cells, probably sloughed off from the endodermal epithelium, and green cells identical with the "zoanthelae" found in the mesogloea. One or more copepods and other crustacea were found in five specimens. In one of these one small amphipod was found, and in another the cornea of an unknown crustacean.

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[1] While this paper is passing through the press a paper has appeared by E. W. Berger (**1900**), in which he gives the results of experiments made by F. S. Conant upon Polyclonia and Cassiopea to test the effect of removing the rhopalia.

Diatoms and other algae, exclusive of the above-mentioned zoanthelae, were found in four cases out of the twenty-two. Almost always the first impression on opening a stomach was that it was empty; and it was only by careful examination that the contents of the stomach could be discovered. In two cases, however, a considerable amount of material was found in the stomach. In one of these the stomach contained, besides the usual eggs, zoanthelae, debris, etc., the remains of many copepods, some nematods, a zoea, and some diatoms. In the other one there was found a compact greenish mass, about one centimeter in diameter, composed of granular debris and diatoms of various species, together with some desmids, Oscillaria, foraminifera, infusoria, Vorticella, and some fine filaments with spirally arranged contents.

This species exhibits the power of regeneration of lost parts to a marked extent. Specimens were frequently met with in which branches of the oral arms, or even portions of the margin of the umbrella, had evidently been formed recently to replace parts that had been destroyed. Moreover, branches of the oral arms that had been cut off were observed to regenerate oscula and vesicles at the central end.

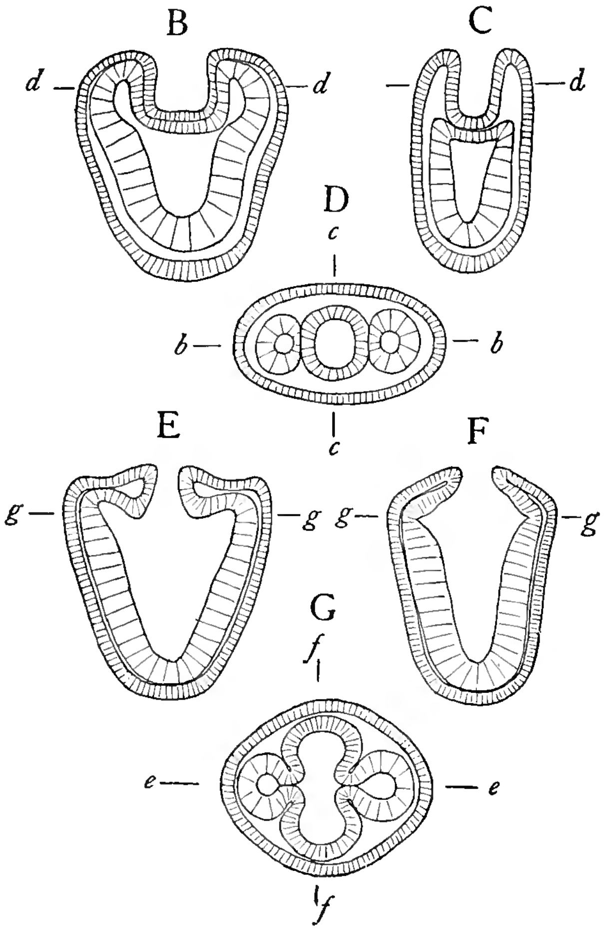
Ontogeny.

Historical Review. — Numerous studies upon the reproduction of various animals by budding have shown that the formation of organs in the bud may take an entirely different course from the development of homologous organs in the sexually produced embryo. As the observations to be described in the sequel were made entirely upon larvae that were observed, or supposed, to be asexually produced, they cannot settle any of the disputed points in regard to the development of sexually produced larvae. Nevertheless it will be of interest to compare the sexual with the asexual mode of ontogeny, especially as the development of a scyphistoma from a bud has never before been fully described.

The development of scyphomedusae from the egg has been studied in comparatively few forms. Several species of Aurelia have been studied by Sars, Haeckel, Schneider, Claus, Goette, Frank Smith, and Hyde. Two species of Cyanea have been studied by McMurrich and Hyde. A species of Chrysaora has been studied by Claus; and Kowalewsky, Metschnikoff, Krohn, and Goette have traced the very interesting abbreviated development of *Pelagia noctiluca.* The nearest ally of our species that has been studied with any degree of completeness is the Mediterranean rhyzostome *Cotylorhiza tuberculata,* which has been the subject of investigation by Claus and Goette.

From the description of the process of budding given in the next section, it will be noted that the larvae produced by budding are set free in a form resembling planulae, and it is the planula stage in sexual reproduction which is the earliest that can be compared with any stage to be described in this paper.

All agree that the planula of the Scyphomedusae is a more or less oval, ciliated larva, somewhat flattened on one side. It consists of two layers of cells surrounding a cavity which is completely shut off from the exterior. The first step toward the development of the scyphistoma is an invagination of the ectoderm at the posterior pole of the planula. According to Goette and Miss Hyde, the endoderm is invaginated at the same time in such a way that two endodermal pouches remain in the plane of the long diameter,—"Hauptebene," Goette,— (Fig. B, and *b–b* Fig. D), one on each side of the invagination, while the endoderm is pushed entirely away from the oral pole in the plane of the short diameter (Fig. C, and *c–c* Fig. D). The ectodermal invagination is the oesophagus (Schlund), its external opening is the mouth, and the endodermal evaginations are the first pair of gastric pouches. Soon an opening is formed (Schlundpforte) between the base of the oesophagus and the central stomach, and at the edge of the opening the ectoderm fuses with the endoderm. Then the second pair of gastric pouches is formed. According to Goette these are produced in Cotylorhiza and Pelagia entirely from the ectoderm of the lower part of the oesophagus (Fig. F). According to his view the lower edges of these evaginations coincide with the margin of the gastro-oesophageal opening (Schlundpforte), and are therefore at the level of the upper edges of the first pair of pouches. As these pouches extend out-



Figs. B–G. Two stages in the development of the mouth and gastric pouches in a sexually produced scyphistoma, according to Goette. Figs. B to D are sections in the three dimensions of space of a larva in which the oesophagus is invaginated and the first pair of gastric pouches are formed. Figs. E to G are similar sections of a larva in which the opening from the oesophagus into the stomach (Schlundpforte) has been established and the second pair of gastric pouches are in the process of formation. *b*, *c*, *d*, etc., indicate the plane of Figs. B, C, D, etc.

ward the ectoderm is pushed out until the principal radii) *e–e* and *f–f*, Fig. G) gradually become equal. This results in the formation of the flattened peristomal disc (Figs. E and F). At the same time the wall separating the oesophagus from the first pair of gastric pouches (Taschenvorhang) is split upward until the openings into the two pairs of pouches are upon the same level, and the "Taschenvorhang" is reduced to a low ridge, while the oesophagus is very much shortened. Portions of the original lining of the lower part of the oesophagus persist as the covering of the inner edges of the septa which separate the four gastric pouches. The larva is now in what Goette calls the scyphula stage. He regards this stage as of great phylogenetic importance, showing clearly, he thinks, a close genetic connection between the Scyphomedusae and the Anthozoa; so that these groups should be placed in a single class, Scyphozoa, to distinguish them, on the one hand, from the Hydrozoa, including the hydroids, hydromedusae, and, on the other, from the Siphonophorae.

This view, which is confirmed by Miss Hyde, is antagonized by Claus, and has given rise to a prolonged controversy. The parties to this dispute are practically in accord in regard to the facts of observation, as represented by the figures in their latest contributions. It is in the interpretation of these facts that they differ mainly. Claus ('90) admits that there is an ectodermal invagination previous to the formation of the mouth, and that the lining of the proboscis is ectodermal. He maintains, however, that the condition represented in Figs. B, C, and D, is due to a severe contraction of the animal, and is without morphological significance. He denies that there is any oesophagus, "Taschenvorhang," or "Schlundpforte," in the sense that Goette uses these terms; and with these he rejects the idea of a close affinity between the Anthozoa and scyphomedusae, with the correspondingly sharp distinction between the latter and the hydromedusae. He admits, however, that a distinction of importance between scyphistoma and hydropolyp is to be found in the possession by the former of an ectodermal lining of the proboscis, and in the presence of gastric pouches and septa.

Goette's position has been strengthened considerably by his latest contribution on this subject ('93), and his conclusions are confirmed in nearly every particular by Miss Hyde. Goette's figures appear to be camera drawings of serial sections, and are a great improvement over the rather diagrammatic illustrations in his earlier papers. They are not entirely convincing, however, for the ectoderm and the endoderm grade into each other so that it is impossible to determine the exact boundary; and the material is so subject to distortion during the preservation that it is often difficult to determine whether a given fold of the epithelium is of morphological value or is merely an artifact.

Miss Hyde fails to confirm the view that the whole of the second pair of gastric pouches (and hence, according to Goette, five eighths of the peripheral digestive tract of the medusa) is of ectodermal origin. On page 550 of her paper she speaks of only the roof, i. e., the lining of the oral side, of these pouches as formed from oesophageal ectoderm, and her sections bear out this view.

The foregoing brief summary of the present state of knowledge regarding the early stages in the development of the sexually produced scyphistoma will serve as an introduction to what is to follow. Mention of the work of others upon the later stages will be made when we come to the corresponding periods in the development of *Cassiopea xamachana*.

The Formation of the Bud. — In 1841 Sars described the budding of scyphistomas that were supposed to belong to a species of either Aurelia or Cyanea. The buds, according to this account, may grow out directly from the main part of the body of the larva, or they may be produced on stolons extending outward from the foot. In either case, several buds may be formed, apparently in various positions on the scyphistoma at one time. The figures show the buds attached to the parent and provided with a well-developed crown of tentacles at the distal end. Agassiz (**'60**) found a similar process of budding to occur occasionally in Aurelia. Goette (**'87**) has confirmed these observations, and has found that the larvae of *Cotylorhiza tuberculata* also produce buds.

In Cotylorhiza the bud is formed as an outgrowth from the body of the scyphistoma; and as it grows it gradually approaches the shape of its parent, but its relative position is just the reverse of what Sars found; for the distal end forms the stem, and the proximal end begins to flatten out into a circumoral disc. In this condition the bud is set free, and swims about, rotating on its long axis, with its distal end forward. The mouth is formed at the point where the constriction finally separates the bud from its parent, and the larva fixes itself by the opposite end.

Claus (**'92**) has found that the scyphistomas of Cotylorhiza not only produce buds, but that they produce them in large numbers. Scyphistomas reared from eggs that had been laid in September, 1890, were kept alive in the aquaria at Trieste and Vienna throughout the following winter and spring. No change was observed after the larvae had reached the sixteen-tentacle stage, until the following July, when budding occurred. The process was not restricted to a few well-nourished individuals, but seemed to be a general and repeated phenomenon, and it resulted in a large increase in the number of larvae. Claus's brief description of the formation and fate of the bud, accompanied by three figures, corresponds perfectly with what I have to describe in the following pages. The strobilization, he says, took place in August, and was monodiscous.

Another case of rapid multiplication of scyphistomas by budding is described by Lacaze-Duthiers (**'93**). A colony of these larvae, of unknown origin, was discovered in an aquarium at Banyuls in 1892. No strobila or ephyra was observed up to October, 1893, but in the meantime the number of scyphistomas had increased enormously. The buds appeared as elevations on the side of large individuals. The base of this elevation became elongated into a filamentous stolon carrying the bud at its tip. The bud fixed itself to the glass, gradually developed tentacles, and finally became independent by the disappearance of the stolon.

In *Cassiopea xamachana* the process of budding is an important, if not the chief, factor in the perpetuation of the species. On looking over collections of scyphistomas taken from the Great Salt Pond during May, June, and July, a considerable number was found with buds attached in various stages of development (Figs. 1, 2, and 26), and budding continued in the aquaria.

There is no stolon. The first visible rudiment of the bud is a slight swelling on one side of the calyx just above where it tapers into the stem. It involves all three layers of the body wall (Fig. 36). At an early stage in the growth of the bud the four septal muscles may be found as four slender cords of cells embedded in the mesogloea and apparently growing out from a thickened area of the ectoderm at the apex of the bud (*sm*, Figs. 38 and 39). This appearance seems to indicate that the septal muscles of the bud are formed, as in sexually produced scyphistomas, by an ingrowth of the ectoderm.

Careful study of serial sections through young buds shows, however, that the septal muscles of the bud are connected with septal muscles of the parent. In Fig. 37 the course of the septal muscles is reconstructed from a series of longitudinal sections. The muscle sm_1 passes around the base of the bud on the side away from the observer and gives rise to two branches, sm'_1 and sm'_3. These extend toward the apex of the bud, and each one divides dichotymously. Muscle sm_4 gives off a branch which fuses with sm_1, at the base of the bud. Sm_2 produces three branches which unite into a single branch. This branch extends into the base of the bud, but it was impossible to trace it further. It may be connected, perhaps, with the muscle sm'_2, which was traced for a short distance from the apex of the bud.

On account of the presence of the muscles, it is possible to study the relation of the plan of symmetry of even young buds with the symmetry of the parent. A series of sections made at right angles to the long axis of the bud shows that the vertical perradii of the bud lie in the plane of one of the perradii of the parent. But in transverse sections it is impossible to trace the muscles of the bud, except for short distances, owing to their extreme fineness.[1]

However, the study of longitudinal sections makes it reasonably certain that the sep-

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[1] The position of the bud is always perradial, although in some preparations it appears to be interradial, owing to the obliquity of the sections, as in Fig. 36.

tal muscles of the bud are derived from outgrowths of one or both of the septal muscles of the parent which lie in the interradii adjoining the perradial area of bud formation. If this be true, then every part of the young bud is formed from the corresponding part of the parent, viz., — ectoderm from ectoderm, mesogloea from mesogloea, endoderm from endoderm, muscles from muscles, and digestive tract from digestive tract. There is no indication of any method of budding of the kind described by Lang ('**92**).

In the young bud the mesogloea is very thin, so that the ectoderm and endoderm are very nearly in contact. The evagination gradually increases in size, becoming first hemispherical and then more elongated. At the same time a constriction appears close to the body of the scyphistoma, which deepens until the bud becomes a spindle-shaped body attached to its parent by a short and narrow stem consisting of a film of mesogloea covered with ectoderm, the digestive cavity of the bud being entirely closed (Fig. 1).

Scyphistomas are never found with more than two buds attached. When two buds are present they are always of different ages, and the elder is always attached to the apex of the younger (Fig. 2).

The Planula-like Larva. — When finally constricted off, the bud is a simple, spindle-shaped, hollow body, without trace of mouth or tentacles. It is like a planula in form and habits. The whole surface is covered with cilia, and it swims about, rotating from right to left upon its long axis. In swimming, the distal end is directed forward. While swimming, the larva is constantly changing its shape, assuming in a few minutes various forms from an elongated spindle to a short heart-shape (Fig. 3, *A*, *B* and *C*). It swims near the bottom, hiding under any object that it may find there. When it strikes an obstacle, it may rest there quietly, or it may rotate slowly upon its long axis. In all its movements it reminds one very strongly of Agassiz's description of the planulae of Aurelia.

The larva is white, speckled with a few greenish brown spots. It is rather opaque, but much of the structure may be seen in a living specimen. A longitudinal section shows that the ectoderm consists of a deep layer of very narrow and closely-packed columnar cells (Fig. 39). The mesogloea contains a few green cells (producing the greenish brown spots), and some widely scattered colloblasts. The layer is thickest at the equator, diminishing gradually to a very thin layer at both ends. The four septal muscles (*sm*) are seen clearly at the distal end of the larva, embedded in the mesogloea and united with the ectoderm near the apex (Fig. 38). In one specimen, not yet detached from the parent, it was possible to trace one of the muscles all the way from the proximal to the distal end. The muscle fibres are already differentiated and line the tube of mesogloea, while the nuclei occupy a central position.

The endoderm is a columnar epithelium, rather thin, with the cells closely packed together and coarsely granular at the proximal or posterior end of the larva. Toward the equator the cells become higher; and at the distal, or anterior, end they are large and clear. The character of the endoderm makes it possible to identify the anterior end of the swimming larva with the distal end of the bud.

The Formation of the Mouth.—The first change to be seen in the swimming larva is the formation of the mouth, which occurs two or three days after the larva has been set free. When writing my preliminary paper ('92 a), I was in doubt as to the relation between the poles of the bud and those of the larva. The better and more abundant material obtained during the second visit to Jamaica proved conclusively that the proximal end of the bud forms the oral end of the larva, just as it does in Cotylorhiza, according to Goette. The identification is made easy by the polar differentiation of the endoderm described in the previous section.

When first seen the mouth looks like a minute pin-hole in the posterior end of the larva (*m*, Fig. 4 *B*). In longitudinal sections at this stage the first indication of the formation of the mouth is the disappearance of the mesogloea from a small area at the posterior end, so that there is no longer a distinct boundary there between the ectoderm and endoderm (*m*, Fig. 40). At the same time a small dent appears in the outer surface. This deepens until it forms a minute tube connecting the endodermal cavity with the exterior (Fig. 41). The mouth thus formed gradually widens and becomes slightly funnel-shaped.

Further stages in the development of the mouth are represented in Figs. 5, 6, 7. In In Fig. 6 there is a distinct circular groove which outlines the base of the proboscis and separates it from a rudimentary peristome. In Fig. 7 the peristome is well developed, and the mouth is widely open.

There is no invagination of the ectoderm connected with the formation of the mouth, and there is no oesophagus, "Schlundpforte" or "Taschenvorhang." So, if Goette's account of the formation of the mouth in the sexually produced scyphistomas be accepted, we have here a case where an agamogenetic differs to a marked degree from the gamogenetic course of development.

The Scyphistoma.—With the elongation of the forward end, the formation of tentacles, and the development of four gastric pouches, the free-swimming larva becomes a typical scyphistoma.

By the end of the third or fourth day after the bud has been set free, the forward end of the larva has elongated to form a stem equal in length to the rest of the body (Figs. 7, 8, 9, and 11). The end of the stem becomes expanded, generally flattened, and the epithelium covering it becomes deeper than the rest (Fig. 42). This epithelium produces a secretion which serves to fasten the larva to some solid object. Fixation usually takes place during the fourth or fifth day, but the time varies greatly.

Development of the Tentacles. — During the third day the peristome appears as a minute ridge surrounding the posterior end of the larva, a short distance from the mouth. The first series of tentacles arises during the following twenty-four hours as four perradial angles in the margin of the peristome (Fig. 8). Four interradial tentacles appear almost simultaneously with these, or sometimes considerably later (Figs. 9, 10, 11, and 12). The elongation of the tentacles takes place rapidly, so that at about the end of the sixth day the peristome is surmounted by a crown of eight tentacles, which equal the proboscis in length.

With the broadening of the peristome the differentiation of the body of the scyphistoma into stem and calyx becomes apparent externally (Figs. 13 and 14). When the eight perradial and interradial tentacles have become long enough to reach some distance beyond the mouth, eight adradial tentacles appear in the angles between them. In Fig. 14 the adradial tentacles are distinctly developed, and two of the tentacles of the first series are bifurcated near the base. Figs. 15 and 16 represent the typical scyphistoma in the sixteen-tentacle stage. The tentacles are now long and graceful, and thickly dotted with batteries of nettle cells.

When fully developed, the scyphistoma is about one millimeter and a half in diameter; and it is provided typically with thirty-two tentacles.[1] But there is as much variation in the number of tentacles in the scyphistoma as there is in the number of sense organs and parameres in the adult. The number of tentacles is seldom less than thirty-two, often greater. The way in which this variation takes place is indicated in Figs. 21 and 14. All degrees of anomaly may be observed, from a bifurcated tentacle shown at *x* in Fig. 21, through the condition represented in Fig. 14, to two completely separated tentacles occupying the position of one typical one.

The tentacles of a well-developed scyphistoma, when fully expanded, exceed the length of the body several times. According to the position in which they are held, the tentacles may be divided into two series. Those of one series are held nearly erect, while those of the other series, consisting of the alternate tentacles, are bent backward until their tips nearly touch the ground upon which the animal rests. The action of the tentacles in capturing prey may be observed in a small aquarium, under the microscope. As soon as a tentacle comes into contact with a small floating body, such as a copepod, it is whipped quickly into the mouth, and at the same instant the side of the mouth toward the tentacle is opened more widely. On one occasion I saw two tentacles make captures at the same time, and the mouth expanded in both directions at once, showing a close co-ordination between the movements of the tentacles and of the mouth.

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[1] Specimens have been found with twenty-four tentacles, but it is uncertain whether this is a regular stage in development between the sixteen- and thirty-two-tentacle stage, or a duplication of tentacles of the earlier stage.

Development of the Gastric Pouches.—While the final result is the same, the method of development of the gastric pouches differs entirely in our larva from the process as described by Goette. The free-swimming larva is somewhat flattened laterally (Fig. 4), and the long and short diameters are in the planes of the perradii. But there is no evidence that the gastric pouches in the long diameter are formed any earlier than those in the short diameter, and the ectoderm plays no part in their development. The formation of the gastric pouches is usually described as a process of evagination; but in this case, at least in the earliest stages, the delineation of the pouches seems to be due rather to the ingrowth of the septa.

These appear at the time of the formation of the first tentacles (Fig. 8) as four minute vertical folds of the endoderm (*sep*, Fig. 43), placed equidistantly in the angle formed by the peristomal fold (compare Fig. 42). The mesogloeal portion of the septum is at first very thin, and in the four-tentacle stage (Figs. 8 and 43) is no higher than the thickness of the endodermal layer of cells. The septal muscles do not penetrate the septa at this stage. While well-developed below, they can be traced upward only to within 35 or 41 μ[1] from the base of the septa.

In the eight-tentacle stage (Fig. 13) the septum is still very small, and the septal mesogloea near the margin of the peristome is very thin, hardly thicker than a cell wall. But at the central margin it has increased in thickness, and now the septal muscle may be traced from the stem upward through this thickened portion of the septal mesogloea to the peristomal ectoderm (*sm*, Figs. 44 and 47). It is impossible to determine whether the new portion of the septal muscles is formed by growth upward of the muscles already present in the stem, or whether it is the result of a proliferation of the peristomal ectoderm which may grow downward and fuse with the older portion of the septal muscles.

The four septa are now complete, and divide the digestive cavity into a large central stomach, extending into the stem, and four shallow marginal gastric pouches. The gastric pouches expand with the growth of the peristomal disc, so that the ectoderm and endoderm remain in close contact at the margin; while the central edges of the septa retain their original relative position. Thus the gastric pouches and the septa become deeper as the larva increases in size. This is evident in the sixteen-tentacle stage (Figs. 15 and 45 to 49). It will be shown later that the relation of the interradial tentacles to the septa is variable. In this stage, however, the distal part of the septal mesogloea has begun to disappear, so that immediately under the interradial tentacles the endoderm of adjacent pouches is fused (Figs. 45, 46, and 47). In the fully developed scyphistoma this area of fusion is perforated, so that there is a communication between adjacent pouches, forming the "Ringsinus" of German authors. In the specimen with

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[1] 35 or 41 μ = about one seventh of the length of the larva.

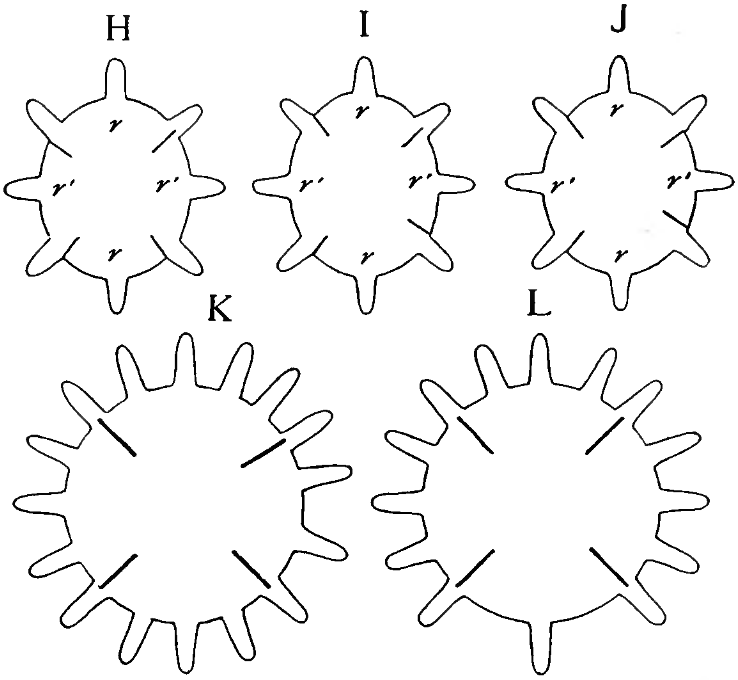
forty-two tentacles, from which the section represented in Fig. 51 was taken, this perforation was very small. Figs. 52 and 53 represent a little later stage, in which the opening has become much wider.

Each septal muscle is a solid cord of cells, with a single layer of longitudinal muscle fibres in its periphery. In the peristome the fibres of the septal muscles spread out in a fan-shaped arrangement toward the margin.

Four slight interradial depressions in the peristome may be observed as early as the four-tentacle stage. They are deeper in the eight- and sixteen-tentacle stages, and the septal-muscles may be seen to join the ectoderm at their bottoms. These depressions may be homologous with the septal funnels of the Stauromedusae, or they may be merely the result of the contracted condition of the larva. The question is of no importance, for there can be no doubt about the homology of the muscles; and whether they are solid or hollow is merely a matter of detail. In later stages (Figs. 51 and 52) sections seem to show that the peristomal depressions have deepened centrally so as to leave the insertion of the septal muscles high up on the peripheral side. But here, again, before any morphological conclusions can be drawn, account must be taken of the growth of the perradial angles of the proboscis and of the effect of the contraction of the septal and peristomal muscles.

Relation of Septa to Interradial Tentacles. — According to Goette, the interradial tentacles are always interseptal in origin. That is, two of these tentacles are produced as diverticulae from each of the second pair of gastric pouches (ectodermal), and their subsequent position in the planes of the septa is due to a secondary shifting. He finds in this important evidence in favor of his theory of the close affinity between the Scyphomedusae and the Anthozoa, for the tentacles of the latter are also invariably interseptal. Claus, on the other hand, finds that the interradial tentacles of Aurelia and Cotylorhiza are variable in origin. According to his observations ('91 and '92), an interradial tentacle may be interseptal, that is, arise as a diverticulum of a single gastric pouch, the endoderm growing out and pushing the ectoderm before it; or it may arise in the plane of a septum by the union of two endodermal diverticulae, one from each of the adjacent pouches. He holds, therefore, that the origin of the tentacles cannot be used as evidence to uphold Goette's theory.

My observations on Cassiopea are in perfect accord with those of Claus. A number of series of transverse serial sections made from young scyphistomas in the eight- and sixteen-tentacle stages were studied carefully with the aid of camera sketches drawn on transparent paper. By this means the relations of the parts could be determined accurately; and the results are embodied in the series of diagrams, Figs. H to L. In the eight-tentacle stage, according to Goette, the gastric pouches in the long diameter, *r r*, should each give rise to a single tentacle, while the pouches in the short diameter, *r′ r′*, should each produce three. From a glance at Figs. H and J it will be seen that this is not the case in Cassiopea. To be sure, most of the tentacles at this stage are interseptal in position, but the interradial tentacles arise as often from pouches in the long diameter, *r r*, as from those in the short diameter, *r′ r′*; and in both Figs. H and I there is one interradial tentacle that is distinctly septal in position. The septa are still complete, so that there can hardly be any chance of a shifting of position. In the sixteen-tentacle stage, there is a tentacle in the plane of each septum (Figs. K and L); but here the perforation of the septa has commenced, and a shifting of relative position is possible. Even at this stage irregularities are common. For example, one of the septa in Fig. K is placed asymmetrically with relation to the tentacles, and two tentacles are wanting in Fig. L.



Figs. H–L. Diagrams illustrating the space relations between the septa and the tentacles, observed in five young scyphistomas of *Cassiopea xamachana*. r — radii of the long diameter, r′ — radii of the short diameter.

The Strobila, — Development of the Rhopalia. — When the scyphistoma has reached a diameter of about two millimeters, there appear the first characters that are distinctive of the strobila. The first noticeable change in this direction takes place at the bases of the tentacles of the more erect series. This change may be regarded either as the outgrowth of a conical lobe from the margin of the circumoral disc bearing the tentacle at its tip, or as a conical widening of the basal portion of the tentacle. The former view is probably the better. At about this time there appear in the tentacle, just beyond the apex of the cone from which it springs, a few glistening white bodies. These are the so-called otoliths, and mark the beginning of the formation of the rhopalium (Figs. 17 and 18). The tentacles containing these will be called the rhopalial tentacles.

These concretions, or otoliths, increase in number until they form a conspicuous mass, while the basal cone begins to broaden laterally. This is now distinctly noncontractile, and may be spoken of as a marginal lobe of the peristome (Figs. 19 and 20). In the specimen shown in Fig. 21 we see the first indication of strobilization. The upper, expanded part of the calyx is separated from a conical, lower portion by a slight groove. The marginal lobes have become semicircular in outline, and a slight elevation is noticeable on the aboral side of each rhopalial tentacle immediately external to the mass of concretions. The epithelium at this point is pigmented, and forms the first rudiment of the eye (*oc.* Fig. 22). Fig. 23 illustrates a more advanced stage, where the proximal part of the tentacle is beginning to take on its final shape, and is separated by a pronounced bend from the distal portion, which is still functional as a tentacle.

We come finally to a stage in which, while the long distal part of the tentacle retains its characteristic structure and remains completely functional, the short proximal part has become completely differentiated into a rhopalium. Fig. 54 is from a longitudinal section of such a tentacle. The rhopalial part has assumed nearly its final shape. The differentiation of its ectoderm into sensory epithelium, eye-spot, and layer of nerve fibres, is complete. It has a lumen that extends outward to the solid chorda-like endoderm of the distal part of the tentacle, and opens toward the centre into a gastric pocket. The endodermal lining of the lumen is a columnar epithelium, the more distal cells being deeper and containing the concretions. Compare Fig. 54 with Fig. 53, which, being interradial, was certainly destined to be a rhopalial tentacle.

The growth of the marginal lobes, which were semicircular at the stage of Fig. 21, has continued, and each lobe has now produced two secondary ones, one on each side of the rhopalial tentacle. These are connected by a slight ridge that crosses the base of the tentacle on its aboral side (*h.* Fig. 54). The secondary lobes are the rhopalial lobes of the margin of the umbrella (Flügellappen of German authors), and the connecting ridge is the hood (Deckplatte) that covers the rhopalium. These marginal structures may be seen in Fig. 24, and this brings us to another stage in the development of the rhopalium, the absorption of the distal part of the tentacle.

In the strobila shown in Fig. 24, the rhopalial tentacles have a very different appearance from what we have seen before. They are shorter than the other tentacles, and are much swollen at a point just beyond the eye-spot. The distal portion is beginning to degenerate. This process, when once begun, proceeds rapidly. During the few hours that were spent in making this drawing, the rhopalial tentacles were reduced in length nearly one half. The eye-spots and concretions were conspicuous, and in each of the former there was a slight cup-shaped depression. This is the earliest stage in which I observed slight medusa-like movements of the ephyra disc. The tentacle at this stage is in a process of degeneration for about fifteen hundredths of a millimeter outward from the ocellus. In this area of degeneration (*t.* Fig. 55) the endodermal cells are broken down, the supporting membrane has disappeared, and the inner boundary of the ectoderm is indistinct. The axial mass of this part of the tentacle is made up of loose particles of a finely granular substance, in which may be seen many small and deeply stained nuclei. There are also a number of green cells that apparently escaped into the central mass when the supporting membrane broke down. There is evidently a free communication between this mass of disintegrating material and the digestive cavity, through the rhopalial canal.

The method by which the shortening of the tentacle is brought about would seem to be as follows: The axial cells adjoining the cells that bear the concretions (Fig. 54) first break down. Why they should do so, and at this particular time, I cannot say. This disintegration proceeds centrifugally, and it is accompanied by a dissolution of the supporting membrane. The ectodermal cells then either begin here and there to break down while still in place, and the resulting debris is squeezed into the central cavity; or else, the cells migrate, or are squeezed inward and then disintegrate. The continuity of the remaining ectoderm is maintained, however. The products of degeneration probably pass through the rhopalial canal into the digestive tract. As this process continues, the inward movement of the ectodermal cells is more rapid than their disintegration, so that when the distal part of the tentacle is reduced to the size of the rhopalial part (Figs. 25 and 55), it is a solid mass of small cells with small nuclei that stain dark. Some of these cells contain a large vacuole and have the nucleus pushed to one side. Scattered among the small cells, there are a number of globular bodies as large as, or larger than, the green cells, and completely filled with coarse granules that stain deeply with safranin; no nucleus is visible in them. The ocellus has now become distinctly cup-shaped (*oc.* Fig. 55).

At about this time the interrhopalial tentacles begin to be absorbed in their turn (Fig. 25). The umbrellar margin has in the mean time grown out beyond the insertion of each interrhopalial tentacle, on its aboral side, into two lobes with a hood between (Figs. 25 and 26). This structure, although smaller, corresponds exactly to the rhopalial lobes and hood, and is further evidence for the homology between the tentacles and the rhopalia. The drawing reproduced in Fig. 25 was made between the hours of eleven in the morning and two in the afternoon. At five o'clock of the same day the tentacles had been reduced to one third the length shown in the figure, and the absorption of the rhopalial tentacles was very nearly completed.

In the later stages of the absorption of the interrhopalial tentacles, the broken-down material is evidently forced in some way into the radial canal. The rhopalium (Fig. 56) is practically complete at this stage. The point (x) where the last trace of the tentacle proper disappeared, is still distinguishable in sections by the presence of small cells with indistinct cell walls, and by the absence of otoliths.

These observations, then, confirm those of Claus ('**83**,) who, without going into the details of development, maintained that the rhopalia are modified basal portions of the tentacles of the scyphistoma; and they contradict Goette's statement that the rhopalia are developed independently of the tentacles.

Other Phenomena of Strobilization.— While the marginal structures are undergoing the metamorphosis that has just been described, important alterations are taking place in the general shape of the body. The horizontal constriction first noticed in Fig. 21 has deepened (Fig. 24), while the fold below it has heightened, and the upper portion has broadened and flattened, until the condition shown in Fig. 26 is reached. At this final stage the upper portion has all the characteristics of a free-swimming medusa (ephyrula), except that it is attached by a slender aboral stem to the centre of a goblet-shaped basal polyp. The four interradial depressions in the peristome of the earlier stages have become nearly flattened out, all that remains of them being the hollows between the projecting radial angles, or pillars, of the proboscis, which have now become very prominent.

At the stage of Fig. 21, there may be noticed on the proboscis eight patches of thickened ectoderm containing many nettle cells. These nettle batteries are arranged symmetrically, one on each side of each pillar of the proboscis. At a little later stage (Fig. 24) the batteries have become invaginated, forming cup-shaped depressions, thickly crowded with nettle cells in all stages of development.

During the time when the larva is being differentiated externally into an upper and a lower portion, internal changes are taking place in the former, which result in the disappearance of structures characteristic of the scyphistoma and the appearance of others distinctive of the medusa.

The orifices in the gastric septa have become relatively larger (*cs.* Fig. 52 and *rc.* Fig. 57) until the septa are reduced to columnar pillars, columellae, connecting the upper and lower walls of the body and pierced longitudinally by the septal muscles (*c.* Fig. 58). The columellae are called by German authors "Septalknoten," but they are not homologous with the so-called "Septalknoten," or areas of adhesion, in the Peromedusae. The columellae of the Peromedusae are the walls of the large septal funnels where they pass from the subumbrella to the exumbrella, and, according to Haeckel's figures, are separated by the gonads from the areas of adhesion.

In the fully developed scyphistoma of Cassiopea, the septal muscles are solid throughout their length, and there is no cavity corresponding to the septal funnels, which, according to Goette, are well developed in Aurelia. But in the strobila there does appear a slight depression extending a very short distance into the end of each septal muscle. In Figs. 57 and 58, where this is well marked, much of the depression may be due to the strongly contracted condition of the specimens; but other specimens not so contracted show at least the deeper part of the cavity, which therefore, may be truly a vestige of the septal funnel.

At an early stage of strobilization there may be noticed a short conical projection from the central edge of each columella. It extends also around the sides. These projections are probably the rudiments of the first four gastric filaments, which are distinctly developed at the time when the ephyrula is set free (*gf*, Fig. 58).

While the septa are shrinking to become the columellae, ridges appear opposite each other on the upper and lower walls of the peripheral part of the digestive tract between the bases of the tentacles. The epithelial membranes at the summits of opposite ridges unite, and thus there is formed a series of lines of adhesion extending inward from the periphery and dividing the space into a series of radial canals, each ending in a tentacle. The two discs of mesogloea never fuse along these lines of adhesion, but the endoderm remains between them as the endodermal lamella, or cathammal plate. At the stage of Fig. 24 the lines of adhesion occupy about half the space from the margin to the columellae.

The lower disc of the strobila remains simply an annular fold of the body wall until the metamorphosis of the upper disc is nearly complete. The septal muscles in this region bend outward with the rest of the body wall (Fig. 57). At length, however, the endoderm grows out toward the periphery as four shallow pouches, leaving septa between them which contain the longitudinal muscles. Very soon after this the septa are perforated so as to allow a fusion of the endoderm at their upper angles (Fig. 58). In the last stage of strobilization (Figs. 26 and 59) the longitudinal muscles may be traced from the peristome through the columellae and the mesogloea of the exumbrella to the narrow isthmus where the ephyrula disc joins the basal polyp. The latter has now a well-developed peristome (Fig. 59), and the mesogloea in this region is very thin. Just in the isthmus the muscles have disappeared, but they may be found again in the peristome of the basal polyp and traced for a distance close under the epithelium to the edges of the septa, where they bend abruptly downward, and continue through the septa into the stem.

Although seldom visible in the living specimen, sections show that the basal polyp at this stage possesses eight short tenacles (Fig. 59). It has also an annular fold of the ectoderm, closely surrounding the isthmus (Fig. 59 and *p*. Fig. 60). This fold is the rudiment of a new proboscis, which is without doubt entirely ectodermal in origin. But, as Goette has pointed out, it does not follow from this that the lining of the proboscis is ectodermal in scyphistomas developed from the egg. Pulsating contractions of the umbrella are first noticed at the time when the rhopalial tentacles begin to be absorbed (Fig. 24). They are then feeble and at long intervals. At the stage of Fig. 26 these movements are rapid and violent. The rhythm is interrupted by few pauses, and these are short. The result of these movements is that the thin wall of the isthmus is ruptured, and the ephyrula is set free.

After this separation, the basal polyp has the appearance represented in Figs. 27 and 28. It is a scyphistoma with seventeen short tentacles and a rudimentary proboscis (Figs. 61 and 62). The proboscis and the tentacles grow rapidly, so that in a few days it is impossible to distinguish a regenerated basal polyp from a young scyphistoma in the sixteen-tentacle stage, except that the former has a somewhat thicker stem. It may be inferred from this complete regeneration of the basal polyp that it undergoes repeated strobilization, as Claus[1] has found to be the case in Aurelia.

The Ephyrula.—The ephyrula of Cassiopea is very different in appearance from the corresponding stage in ordinary scyphomedusae with eight rhopalia. Cotylorhiza has an ephyrula resembling the same stage in the semostomatous medusae. Good figures of this are given by du Plessis and Claus, and there is a striking difference between these figures and Figs. 29 and 30 in this paper, which are camera drawings of well-preserved ephyrulas of Cassiopea, mounted in balsam. Fig. 29 represents a young Cassiopea that has not long enjoyed a free existence. The general shape of the umbrella is like that of the adult, and there is the same concavity in the centre of the exumbrella, while the margin curves in the opposite direction, as in Fig. 64. The typical ephyrula of Aurelia or Cotylorhiza has eight marginal arms with two lobes at the end of each, and between each pair of lobes there is a rhopalium. In Cassiopea structures corresponding to these arms are present to the number of sixteen, or often more. But these do not destroy the general circular outline of the animal, for they are connected by thin areas on the umbrella, alternating with an equal number of ridges, which at an earlier stage bore the interrhopalial tentacles on their under sides.

We have, then, at this stage the marginal zone of the umbrella marked by a number of short radial ridges separated by an equal number of thin areas. The ridges are in line with the radial canals. At the peripheral end of each ridge the margin of the umbrella is produced into two lobes, those adjoining the rhopalia being well marked, the others small and inconspicuous (*il.* Fig. 30).

In Fig. 29 there are seventeen, and in Fig. 30, twenty-three, rhopalia. The latter is an unusually large number, and it will be noticed that the number of marginal lobes has not increased in proportion, so that irregularities of the margin occur in many places, as described in the section on variations.

At this stage the rhophalia have come to lie, as in the adult, wholly within the margin of the umbrella, and project from its subumbrellar surface. The interrhopalial tentacles

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[1] See foot-note, Claus ('92).

have totally disappeared. The lines of adhesion separating the radial canals are faintly visible as radiating lines of greater transparency.

The four lips of the mouth are spread out into a cross-shaped figure, and one may look directly through the lumen of the oesophagus into the stomach and see the four gastric filaments (Figs. 29 and 30). Each one of the four lips is nearly square, and from its two outer angles there are two grooves that extend obliquely inward until they meet and form a V. The point of the V is in an angle of the oesophagus, along which there is a groove that is continuous with the other two grooves, and that extends into the stomach. On the interradial side of each of the eight labial grooves, there may be seen a small roughly circular area that is less transparent than the rest. These areas are the nettle batteries, first seen in the strobila. The margins of the lips are provided with numerous small processes, the digitella, which are arranged in a single continuous series.

Fig. 63 is a section of an ephyrula that has just become free. In this stage there is still an opening through the aboral wall of the stomach, and one may see the last vestige of the connection between the columella and the exumbrella, which contains also the degenerating remnants of the septal muscle.

At a little later stage, when the opening in the roof of the stomach has closed, both the septal muscles and the septal funnels totally disappear. Sometimes one, sometimes the other, is the first to vanish.

The Later Stages.—The later stages in the development of Cassiopea will be treated very briefly. While the umbrella remains at first unchanged, the metamorphosis of the mouth parts is inaugurated by the growth of the two outer angles of each of the more or less quadrate lips, so that they are soon drawn out into extended lobes (Fig. 31). At the same time the pillars of the proboscis thicken, and the mesogloea is continued outward along each of these lobes as a midrib. We have then eight oral arms, each with a longitudinal groove, supported by a midrib, and fringed with digitella,—arms very similar to those characteristic of the genus Aurosa Haeckel ('79). But it is only the mouth parts of Cassiopea that may be said to pass through an Aurosa stage, for the comparison cannot, at this time at least, be carried to the other organs.

Claus has described ('83) some of the principal stages in the metamorphosis of Pilema (Rhizostoma) and Cotylorhiza. He regards the formation of the eight oral arms as a different process in these forms from what occurs in Aurosa. But it appears to be merely the same thing expressed differently.

In the next stage we find two oral funnels, or oscula, and a small vesicle developed at the tip of each oral arm. The other portions of the arm are still open and fringed with digitella, as before, but the outline is no longer a regular curve, for there are folds in the margin. The deepest folds are the most distal, and they become progressively more shallow toward the base of the arm. The central mouth is still widely open. The subgenital cavities are well developed at this stage. Figs. 64, 65, and 66 show how the oral disc is formed, and how the subgenital cavities are produced by the great increase in thickness of the mesogloea at the pillars of the proboscis and the bases of the oral arms. By the growth of these structures, the subgenital cavities are necessarily produced. The only special adaptations are the subsequent growth and folding of the aboral wall and the narrowing of the orifice.

The marginal lobes of the umbrella now begin to broaden, and thus approach the adult condition, but there is only a single "vellar" lobe between two rhopalial ones.

At a little later stage, when there are three oral funnels at the tips of the arms (Fig. 33), the re-entrant angles between the pillars of the proboscis have grown inward, met at the centre, and fused. In this way the lumen of the oesophagus is divided into four tubes (Fig. 32), representing the grooves that were present in its angles in the earlier stages. In the figure the fusion at the centre has gone so far as to involve the edges of the lips, and the labial grooves of the different pairs of arms are not in open communication, but a short cross-shaped tube connects them at the centre, and the oral disc is now completed.

It is interesting to note that Claus has found a stage both in Pilema and in Cotylorhiza that, while showing the characteristic family differences, has also a certain resemblance to this stage in Cassiopea. In all three the walls of the proboscis have fused so as to divide its lumen into four tubes, and the formation of oscula has begun at the tips of the arms in such a way that we have on each arm three oscula with a vesicle in the angles between them. The occurrence of this stage in the ontogeny of three so distinctly separated families must have some morphological significance, and we may regard these eight primary vesicles as homologous in the three groups.

The mode of formation of the oral funnels becomes evident at this stage. They are not formed in Cassiopea simply by a series of fusions of the lips along the line of the labial groove, as Hamann ('81) states to be the case in Cotylorhiza. It is more like the process in Pilema, as described by Claus. Each of the primary funnels is represented at first by one of the folds in the margin of the lips referred to above (Fig. 33). The fold deepens, and its edges are brought together on the ventral side and fuse, leaving an opening at the apex of the fold, the osculum. At the same time the labial groove in this region is converted into a canal by the fusion of the lips on its two sides. After the fusion all trace of what has occurred quickly disappears.

With the division of the oesophagus into four tubes, and the completion of the oral disc, our larva comes to be distinctly a rhizostomatous medusa. Further development of the mouth parts consists in the continued division of the labial, or brachial, grooves into oral funnels and brachial canal, together with the development of oral vesicles. By the time two or three vesicles have been formed on the end of each arm, a vesicle appears in the centre of the oral disc. Except for this interruption, the development of the mouth parts proceeds regularly in a centripetal direction. The funnels and vesicles are formed first at the tips of the arms, and then one after another in regular succession toward the centre. Each of these primary funnels is the rudiment of one of the primary branches of the arm. When the process of forming funnels has reached about half the length of the arm, the distal funnels begin to subdivide. By this subdivision of the primary funnels new ones are produced, of which some are the rudiments of secondary branches; these subdivide again, and so on, as long as growth continues. The subdivision is not dichotomous, but takes place in such a way as to produce alternate branches. The formation of a vesicle takes place at this stage in some way at about the time of the completion of the adjoining funnel. I have not been able to determine whether the vesicle is a funnel with the orifice closed, as Hamann claims it to be, or whether it is an evagination from the pedicle of a funnel, as at first it seemed to me to be, and as Claus thinks it probably is.

According to Haeckel ('79), the genus Archirhiza represents a form that was the ancestor of all the rhizostomatous medusae. Of this genus there are two known species, *A. primordialis* Haeckel, and *A. aurosa* Haeckel. They agree in having four subgenital cavities and eight simple unbranched arms that are provided with a single zig-zag row of closely set oral funnels, and are devoid of other appendages. Hamann says that a stage representing this condition is a feature of the ontogeny of rhizostomatous medusae. From what has been said it is evident that we have no such stage in the development of *Cassiopea xamachana*, for while the labial groove is still open in the proximal half of the oral arm, in its distal half the vericles are formed, and branches are in the process of formation.

The outline of the umbrellar margin has not changed essentially since the last stage. The areas of adhesion have become much wider than the radial canals they separate, and in them there has appeared a network of anastomosing canals, while the gastric filaments have become numerous.

We have now followed the larva of our Cassiopea from its first appearance as a bud to a point where, with the exception of the gonads, all the organs of the adult are outlined. Here we must take leave of it.

Summary and Conclusions.

Cassiopea and Polyclonia are genera of rhizostomatous medusae peculiarly modified in adaptation to a sedentary mode of life in shallow water among the mangroves bordering tropical seas. A comparison of specimens of *Polyclonia frondosa* Ag. with *Cassiopea xamachana* shows that these two forms are specifically distinct, although in general appearance they are very similar and they have the same geographical range and habitat.

C. xamachana is remarkable for its variability. This is especially shown in the appendages to the mouth parts and in the structures at the margin of the umbrella. It will be noticed that the most frequent number of rhopalia, in the twenty-seven specimens examined, was sixteen, which is the typical number for the genus. But the variations are not arranged symmetrically on the two sides of this mode, for specimens having a greater number of rhopalia are more than twice as many as those having less. The species shows a strong tendency toward duplication of the rhopalia and associated structures of the umbrella; and at the same time the symmetrical relations of the parts tend to be preserved. The great majority of scyphomedusae have only eight rhopalia, and in Cassiopea with its sixteen rhopalia we have a beautiful illustration of Darwin's law that "A part developed in any species in an extraordinary degree or manner, in comparison with the same part in allied species, tends to be highly variable." Study of the color markings and measurements of the mouth parts indicates the division of the species into three varieties; and it was in one of these, var. *A*, that the duplication of marginal organs was especially prevalent.

The color of both larvae and adults is due to a great extent to the presence in the mesogloea of minute symbiotic algae. That these are plant cells was demonstrated by micro-chemical tests. Their presence undoubtedly enables the medusae to live in water that would be too poor in oxygen for most marine animals.

The search for developing eggs proved unsuccessful, but scyphistoma larvae were abundant, and it was found that they were multiplying rapidly by budding.

The bud arises as an evagination of the body wall of the scyphistoma. There is no evidence of any special gemminal epithelium. The bud, when set free, differs from a planula chiefly in the possession of a well-defined mesogloea and four septal muscles. The septal muscles are shown to be formed as branches of the two adjacent septal muscles of the parent. The mouth of the young scyphistoma is formed by a minute perforation at the former point of attachment, while the distal end of the bud becomes the stem. This remarkable orientation agrees with what Goette and Claus have found in Cotylorhiza. In the formation of the mouth there is no evidence of any invagination of ectoderm Apparently the oesophagus, as well as the gastric pouches, is lined with endoderm. On the other hand, the oesophagus of the lower disc of the strobila is formed wholly of ectoderm.

The four radial tentacles are formed simultaneously, and the four interradial ones appear at the same time or slightly later. These are followed by eight adradial tentacles and sixteen more are added a little later, making thirty-two in all. It was found that the rudiments of the interradial tentacles are not at all constant in position with relation to the septa. Some were septal, others were interseptal, sometimes on one side of the septum, sometimes on the other, thus agreeing with the observations of Claus on Aurelia and Cotylorhiza.

The four gastric pouches are formed at the same time by the ingrowth of the septa. They are soon brought into communication at the periphery by the perforation of the septa, which become reduced to columellae surrounding the longitudinal muscles.

Contrary to Goette's opinion, it may be stated positively that the rhopalia are differentiated in the bases of alternate tentacles. After the rhopalium is fully developed, the distal part of the tentacle undergoes degeneration and is absorbed. The development was traced for the first time through all its stages, and the opinions of Agassiz, Claus, and Lendenfeld are fully confirmed.

The scyphomedusae are the only coelenterates, which possess four longitudinal muscles of ectodermal origin completely imbedded in the mesogloea between the points of insertion. The buds of Cassiopea have this distinctively medusoid characteristic long before they are detached. Moreover, the methods by which the mouth and the gastric pouches are formed differ entirely from what is said to take place in larvae that pass through an anthozoan stage. Therefore, whatever may be true of the larvae derived from eggs, this stage is certainly omitted in larvae produced by budding.

The first step toward the formation of the free-swimming medusa is the perforation of the gastric septa which takes place in the young scyphistoma before it is fully developed. Then follows a period of growth and reproduction by budding, and further metamorphosis begins finally with the process of strobilization. Besides the differentiation of the sense organs and the development of the marginal lobes of the umbrella, the most important events are the development of the angles of the mouth into quadrate lobes and the fusion of the two layers of endoderm along certain areas of adhesion so as to divide the periphery of the digestive tract into a series of radial canals. Only one medusa is formed; but, separated from this by a constriction, is a small basal segment which, a short time before the medusa becomes free, begins to develop gastric pouches, tentacles, and a proboscis. This becomes eventually a perfect scyphistoma, and after a period of growth probably undergoes strobilization again.

There has been considerable discussion in regard to the nature of strobilization; the question being whether the medusa is to be regarded as a metamorphosed scyphistoma, or as derived from the scyphistoma by a process of budding. In the monodiscous strobila of Cassiopea we have clearly a metamorphosis. The form of the medusa is the result of a series of changes which begin very early and involve all the essential organs of the scyphistoma. The portion not involved in these changes merely serves as a mechanical support. That this part is separated off and regenerates the lost parts, instead of being absorbed, may be regarded as merely an incidental fact.

If there be any question of budding it refers to this basal segment. And this suggests a striking analogy between the basal polyp and the peculiar planula-like buds. In the first place they have the same orientation relative to the upper disc. In both, the distal end forms the stem and the proximal end forms the mouth. In the second place, they have essentially the same structure. Each one consists of a simple sac with a wall made up of three layers, ectoderm, mesogloea and endoderm, and each is provided with four longitudinal muscles imbedded in the mesogloea. What differences appear in the subsequent development, may be attributed to the different ways in which the two become separated from the disc and to the greater size of the longitudinal muscles in the basal polyp. The production of supernumerary tentacles, rhopalia, and marginal lobes, is common in this species. Why may we not regard the buds as supernumerary basal polyps, and their subsequent development as a process of regeneration preserved and modified by natural selection for its obvious advantage?

The ephyrula of Cassiopea has the same number of rhopalia as the adult, and differs in shape from the corresponding stage of ordinary scyphomedusae with eight parameres.

The most important event in the later stages is the metamorphosis of the mouth parts. The angles of the four quadrate lips become extended to form eight oral arms somewhat similar to those found in the adult Aurosa. There is no Archirhiza stage, but there follows a stage with the oesophagus divided into four tubes, and with three oscula and an oral vesicle on each arm. A similar stage has been found in Pilema and Cotylorhiza, and it may have some phylogenetic significance.

The studies of numerous investigators upon the Ascidians have demonstrated that a knowledge of the gamogenetic development of an animal will not always enable one to predict how the organs will be formed in the agamogenetic process. So it may be objected that the results set forth in this paper do not afford a valid basis for the criticism of work done by others on larvae developed from the egg. On the other hand, the eight-tentacle stage of the bud larva of Cassiopea is so like the same stage of the sexually produced larva of its near relative Polyclonia that it would be impossible to tell them apart, and, in the absence of any evidence to the contrary, there seems to be no necessary reason for supposing that their later history is different. At any rate, we have here the first fairly complete history of the development of a scyphomedusa from the bud; and when the sexual development of *Cassiopea xamachana* or an allied species is studied, this memoir will serve as a means of comparison, and will make it possible to determine whether or not the two modes of ontogeny are alike.

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EXPLANATION OF PLATES.

All the figures from 1 to 28, and Figs. 34 and 35, are freehand drawings made from the living animals. Figs. 29 to 33 are from well-preserved specimens mounted in balsam, and were outlined with the camera lucida. The remaining figures, except Fig. 37, are camera-lucida drawings of microtome sections. All the figures are reduced uniformly to slightly less than one half the diameter of the original drawings.

LETTERING COMMON TO ALL THE FIGURES.

b. — bud.
c. — columella.
c d. — circum-oral disc, or peristome.
c s. — circular sinus.
cx. — calyx.
d. — digitellum.
ect. — ectoderm.
e l. — endodermal lamella, or cathammal plate.
end. — endoderm.
e u. — exumbrella.
g. — stomach.
g f. — gastric filament.
g p. — gastric pouch.
h. — hood.
i l. — interrhopalial lobe.
i t. — interrhopalial tentacle.
l g. — labial groove.
m. — mouth.
mes. — mesogloea, or supporting membrane.
n f. — nerve fibres.
o a. — oral arm.
oc. — ocellus.
o d. — oral disc.
oe. — oesophagus.

oe. t. — oesophageal tube, or canal.
os. — osculum.
ot. — rhopalial concretion (otolith).
p. — proboscis.
p p. — pillar of the proboscis.
r c. — radial canal.
rh. — rhopalium.
rh. c. — rhopalial canal.
rh. t. — rhopalial tentacle.
s. — stem.
s e. — sensory epithelium.
sep. — septum.
s f. — septal funnel.
s g. — subgenital cavity.
s m. — septal muscle.
s n. — subumbrella.
t. — tentacle.
v. — vesicle.
za. — brownish green cells, symbiotic algae.

PLATE 31.

Fig. 1. Portion of the calyx and stem of a scyphistoma with a fully developed bud (*b*) attached. *A*, the outline of the same bud when contracted.

Fig. 2. Similar to the preceding, except for the formation of a second bud (b') which bears the older one (*b*) upon its apex.

Fig. 3. The form of the planula-like bud during the first two days after becoming free. *A*, *B*, and *C*, are the successive changes in shape observed in one specimen during a few minutes. The arrows show the direction in which it swims.

Fig. 4. Larva of probably the third day. *A*, lateral aspect; *B*, oral aspect.

Fig. 5. A larva of about the same age, 48 hours or over.

Fig. 6. Another larva of 48 hours or over.

Fig. 7. Larva of the fourth day.

Fig. 8. Free scyphistoma of the fifth day, with rudiments of four tentacles. The arrows show the direction of progression and rotation.

Fig. 9. A scyphistoma of about the same age, with the rudiments of eight tentacles.

Fig. 10. Oral aspect of a similar larva, perhaps somewhat younger.

Fig. 11. A scyphistoma a little more advanced, probably in the fifth day.

Fig. 12. A still more advanced scyphistoma of the fifth day. The four tentacles first formed are much longer than the other four.

Fig. 13. Scyphistoma of the sixth day, attached, and with eight tentacles.

Fig. 14. Scyphistoma with rudiments of the second set of eight tentacles. Two tentacles of the first series are bifurcated.

Fig. 15. Scyphistoma with sixteen tentacles fully developed, in the attitude of feeding.

Fig. 16. Oral aspect of a similar specimen.

PLATE 32.

Fig. 17. Scyphistoma showing first traces of rhopalial structure.

Fig. 18. A small portion of the margin more highly magnified.

Fig. 19. Scyphistoma at a slightly older stage.

Fig. 20. Small part of the margin of a similar larva.

Fig. 21. An early stage in strobilization.

Fig. 22. A rhopalial tentacle of the same specimen seen from the side.

Fig. 23. An older rhopalial tentacle.

Fig. 24. Strobila in which the rhopalial tentacles have begun to degenerate.

PLATE 33.

Fig. 25. Strobila, in which the degeneration of the rhopalial tentacles is nearly completed, and the interrhopalial tentacles have begun to degenerate.

Fig. 26. A complete strobila. The basal polyp bears a bud which broke off and swam away while the drawing was being made. The ephyrula was detached during the following night. The rhopalia are visible through the umbrella. At *y*, is a pair of twin rhopalia ; compare *y*, Fig. 30.

Fig. 27. The basal polyp of the same specimen, a few hours after the separation of the ephyrula.

Fig. 28. Optical section of the same.

Fig. 29. An ephyrula recently set free. Oral aspect. The gastric filaments are visible through the mouth. × 31.

Fig. 30. A specimen of about the same age, showing variations of the margin at *u*, *w*, *x*, *y* and *z*. × 31.

PLATE 34.

Fig. 31. Mouth parts of a young medusa in the Aurosa stage. The gastric filaments may be seen through the central mouth opening. × 33.

Fig. 32. Oral disc of an older specimen. The oesophageal tubes appear as light areas, one at the junction of each pair of labial grooves.

Fig. 33. One of the oral arms from the same specimen as Fig. 32.

Fig. 34. Floor of the stomach and the oral arms of an adult viewed from the aboral side. The roof of one subgenital cavity is removed, and a thread is represented as passing through the external orifice into this cavity, at *x*. The ultimate branches are represented on only one of the oral arms.

Fig. 35. Portion of the aboral surface of an adult. About half natural size.

PLATE 35.

Fig. 36. Section of a young bud. × Zeiss DD + oc. 2.[1]

Fig. 37. Diagram to show the branching of the septal muscles, sm_1, sm_2, sm_3 and sm_4, and the connections of the septal muscles of the bud, sm'_1, sm'_2, and sm'_3. Reconstructed from the series of sections of which Fig. 36 is one.

Fig. 38. Section through the distal apex of an older bud, showing the attachment of a septal muscle to the ectodermal epithelium. × Zeiss H + oc. 2.

Fig. 39. Longitudinal section of a planula-like larva. *D* was the distal, and *P* the proximal, end of the bud while attached. × Zeiss DD + oc. 2, dt. 160.

Fig. 40. Longitudinal section through the posterior end of a swimming larva, in which changes preparatory to the formation of the mouth are taking place. × B & L $\frac{1}{8}$ + Zeiss oc. 2.

Fig. 41. Similar section of a slightly older larva, showing the mouth as a small opening not exceeding in width the thickness of the section. × B & L $\frac{1}{8}$ + Zeiss oc. 2, dt. 160.

Fig. 42. Adradial section of a scyphistoma a little older than Fig. 9 (5th day). × Zeiss DD + oc. 2.

Fig. 43. Obliquely transverse section of a specimen of the same age, showing the greatest width of one septum. × B & L $\frac{1}{8}$ + Zeiss oc. 2, dt. 160.

Fig. 44. A tangential section of an older larva, showing the connection of a septal muscle with the circum-oral disc. × Zeiss H + oc. 2.

PLATE 36.

Figs. 45 to 47 are consecutive transverse sections of one individual. Fig. 45 shows the continuity between the endoderm of adjacent gastric pouches at the base of an interradial tentacle. Fig. 47 is lower, and here the gelatinous septum completely separates the two pouches. × Zeiss H + oc. 2.

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[1] Unless otherwise noted, the microscope was used with the draw tube not drawn out. Length of tube (dt.) = 137 mm.

Figs. 48 and 49 are from the same series. Fig. 48 is the second section below Fig. 47. It just clears the oesophagus. Fig. 49 is through the upper part of the stem. × Zeiss DD + oc. 2.

Fig. 50. Longitudinal section of a scyphistoma with sixteen tentacles, probably a little younger than Fig. 15. × Zeiss. DD + oc. 2, dt. 195.

Fig. 51. An obliquely transverse section of a fully developed scyphistoma, showing the relations of the septal muscles to the depressions in the circumoral disc. The mesogloea is shaded. × Zeiss B + oc. 2, dt. 160.

Fig. 52. Part of an interradial section from a scyphistoma a little older than the last. Owing to a slight obliquity of the section, the full extent of the circular sinus at the base of the tentacle is not shown. It extends to the point marked x. × Zeiss C + oc. 2.

PLATE 37.

Figs. 53 to 56 illustrate the development of the rhopalia.

Fig. 53. Median section of the interradial tentacle shown in Fig. 52 ; x marks a corresponding point in the two sections × Zeiss H + oc. 2.

Fig. 54. A radial section from the base of a rhopalial tentacle somewhat older than Fig. 23. × Zeiss H + oc. 2.

Fig. 55. Radial section of a rhopalium in the stage of Fig. 25. × Zeiss H + oc. 2.

Fig. 56. Radial section of a rhopalium in about the stage of Fig. 26. × Zeiss H + oc. 2.

Fig. 57. Radial section showing the course of a septal muscle in a strobila, at the stage of Fig. 24. × Zeiss DD + oc. 2.

Fig. 58. A similar section from a specimen a little older than Fig. 25 ; x, point of separation between the two discs. × Zeiss DD + oc. 2.

PLATE 38.

Fig. 59. Median vertical section of a strobila in the stage of Fig. 26 ; x, boundary between ephyrula and basal polyp. × Zeiss B + oc. 2.

Fig. 60. Portion of section from the same specimen, showing the proboscis of the basal polyp ; x marks same point as in preceding. × B & L $\frac{1}{6}$ + Zeiss oc. 2, dt. 160.

Fig. 61. Median vertical section of a basal polyp, stage of Fig. 27. × Zeiss B + oc. 2.

Fig. 62. Part of a section from the same specimen, showing the proboscis, p, and the vestige of the former connection with the ephyrula at x. × B & L $\frac{1}{6}$ + Zeiss oc. 2, dt. 160.

Fig. 63. Median vertical section of an ephyrula that has recently become free ; x is opposite the opening that formerly led into the cavity of the basal polyp. Cf. Fig. 29. × Zeiss DD + oc. 2.

Fig. 64. Median vertical section from a young medusa intermediate in age between Figs. 31 and 32. The section is nearly interradial in position. × Zeiss AA + oc. 2, dt. 160.

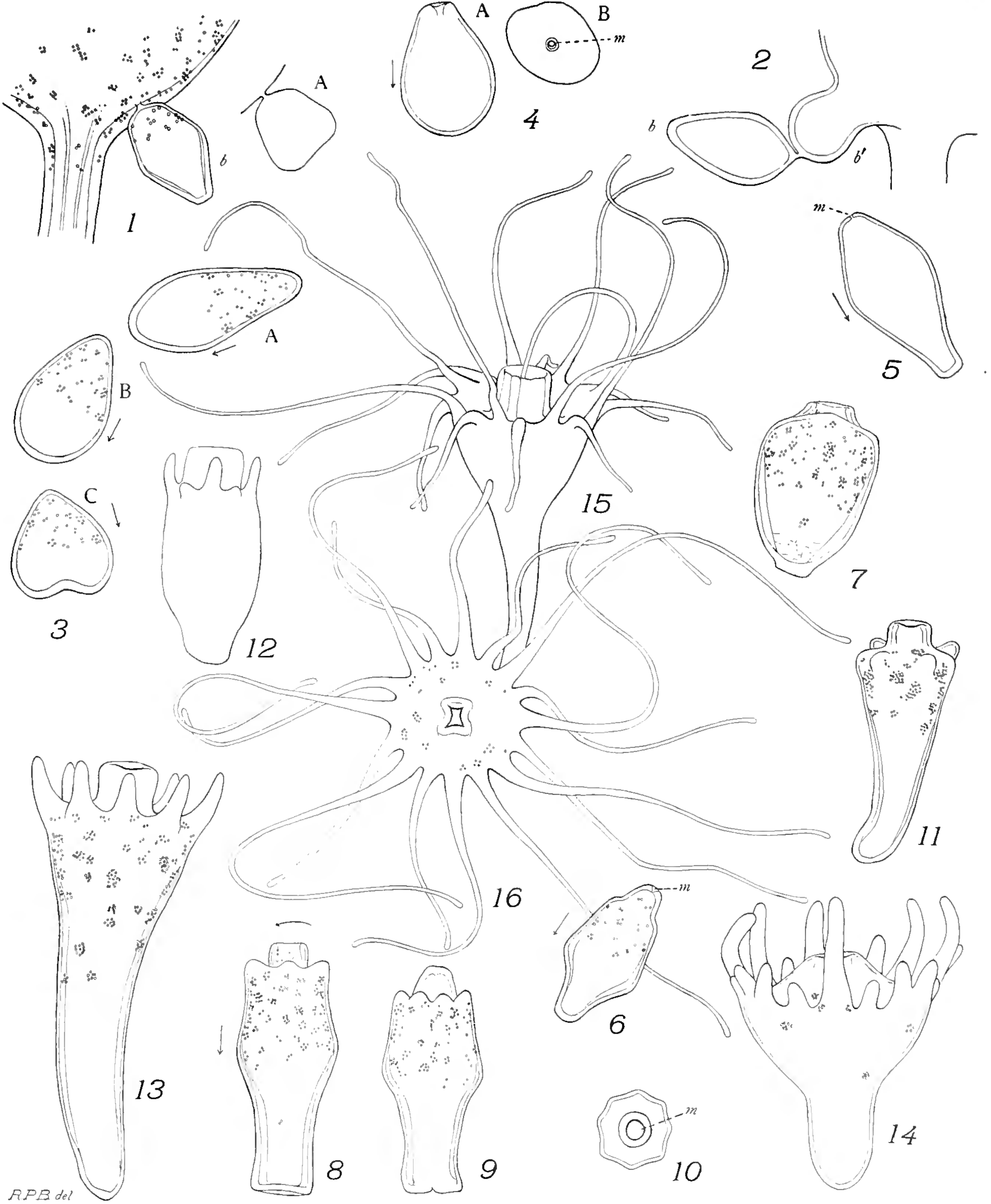
Figs. 65 and 66. Tangential sections of the same specimen, parallel to the last, nearly at right angles to an interradius. Fig. 66 is the one nearer the periphery. × Zeiss AA + oc. 2, dt. 160.

Printed, August, 1900.

VITA.

The author of this thesis, Robert Payne Bigelow, is the son of Otis and Margaret Payne Bigelow, and was born in Baldwinsville, New York, on the 10th of July, 1863. Since 1868 he has resided in the City of Washington, where he attended the public schools and afterward studied for two years, until 1882, in the Preparatory School of the Columbian University. A year was spent as bookkeeper for the firm of Otis Bigelow & Co., after which he entered the Lawrence Scientific School at Harvard University, whence he was graduated in 1887 with the degree of Bachelor of Science, *magna cum laude*.

Another year was spent in business, and then he entered the Johns Hopkins University as a candidate for the degree of Doctor of Philosophy, taking Animal Morphology as his principal study, with Physiology and Botany as subordinate subjects. While in this University he has held the positions of University Scholar, Fellow, and Adam T. Bruce Fellow.



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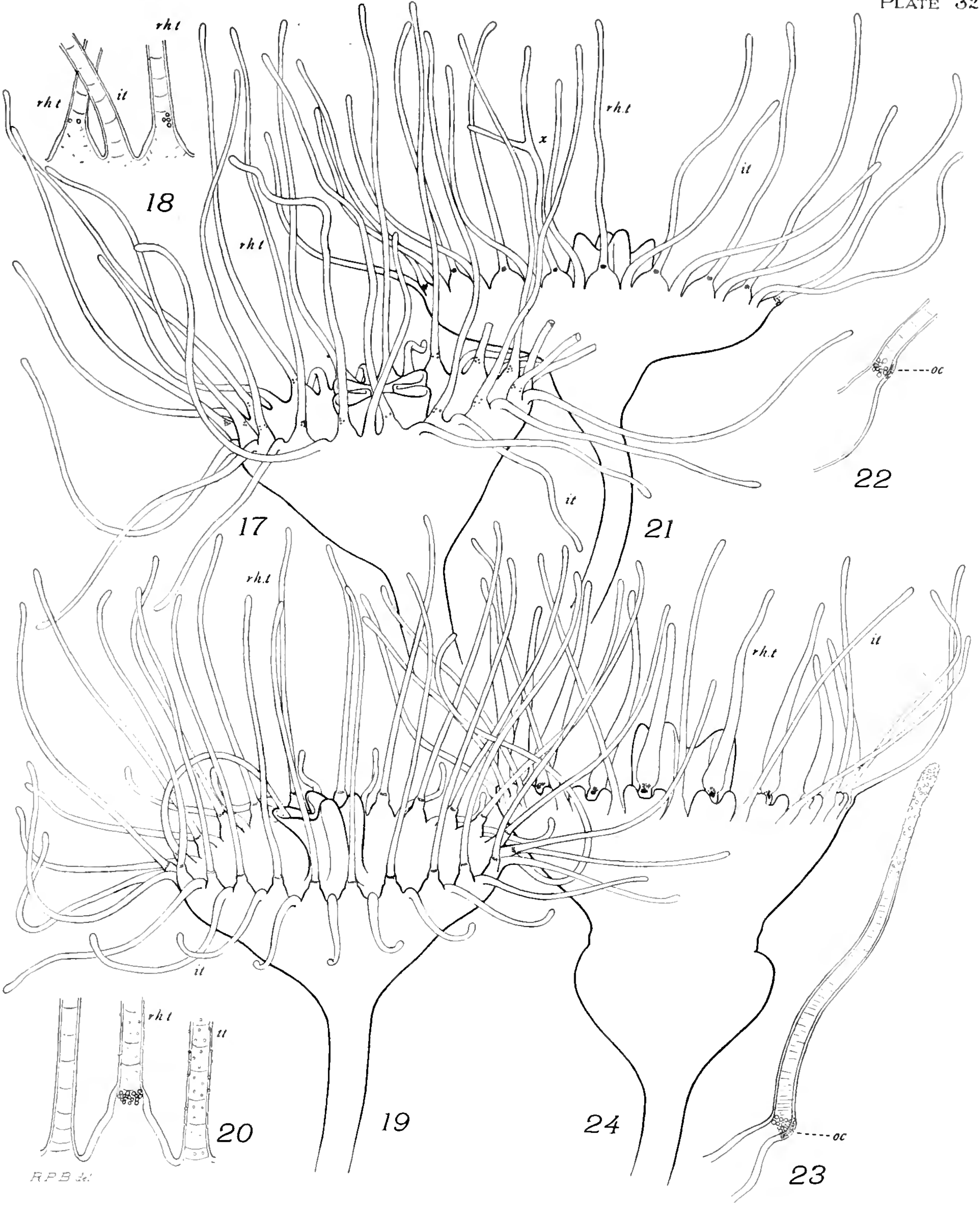

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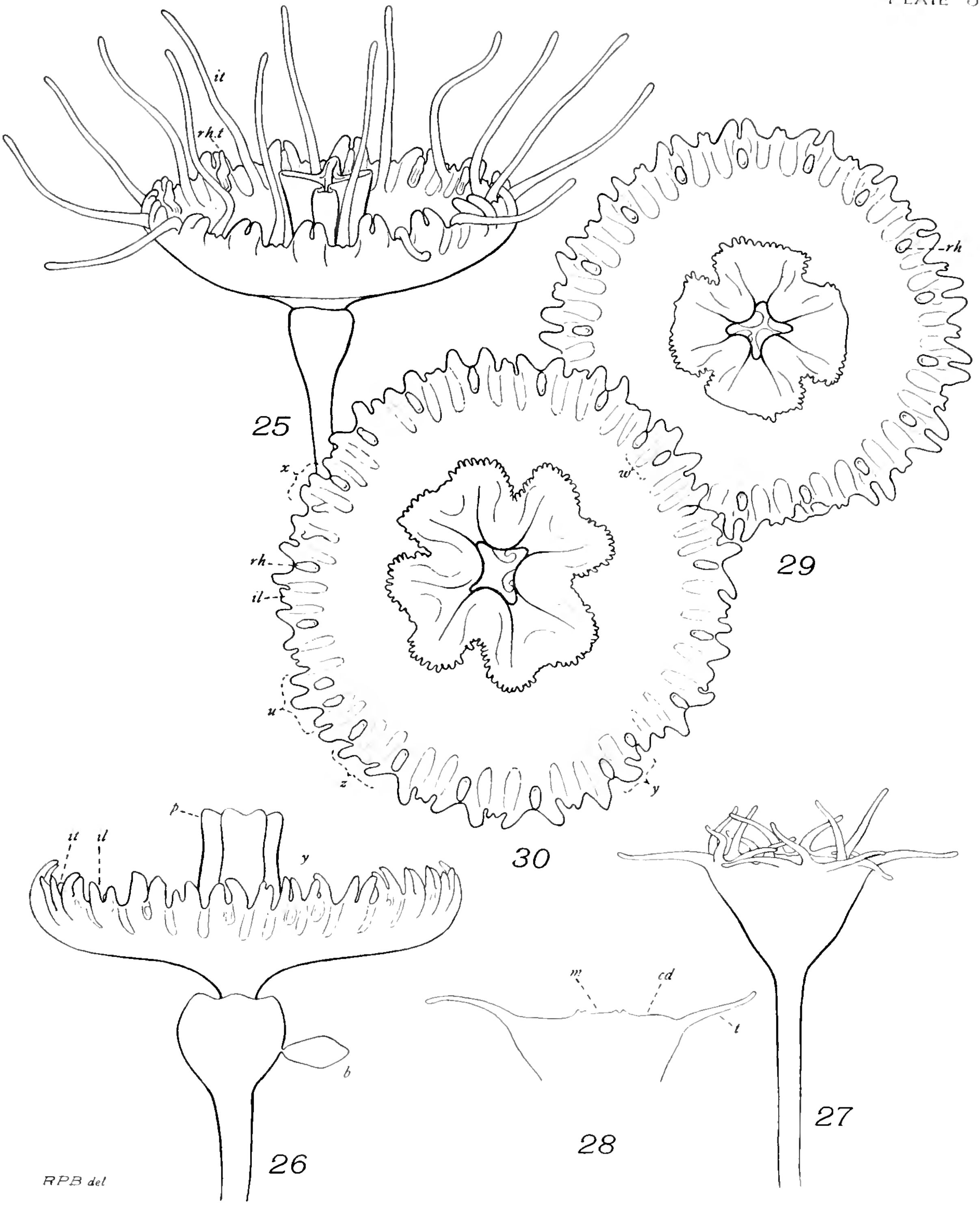

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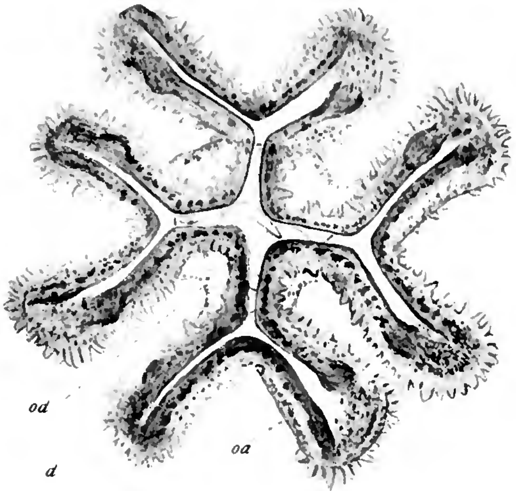

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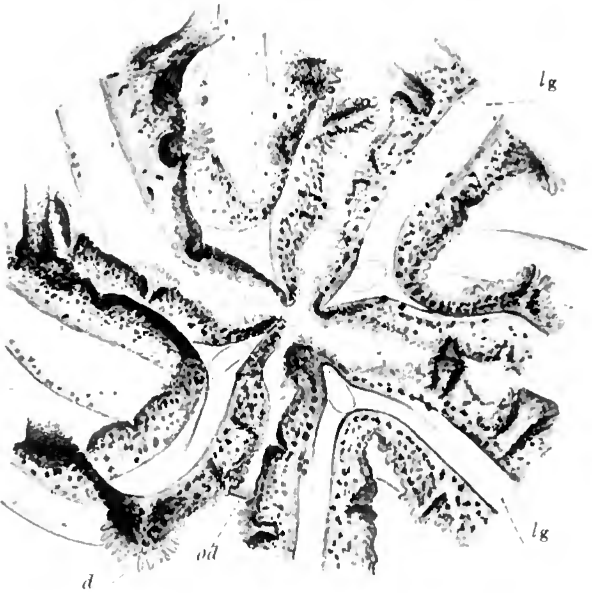

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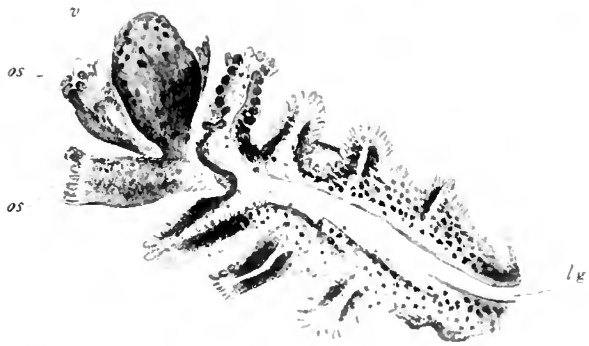

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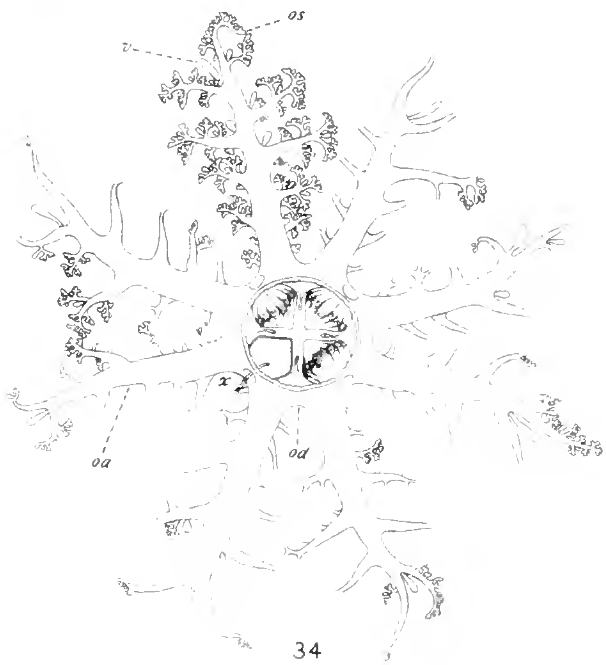

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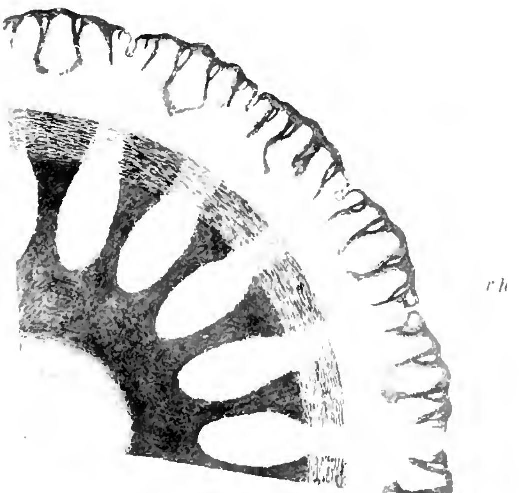

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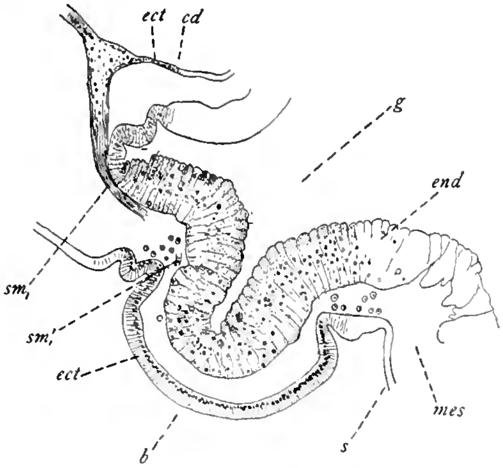

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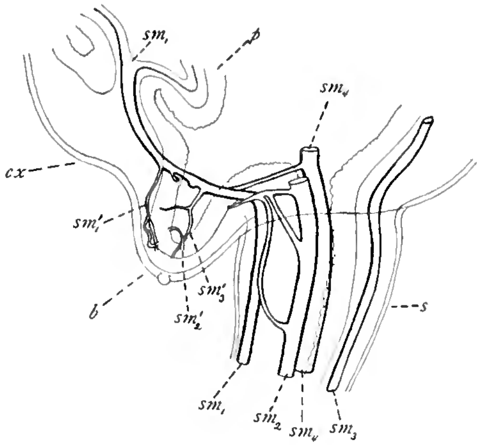

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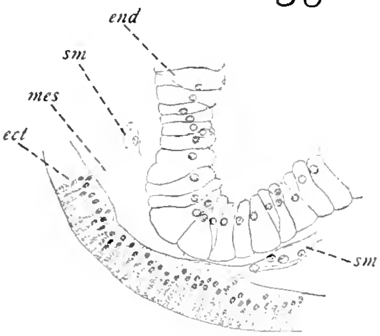

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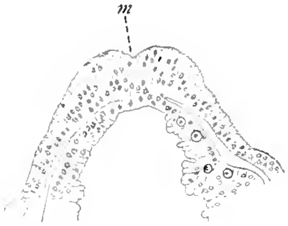

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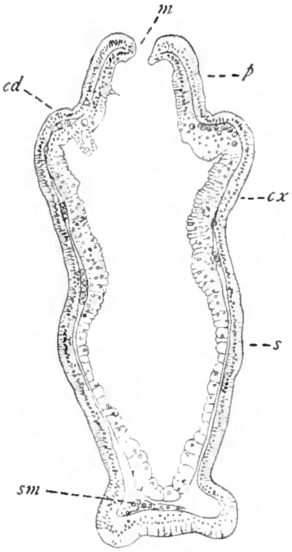

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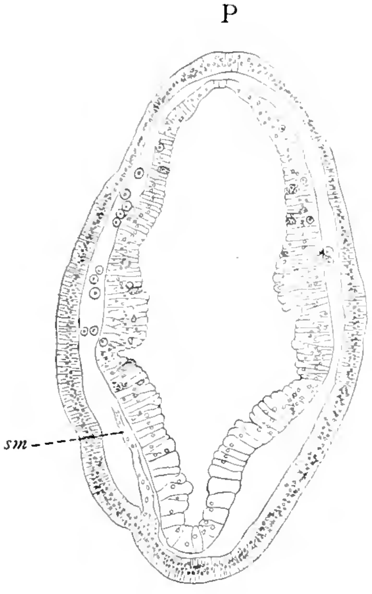

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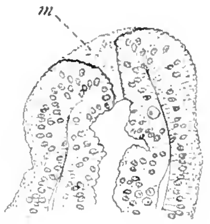

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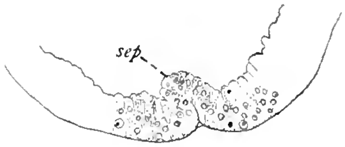

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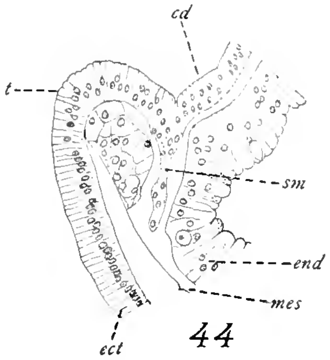

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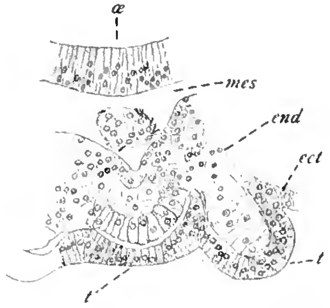

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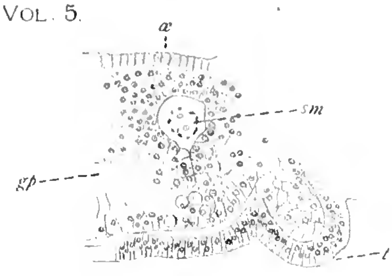

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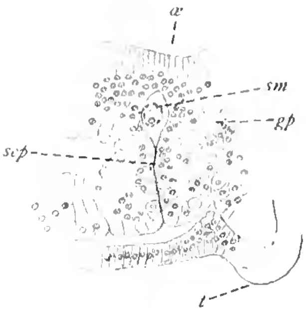

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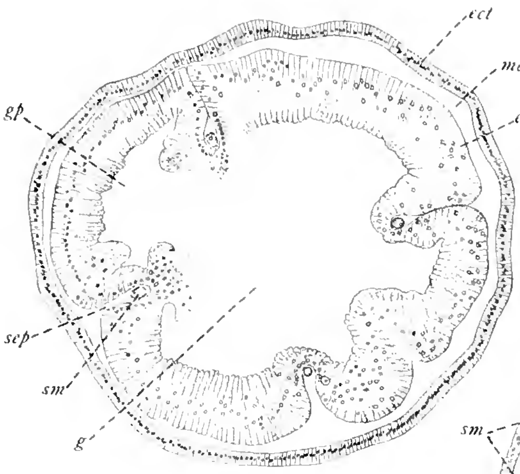

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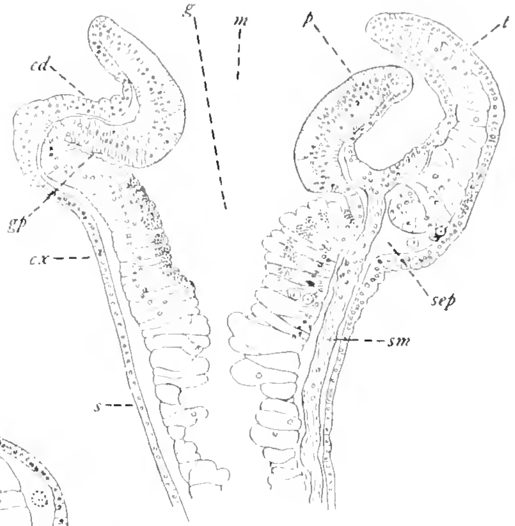

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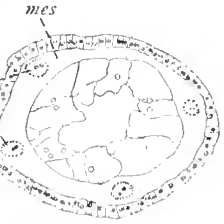

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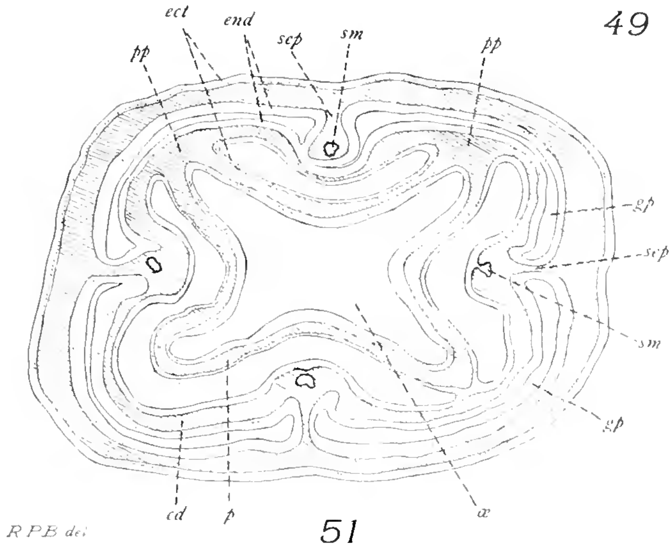

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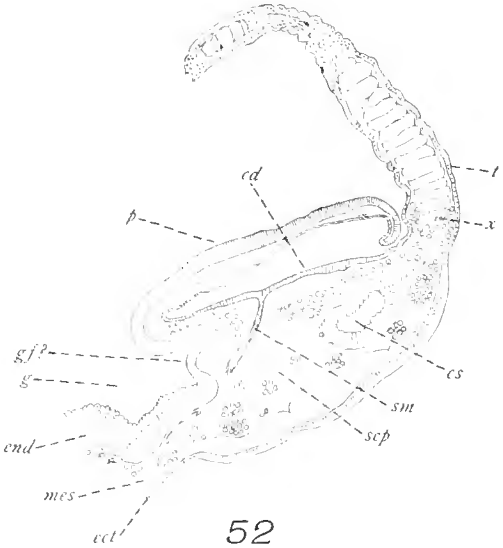

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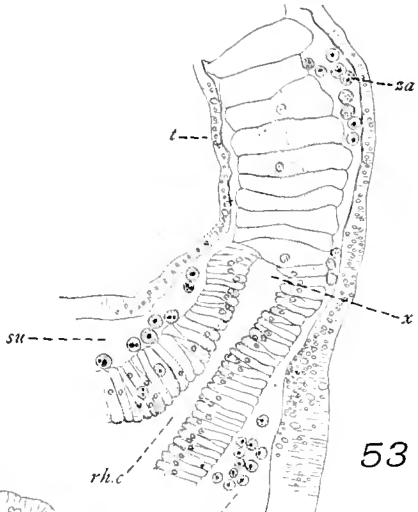

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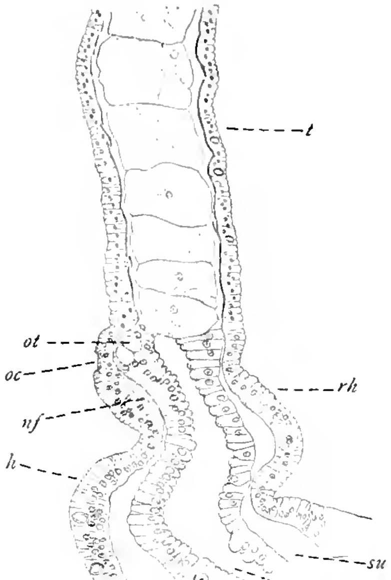

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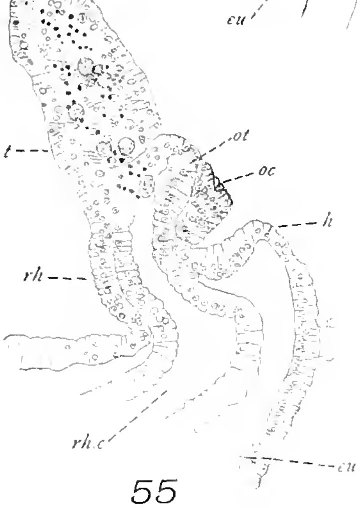

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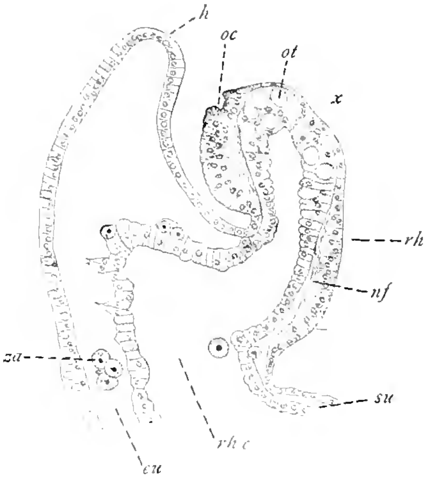

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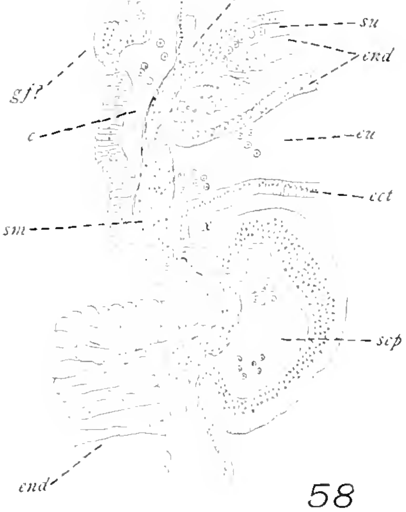

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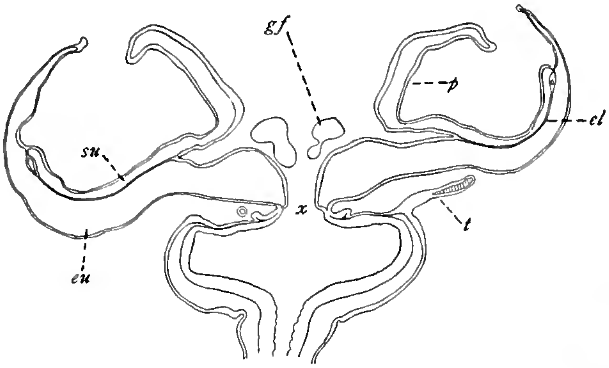

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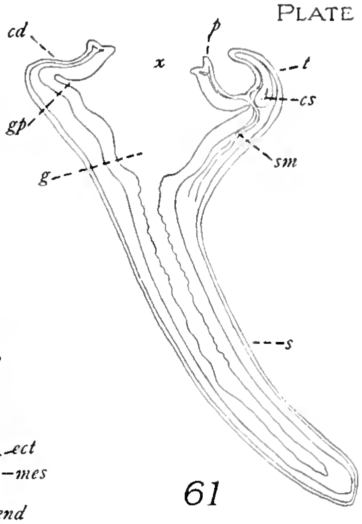

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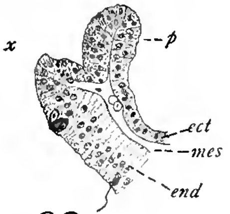

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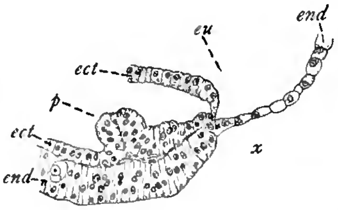

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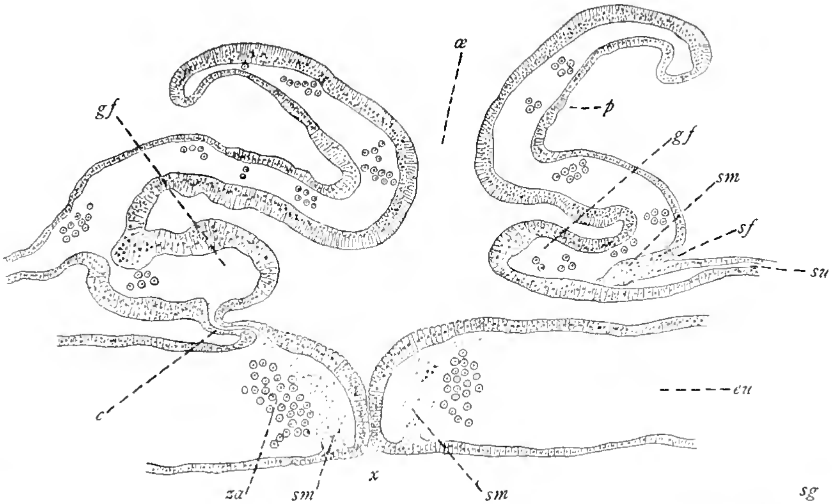

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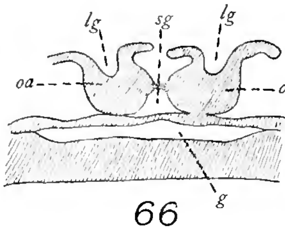

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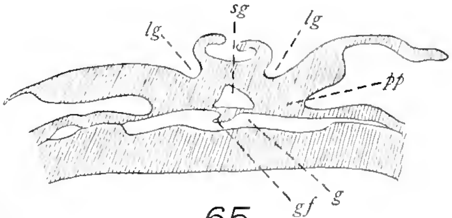

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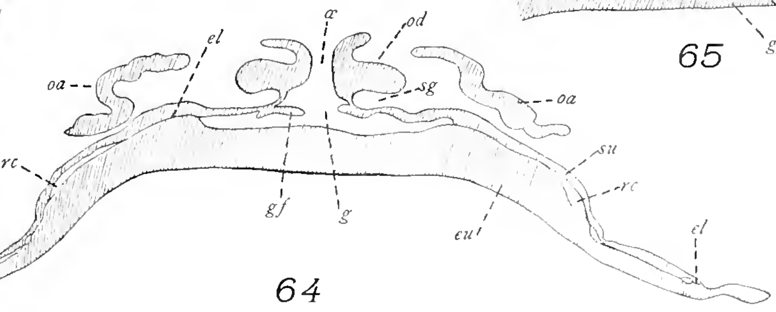

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