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SYNAPTA VIVIPARA

A CONTRIBUTION TO THE MORPHOLOGY OF ECHINODERMS

A DISSERTATION

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

BY HUBERT LYMAN CLARK.

(Read November 3, 1897.)

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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 picro-

nitric acid. Corrosive-sublimite 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-carmin (70% alcohol) and Lyons blue (70% alcohol) proved the most satisfactory. The early stages of the larvae were oriented and imbedded in celloidin 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 Örsted ('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 synonymy 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 inhaerans*, 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. inhaerans*, 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 pentaactula, 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 ectoderm-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 madreporic 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 madreporic 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 interradiial 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 interradiial 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) similar 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-tentacled 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 pentactula; 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 out-

growth" 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 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 considerable.

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 radial 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 madreporite (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 60-70 μ 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 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 sub-

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