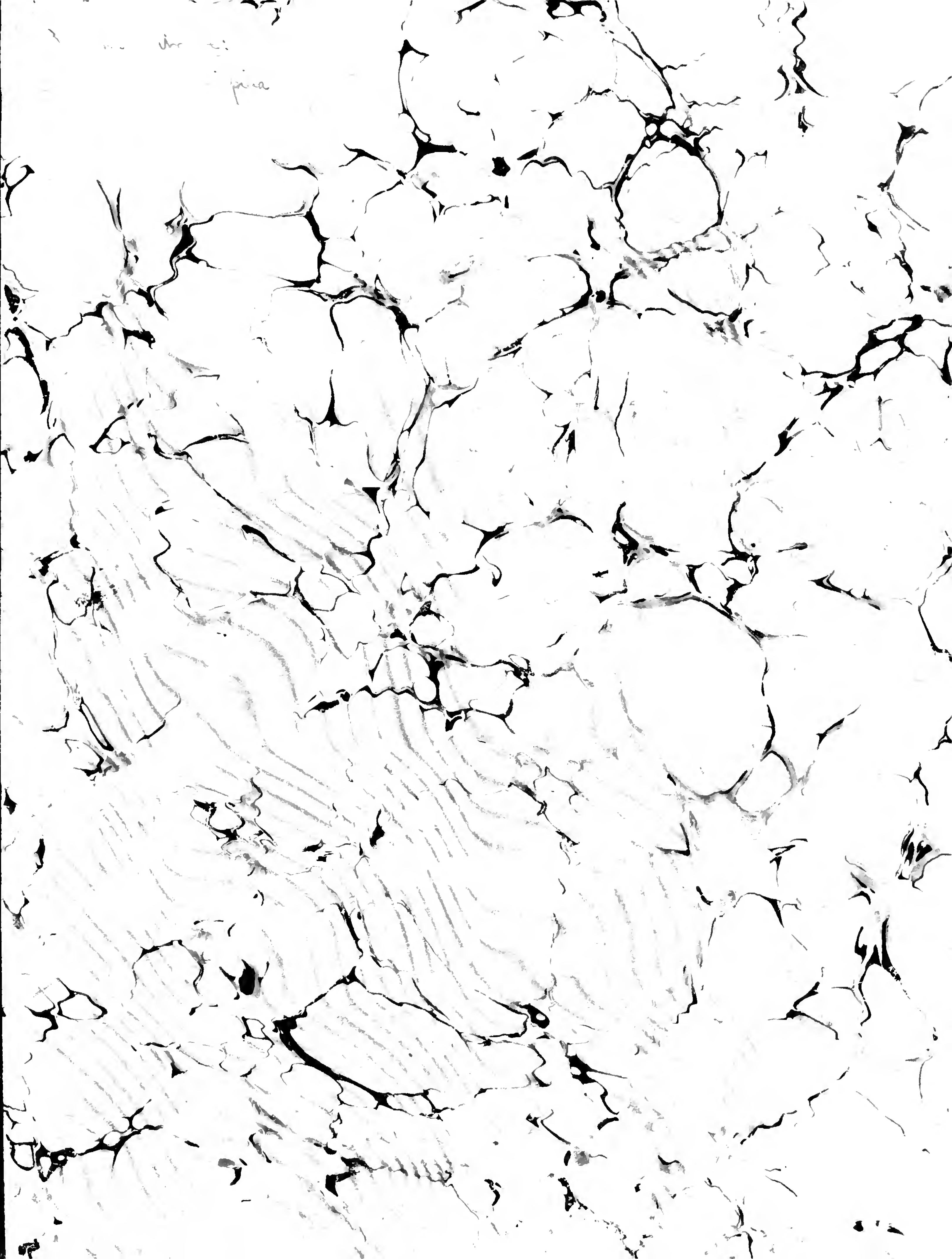

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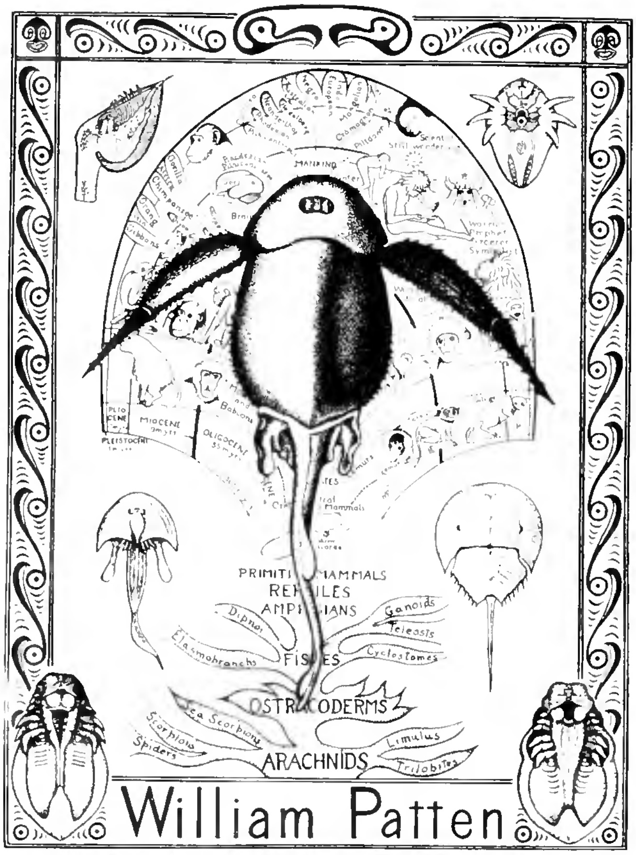

Brooks, William Keith

Ophiura brevispina

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OPHIURA BREVISPINA.

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As my name appears upon the title-page of this memoir, it is proper for me to state that my share in the work has been that of the instructor under whose direction the work has been done. The discovery that this Ophiuran is of peculiar interest and that it is unusually favorable for the study of the problems of the morphology of Echinoderms, was made by Dr. Grave; and the results which are here detailed are his work.

W. K. Brooks.

CONTENTS.

OPHIURA BREVISPINA.

By W. K. Brooks and Caswell Grave.

INTRODUCTION.

During the summer of 1898 it was my privilege to occupy the table of the Johns Hopkins University in the United States Fish Commission laboratory at Woods Hole, and while here I rediscovered the peculiar Ophiuran larva, which was first found and figured by **Krohn** (7).

Finding the larvæ he described in the open sea **Krohn** did not know to what species they belonged; but the larvæ, the development of which is the subject of the greater part of this paper, came from eggs laid in aquaria by *Ophiura brevispina.* It is not likely that the same species of Ophiuran occurs both at Funchal, where **Krohn** did his work, and also at North Falmouth, where my material was obtained, but it is very probable that species belonging to the genus *Ophiura* have similar larval forms.

Among Echinoderms, where a direct development from the larva to adult occurs, that is, without the usual highly specialized intermediate pelagic larva, we usually have to do with a species which in some manner takes care of its brood; but in *O. brevispina* the larvæ are free swimming, they being provided with a well developed locomotor apparatus, yet the usual Ophiurid pluteus larva is as completely omitted as it is from the life history of the viviparous *Amphiura squamata.*

From the fact that the usual pluteus skeleton is begun in the larvæ of *O. brevispina* one is led to suspect, however, that at some period in its history the species possessed a larva more nearly like a pluteus than at the present time. On the other hand, on account of the resemblances which exist between the larvæ of *O. brevispina* and *Antedon rosacea* (treated of in another place) we may suppose a close phylogenetic relationship exists between them. If, as many zoologists believe, the crinoids have retained more nearly than any other group the characters of the primitive Echinoderm stock, then in the larva of *O. brevispina* we may have one which has retained unmodified its primitive characteristics.

In this paper, however, the facts only of development are taken up, and the question of the bearing which this larva may have on any theoretical discussion concerning the interrelationships of the Echinoderms is suggested here in order that the reader may keep the subject before him while studying the paper. The points of resemblance between the Ophiuran and Antedon larvæ are enumerated in a chapter further on.

The method used in the preparation of the material for microscopical study, and which gave good results, is as follows: The larvæ were taken up into a pipet with as little water as possible, and squirted into a small bottle containing a solution of sublimate-acetic (98 parts of a sat. sol. $HgCl_2$ being used to 2 parts of glacial acetic acid). After from two to five minutes the sublimate solution was drawn off gently, leaving the larvæ at the bottom where they had settled. Then 50 per cent alcohol was added, which in a few minutes (5) was drawn off and replaced by 70 per cent alcohol, in which a little iodine had been dissolved. In a few hours (3–12) this was changed for clear 75 per cent alcohol, in which the larvæ remained until needed for laboratory study. After staining lightly in acid carmine, so as to facilitate their orientation, the larvæ were dehydrated in the usual way and cleared in oil of cloves. From the clove oil they were oriented by a modification of the **Patton** method. After an impregnation with 55° paraffin, series of sections three microns in thickness were made in three planes, transverse, longitudinal sagittal, and longitudinal horizontal. The sections were stained on the slide with KLEINENBERG'S hæmatoxylon. Other methods were tried, but none proved so satisfactory as the one just described. The shrinkage in echinoderm tissue, which usually accompanies the unmodified paraffin method, was not to be seen in the tissue of these larvæ, due, no doubt, to its unusual thickness.

It has been thought best to make the following list of terms which are used synonymously in the text of this paper in the description of the larvæ. Those in the same line can, in most cases, be interchangeably used.

Dorsal–aboral–above–over.
Ventral–oral–below–under.
Anterior–forward–before.
Posterior–backward–behind.

In the drawings of the larvæ, when the ventral side is up and the anterior end is nearest the top of the page, then the reader's left is also left in the figure.

For convenience in description, the various stages taken to illustrate the life history of the species have been designated by letters of the alphabet, this method seeming preferable to one in which age is used as a distinguishing character, since the progress of development at any age depends so intimately on the varying conditions of environment.

I take this opportunity to acknowledge my indebtedness to Dr. C. P. SIGERFOOS, at whose suggestion I began the study of Ophiuran development.

I was aided very materially while at the Fish Commission laboratory by Prof. H. C. BUMPUS, who placed at my disposal every facility for work at his command, and to him, also, I am greatly indebted for many suggestions in methods of rearing larvæ at the seashore.

To Professor BROOKS, under whose direction my work has been done, are due my warmest thanks for the interest with which he has followed me in my studies and for the many valuable suggestions he has offered from time to time during the year.

HISTORICAL SKETCH.

The species of Ophiuran, *Ophiura brevispina*, the life history of which is the subject of this dissertation, was first discovered and described by Thomas Say in 1825 (12).

Since this time the species has been rediscovered and renamed as many as three times. It is probably best known at present by one of its synonyms, *Ophiura olivacea*, which was given to it in 1865 by THEODORE LYMAN (8). In his earlier works LYMAN distinguished between *O. olivacea* and *O. brevispina*, but in his *Challenger* report on the *Ophiuridæ* and *Astrophytidæ* (9) he places the two species together as one under its earlier name, which, although less descriptive of the species than that given by Lyman, it is probably best to retain.

In 1852 AYERS described the species under the name *Ophioderma olivaceum* in Vol. IV of the Proc. Bost. Soc. Nat. Hist.

LUTKEN also described it as *Ophioderma serpens* in 1856.

DISTRIBUTION AND HABITS.

Ophiura brevispina is a very widely distributed species, it having been reported from points along the Atlantic coast from Brazil to New England.

It has been taken from the following localities:

1. Bahia, Brazil.
2. Port Antonio, Jamaica.
3. St. Thomas, Bahamas.
4. Cape Florida, Florida.
5. Tortugas.
6. Beaufort, North Carolina.
7. Old Point Comfort, Virginia.
8. Sag Harbor, New York.
9. Dartmouth, Massachusetts.
10. New Bedford, Massachusetts.
11. North Falmouth, Massachusetts.

That part of North Falmouth Harbor which is inhabited by the species is very shallow, its depth at low tide not exceeding 1 fathom.

The bottom is covered with a mat of living and dead grasses and algæ, and in this tangle the ophiurans live, together with a great variety of crustaceans, molusks, and worms.

The usual color of the species is an olive green, with darker bands on the arms and sometimes with a clouded disk.

Through the blending of their colors with the seaweed the ophiurans are greatly protected from their enemies, and it is difficult, even when looking for them, to see them among the seaweed so long as they do not move.

It is quite common to find a small Amphipod crustacean clinging to the arms of dredged specimens, and from the structure of the crustacean it is probable that the two species live together commensally. What benefit either animal can derive from the association it is difficult to see.

One pair of the thoracic legs of the crustacean is so modified as to form a structure beautifully adapted for clinging to the round ophiuran arms. The last segment but one of each of this pair of legs is Y-shaped. At the end of one arm of the Y is attached a movable segment, the end segment of the leg, which when shut down upon the end of the other arm of the Y incloses a triangular space in which the ophiuran arm is held.

The body of the crustacean is colored and banded in such a manner as to simulate closely the color and banding of the ophiuran arms.

When placed in aquaria with their host, the crustaceans cling to the ophiuran arms until the water becomes depleted of oxygen, when they leave the arms and swim about the edge of the dish apparently much alarmed.

In examining the stomachs of the ophiurans one finds bits of other animals, such as crustacean appendages and the skeletons of young horseshoe crabs. From this it is probable that the creatures are scavengers, since an active crustacean would hardly be captured by so slow and poorly armed an animal as an ophiuran. None were ever observed to eat anything when kept in the laboratory, and it is quite out of the question to observe them in their natural habitat, since they are nocturnal animals remaining hidden during the day.

The ophiurans were first examined for sexual elements early in June, and at that time the eggs were very large but adhered closely together in the gonads. The sperm appeared to be fully formed but were nonmotile.

From this time on until the middle of August the species was regularly watched and examined, and on July 16 the first ripe eggs and sperm were obtained. A great number of specimens had that day been dredged and placed in aquaria dishes of fresh, filtered sea water. One week later a great number of adults were again brought in and placed under the same conditions as those which had spawned in the laboratory the week before, but this time very few eggs were obtained, and all subsequent attempts to get the ophiurans to spawn were unsuccessful.

From this it would seem that the breeding season is extremely short.[1]

The time of day at which spawning occurred corresponds well with the time at which I have noted it to take place in *Ophiophilus aculeata* and *Ophiocoma echinata*, that is, between 8 and 10 o'clock p. m.

PHYSIOLOGICAL NOTES.

The locomotor movements of an ophiurid, upon a casual observation, seem to consist of an uncoordinated writhing and twisting not calculated to bring the creature to food or a place of safety except by chance; but a more careful study shows them to be the result of an orderly and nicely coordinated mechanism.

The rapid strides which characterize the movements of a brittle star are in strong contrast

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[1] During the summer of 1899, after this paper had gone to press, my experience with the species was very different from the above. Specimens brought into the laboratory early in June threw eggs and sperm, but the eggs, after passing through the early segmentation stages, ceased to develop. The eggs were probably immature, and were spawned only because of the bad condition of the water in the aquaria, but spawning always occurred early in the evening at the time when it would have occurred under normal conditions. Why unripe eggs should develop at all, or why eggs mature enough to begin their development should not be mature enough to complete it, is an interesting question.

This phenomenon was repeated every few days until July 26, when about one-fourth the number of eggs spawned developed into normal larvæ. This is ten days *later* than the date when eggs became mature at Woods Holl. From the fact that the water is much warmer at Beaufort than at Woods Holl one would expect to find the spawning season earlier at the latter place.

with the slow creeping movements of a starfish or sea-urchin, the difference being due to the employment of different locomotor mechanisms in the two cases; the starfish and sea-urchin depending entirely upon their tube feet and spines while in the ophiurids, the arms themselves are the efficient locomotor organs, they being used much as we use our arms in swimming.

The arm of an ophiurid consists of a large number of segments, each of which contains a central calcarious ossicle. The calcarious ossicles of adjacent segments articulate with each other like the vertebræ of the spinal column, and are joined together by two pairs of muscles in such a manner that motion is possible in all directions. This mechanism is aided in producing the locomotion of the creature not only by the arm spines, where they are present, but by the foot tentacles. These latter organs, which are the homologues of the tube feet of other echinoderms, have been previously regarded as having given up their locomotor function entirely, but I shall show further on that this is not true in the genus *Ophiura*.

The experiments I carried on last summer on the movements of ophiurans resulted in little that is new, but on account of the confirmation my notes and photographs give to PREYERS' work (11) on the same subject, it has been thought advisable to publish them.

In the usual method of progression one arm precedes, it taking no other part, apparently, than to point out the way; the two arms adjacent to and behind the anterior arm make the stroke; the remaining arms are dragged behind, acting as a rudder.

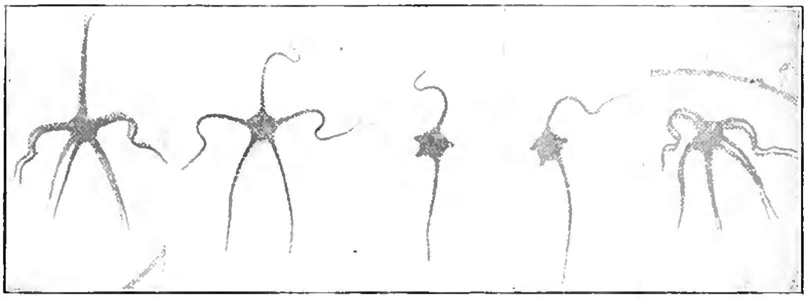

FIG. 1. FIG. 2. FIG. 3. FIG. 4. FIG. 5.

No preference as to which arm should precede could be found in an adult ophiuran, each arm being equally capable of going before, making the stroke, or following behind.

If greater speed is needed, for example, to get away from a strong stimulus, the arm which precedes may also take part in the stroke, its contractions being made simultaneously with those of the side arms. This added force, if produced repeatedly on one side, would soon change the course of progression, but this difficulty is overcome by an alternation of the stroke of the preceding arm, first on one side, then on the other (text fig. 2).

In a third method of normal locomotion the arms are arranged as is seen in text fig. 5, in which only one arm follows, acting as the rudder. This leaves two pairs of arms for the stroke, but the anterior pair is usually most vigorous in its contractions.

Since no physiological differentiation into anterior, posterior, or lateral parts is to be found in ophiurids, the creatures are under no necessity of turning the body when a change in the direction of progression is to be made. The arm which finds itself pointing in the new direction to be traveled takes the lead, although it may have been either lateral or posterior in position in the previous movements.

As has been mentioned before, the foot tentacles aid in making the strokes of the arms efficient in propelling the body. After a stroke has been made, while the arms are being drawn forward and extended for a new stroke, the tentacles can be seen moving actively about, but as the arms come to rest for the backward movement the tentacles are thrust down against the substratum and cease to move. The tentacles thus fit themselves into the inequalities of the surface and afford fixed points for the arms to pull against. The tentacles of the posterior arms act in the same way, and are efficient in preventing the force of the stroke being lost in side motion.

In ophiurans with long arm spines these latter structures may perform the function just described for the foot tentacles, but in the genus *Ophiura* the arm spines are very minute and closely applied to the sides of the arms.

It is interesting to note the wonderful coordination of locomotor movements immediately following the amputation of three of the arms. In this case if the nerve ring has been uninjured one of the remaining arms takes up the part of guiding and balancing, while the other strokes first on one side then on the other (text figs. 3 and 4).

When the central nerve ring is cut at any point the coordination in movement is impaired, and when cut in five places, between the arms, it is lost entirely.

When placed on its aboral surface an ophiuran quickly turns over. The method used is quite definite; two adjacent arms straighten out so that together they form a straight line. On these arms as an axis the body revolves, being pushed over by the three remaining arms, but mostly by the median one of the three.

EARLY STAGES.

The mature eggs are opaque and vary in color from an olive green to an orange yellow. Those of the same individual, however, are constant in their coloration. Until quite well developed the larvæ retain the color which was on the eggs at the time they were laid.

For echinoderms the eggs are very large, being 0.3 millimeter in diameter.

Soon after they are fertilized the eggs throw off two membranes, the first of which is much thicker than the second.

When first laid and during their early development the eggs float, but when their cilia are formed the larvæ are able to swim below the surface.

As I did not know that any special interest would be found in the life history of the species, I did not carefully observe the early stages while living, nor preserve material for future study, and as I have stated elsewhere, all later attempts to get other material were unsuccessful.

This makes it necessary to begin this paper with the description of a late gastrula in which the first pair of enterocœles have already begun to form as lateral pouches from the anterior free end of the archenteron (figs. 1–3).

Larvæ in this stage of development will be designated as "A."

Stage "A," 36 Hours Old.

(Figures 1, 2, and 3.)

At the age of 36 hours the larvæ swim actively, they being uniformly covered with cilia (fig. 1).

The shape of the larvæ is an oval, the length being to the shorter diameter as 2 is to 1.

The animal or anterior pole is slightly more pointed than the posterior vegetative one. The ventral surface is distinguished by the presence of the blastopore, which latter has been pushed from its posterior position to a ventral one by the rapid growth of the ectoderm of the dorsal surface of the larva.

An apical plate of taller cells is present at the anterior end, but I could not see that the cilia at this point were any longer than those which cover the other parts of the larva (fig. 3, ap).

From the blastopore, through which its cavity opens to the exterior, a large archenteron projects forward into the blastocœle.

The remainder of the blastocœle, not taken up by the archenteron or its pouches, is filled with a close network of mesenchyme cells. This mesenchyme tissue is shown in fig. 3, mes, which is a longitudinal sagittal section of "A."

From the anterior free end of the archenteron a large pouch is in process of being cut off. This pouch projects to the right and left as horn-like processes, which latter are to be considered the rudiments of the right and left anterior enterocœles (fig. 2, aer and ael).

As to the method of gastrulation I can not at present speak from observation on larvæ in which it is just taking place, but from a study of the stage now under consideration some idea can be gotten as to how it has proceeded. In figs. 1 and 3 we see a cellular plug (cp) protruding from the blastopore and also extending far into the archenteric cavity. In some cases it extends even into the enterocœle pouch. The contour of this cellular mass is ragged, which is also true of both the outer and inner surfaces of the wall of the archenteron and the inner surface of the ectoderm.

These facts seem to indicate that gastrulation does not take place by invagination, as is usual in echinoderms, but that the larva before gastrulation is a solid, planula-like affair, and later the archenteron is formed by a splitting away of the central core. In the same way the plug of cells is probably formed by the hollowing out of the solid archenteron.

Beside their ragged outline the walls of the larva have another peculiarity in their structure, for, judging by the number and position of the nuclei, they are from two to three cells in thickness (fig. 3).

Cell walls are not distinguishable in any stage of development.

STAGE "B," 42 HOURS OLD.

(Figures 4 and 5.)

According to BURY (2) the hydrocœle does not have the same origin in all the groups of echinoderms. He found that it originates in the crinoids, sea-urchins, and starfishes from the left *anterior* enterocœle, but in the ophiurids it grows out from the anterior end of the left *posterior* enterocœle.

This observation, which BURY records with apparent hesitation, I can completely confirm, as will be seen in the description and figures of "B."

Externally the appearance is the same as in "A," but the internal structures have undergone a great change.

The anterior pouches, the cavities of which in "A" were connected both with each other and with the cavity of the archenteron, are now separate and distinct. The connection between these structures still continues, however, in their fused walls. The left pouch is a little larger than the right and lies behind and to the left of the latter (fig. 4, ael).

Just below the anterior pouches there is to be found a third pouch, which is growing out from the left side and anterior end of the archenteron (fig. 4, hy). It protrudes anteriorly and partially covers the two anterior enterocœles. The cavity of this pouch, which is the rudiment of the hydrocœle, is in wide communication with the archenteron.

From the wall forming the convex sides of the hydrocœle there are, even at this early stage in its formation, five outgrowths which are the beginnings of the radial canals of the adult ophiuran (fig. 4. 1, 2, 3, 4, and 5).

The whole hydrocœle is curving round to the right to encircle the œsophagus, which latter is making its first appearance in this stage as a shallow but definite pit in the central part of the ventral ectodermal wall (fig. 4, oe).

To avoid confusion the hydrocœle was spoken of above as arising from the archenteron, but, as will be seen in the transverse section (fig. 5), taken in a plane posterior to the origin of the hydrocœle, a differentiation is taking place in the archenteron which enables us to distinguish in it the rudiments of two structures, the posterior enterocœles and the stomach. By a longitudinal circular furrow the archenteron is being cut horizontally into a large ventral pouch, the posterior enterocœles (pe) and a smaller dorsal one, the stomach (s). This stomach rudiment bends around the posterior end of the posterior enterocœle and opens to the exterior through the blastopore (fig. 4).

It is from the left side and anterior end of the ventral pouch that the hydrocœle grows out, hence the confirmation of BURY'S statement that it arises from the left posterior enterocœle in ophiurids.

In most echinoderms the posterior enterocœles originate as paired structures, and if the statements of BURY and MCBRIDE are correct, that the left posterior enterocœle of the larva forms the hypogastric body cavity of the adult, and the right posterior enterocœle goes to form the epigastric cœlom, then, according to this, the large ventral pouch, which I regard as the fused right and left posterior enterocœles, really represents the left only, because it takes no part in the formation of the epigastric body cavity of the adult ophiurid, but, with the left, does pass directly into the hypogastric.

The origin of the epigastric enterocœle is discussed in the description of Stage "C," in which its rudiment is first found over the stomach.

My reason for regarding the ventral pouch of "B" as the fused right and left posterior enterocœles, is that at the time of its origin it is symmetrically disposed on either side of the plane of larval bilateral symmetry.

Goto (5), too, has shown that the hypogastric enterocœle in the starfishes is not formed from the left alone, but in it are to be found the left and the greater part of the right posterior enterocœles.

The cellular plug of cells, which in "A" fills the archenteric cavity, becomes divided by the furrow which separates the archenteron into enterocœle and stomach and a part of it becomes inclosed in the cavities of each of these structures (fig. 5, ep).

Stage "C," 48 Hours Old.

(Figures 6, 7, and 8.)

The external form of the larva, which in this series of embryos is six hours older than "B," has been changed by the appearance of two lateral thickenings of the ectoderm a little posterior to the median transverse plane (fig. 6).

The blastopore, which in "B" was open to the exterior, has closed, leaving no trace of its former position.

The mouth and œsophagus, which existed in "B" only as a shallow ectodermal pit, now have the form of a deep, hollow tube (figs. 6 and 7, m and oe), which projects vertically inward until it passes through the hydrocœle and beyond the posterior enterocœle, when it curves back under the latter to fuse with the anterior wall of the stomach.

The stomach and posterior enterocœle are still in open communication, as in "B," but the furrow in "C" has deepened, and the process by which the two structures are being separated is almost complete (fig. 7).

Although the walls of the œsophagus and stomach are fused, their cavities are still separate.

This condition renders it easy to see just what part is played by the ectoderm in the formation of the alimentary canal, the entire œsophageal cavity being surrounded by ectoderm.

In "B" the hydrocœle communicates with the posterior enterocœle by a wide opening, and at the same point in "C" the two structures are still in communication, but the connection has been narrowed down to a small tube (fig. 7, hc).

Beside this connection with the posterior enterocœle, a second tube has been formed, joining the left anterior enterocœle with the hydrocœle (fig. 7, st). This new tube, which is the rudiment of the stone canal, enters the hydrocœle at the same point with the tube connecting the latter with the posterior enterocœle.

The left anterior enterocœle lies to the left of the œsophagus, and dorsal to the left half of the hydrocœle (figs. 6 and 7, ael).

It is to be noted that, although we now have a larva possessing both hydrocœle and stone canal, there has been as yet no pore canal formed. This is a marked reversal in the sequence of the formation of these structures from what might be expected from the order of their appearance in other known echinoderms, the pore canal arising usually before the formation of the hydrocœle, while the stone canal appears much later than either.

Returning to the hydrocœle, we find it a horseshoe-shaped structure astride the œsophagus (figs. 6 and 7, hy). The bulging areas which are to form the radial canals of the adult are much longer and more regular in size than in "B." The radial pouch, which lies to the right of the œsophagus and at the end of the right horn of the horseshoe, will hereafter be spoken of as radial canal 1, since it arises from that part of the hydrocœle which was first to bud out from the posterior enterocœle. The other radial canals, passing to the left over the œsophagus, will be designated as 2, 3, 4, and 5. Radial canal 5 lies in this stage over the opening of the stone canal.

The rotation of the hydrocœle around the œsophagus from its original left position, which was begun in "B," has continued to such an extent in "C" that half of it lies to the right of the median sagittal plane of the larva and half to the left. Radial canal 3 lies in this plane and points directly toward the anterior end of the larva (fig. 6).

With its rotation the hydrocœle also moves bodily toward the posterior end of the larva, carrying with it the œsophagus. The œsophagus, coming in contact with the anterior wall of the united posterior enterocœles, causes the latter to be pushed in at the point of contact. As the process continues, those parts of the posterior enterocœles lying on either side of this in-pushing area are forced to flow forward around the œsophagus and under the hydrocœle; thus we have the posterior enterocœles becoming horseshoe-shaped, the two horns of which lie under the horns of the hydrocœle (figs. 6 and 7, he and hy).

Lying dorsal to the stomach we find a small enterocœle which was not present in "B," or if present, not in this position. It is the rudiment of the body cavity, which in the adult lies aboral to the stomach and which has been recently appropriately termed the epigastric enterocœle (figs. 6 and 7, ee).

As to the origin of this structure I have no direct observations to give, but certain facts have led me to believe that it is formed from the right anterior enterocœle. These facts may be summed up as follows: In "B" no epigastric enterocœle exists, but the two anterior enterocœles (fig. 4, aer and ael) lie side by side anterior to the stomach and the posterior enterocœles. In "C" (figs. 6 and 7, ee) an epigastric pouch, equal in size to the right anterior enterocœle of "B" is to be found, but by the side of the œsophagus only the left anterior enterocœle remains (figs. 6 and 7, ael).

During the six hours which intervene between "B" and "C" it seems hardly possible that a complete formation of the epigastric enterocœle should have taken place or that there should have been time for the complete degeneration and disappearance of the right anterior pouch; sufficient time may have elapsed, however, for the migration of the right anterior enterocœle to a position behind the stomach.

Against such an interpretation as the above there is the fact that in no other case has the epigastric enterocœle been observed to take its origin from the right anterior pouch. It has been described as arising from the right *posterior* enterocœle, however, as has been referred to before, in all the groups by BURY, and his observations have been corroborated by both MCBRIDE and GOTO in the starfishes.

STAGE "D," 60 HOURS OLD.

(Figures 9-14.)

The changes which have taken place in "C" to produce "D" are very marked.

The cilia have disappeared, except in four transverse rings or bands, three of which extend entirely around the body of the larva. The third ring, counting from the anterior end, is interrupted by the aboral disk on the ventral surface.

This third ciliated ring first appears on the lateral bulges, which were described in "C," and the fourth ring appears on a second pair of lateral bulges which originate behind the first pair near the posterior end of the larva.

The shape of the larva is no longer oval, but the posterior end has widened laterally and become somewhat dorso ventrally compressed (fig. 9). The anterior end has not changed in shape and may be thought of as forming the handle of the now club-shaped larva.

The enlarged posterior end of the larva contains all its organs and is the part which will enter directly into the formation of the adult ophiurid.

From its homology with the preoral lobe and larval organ of *Asterina gibbosa* I have called the anterior end of the larva the larval organ. It disappears with the metamorphosis into the adult form.

The larval organ is also homologous with the stalk of the Antedon larva, although in the ophiurid larva it never functions as an attachment organ. When swimming, the larval organ precedes. It is filled with a network of mesenchyme cells (fig. 11, mes).

Internally the changes have been even greater than the external ones we have just considered, for it is during this period of development that the rotation and readjustment of organs takes place, which is present in all echinoderms at some stage of their development.

The hydrocœle, which has begun its rotation about the œsophagus as an axis in "C," has completed it in "D" and reached its definite position.

That part of the hydrocœle which in "C" was situated on the left of the plane dividing the larva into bilaterally symmetrical halves, now lies on the right side of the same plane and vice versa. (Compare figs. 6 and 9.)

A revolution of 180° has taken place in the hydrocœle since "C," to which if the 180° of rotation be added, which took place up to the time of "C," we have a total rotation of 360° in the hydrocœle. Radial pouch 1, finally, after having passed around the œsophagus, comes to rest at the point where it originated. Radial pouch 5, it will be noted, is carried only half as far as radial pouch 1, or from its point of origin on the left to a point opposite on the right of the œsophagus. (Compare figs. 6 and 9, (1) and (5).)

This great amount of rotation seemed so peculiar that I hesitated for some time to believe it, and was led to suppose instead that while the hydrocœle moved to the right the other organs lying above it rotated an equal amount to the left.

The early closure of the blastopore and the central position of the mouth in the early stages make such a view as the latter seem possible, and as it may suggest itself to those who study figs. 6 and 7, I will give below the points which seem to me, directly or indirectly, to prove that the hydrocœle revolves under the enterocœles and stomach, rather than that the latter twist over the hydrocœle:

(*a*) The ectodermal bulges, nearer the posterior end in "C" (fig. 6), are the same as those nearer the posterior end of "D" (fig. 9), on which the third ciliated band is situated.

(*b*) If the latter view is the correct one then radial canal 3 points toward the same end of the larva in both "C" and "D" (figs. 6 and 9), but in "C" the end toward which it points is anteriorly directed in swimming and in "D" it points away from the end which precedes. It is hardly thinkable that in any stage in its development the anterior end of a larva should change its physiological function and become the posterior end.

(*c*) By any other view than the one I have adopted the blastopore, or the point where it existed before closing, would be anterior and the larval organ posterior in position. In all known echinoderm larvæ, however, the blastopore marks the posterior end, and in all cases where it occurs the larval organ originates from the anterior end of the larvæ.

(*d*) It may be recalled, also, that in the readjustment of parts which takes place during the metamorphosis of other echinoderm larvæ the rotation is almost entirely confined to the hydrocœle.

As the hydrocœle passes around the œsophagus the tube connecting it with the left horn of the hypogastric enterocœle becomes broken and the left anterior enterocœle, together with the tube connecting it with the left horn of the hydrocœle, are carried anteriorly around the œsophagus (fig. 9, ael and st). In "D," then, we find the stone canal on the right side of a line dividing the larva into symmetrical halves, instead of to the left of the same line as it is in "C." (Compare figs. 6 and 7 with 9.) The anterior enterocœle comes to rest immediately in front of the stomach and œsophagus.

From the point where the stone canal enters the anterior enterocœle the pore canal grows out, passes dorsally to the ectoderm, with which latter its walls fuse, and an opening the water pore (figs. 9 and 11, pc.) breaks through. Thus in this stage the cœlom and hydrocœle are first connected with the exterior.

In "C" the circular water-canal had not closed, but existed in the form of a horseshoe, the concave side of which opened posteriorly, but as the rotation of the hydrocœle takes place its horns grow toward each other until they meet. A fusion of their walls then takes place at the point of contact and a complete ring is thus formed. The part of the ring canal, the formation of which has just been described, lies between radial canals 1 and 5 in fig. 9. The opening of the stone canal into the water ring is situated in "C" at the base of radial canal 5, but by means of the rotation of the hydrocœle about the œsophagus, together with the growth of the ends of the horseshoe, this opening is carried away from its position at the base of radial canal 5 toward radial canal 1. It always remains, however, nearer the former than the latter; in other words, it comes to lie definitively in the *right adradius* between radial canals 5 and 1. (Compare figs. 6 and 9.)

The radial canals, which existed in "C" as simple pouches from the convex side of the hydrocœle, have in "D" each become three-lobed. Near the tip and from the sides of each canal a pair of pouches has budded out, each of which is about equal in size to the end of the canal which lies between and beyond them (fig. 9, et and tl). In these three structures we have the rudiments of the end tentacle and the first pair of foot tentacles of the ophiurid arm.

When we were last considering the hypogastric enterocœle it was in the form of a crescent, the horns of which were very short and its central part very wide. Into its concavity, which was anteriorly directed, the œsophagus fitted. The horns of this enterocœle, beginning in "C" to grow over the hydrocœle, continue the process during the rotation of the latter, the horns of the crescent growing at the expense of the thickness of its central part, and in "D" we have this enterocœle lying directly over the hydrocœle in the form of a perfect horseshoe (fig. 9, he).

Between the ends of the horns of the hypogastric cœlom lies the anterior enterocœle. The walls of these structures come together and fuse in such a way that they together form a hollow circular cœlom surrounding the stomach and lying over the somewhat smaller water vascular ring (fig. 9).

In the four interradii, marked by their positions between radial canals 1 and 2, 2 and 3, 3 and 4, and 4 and 5, four pouches of the hypogastric enterocœle grow downward, outside the water vascular ring, forcing themselves between the radial canals; a fifth pouch, similar to those just described, is formed from the left anterior enterocœle in the remaining interradius between radial canals 5 and 1 (figs. 9, 12, 13, and 14, hip 1–2, 2–3, 3–4, 4–5, and ipax 5–1). These five pouches are the rudiments of the *outer* perihæmal ring, which will be more fully considered in the succeeding stages.

The stomach, after being entirely cut off from the hypogastric enterocœle, was drawn forward during the rotation of the hydrocœle, and the œsophagus was carried in the opposite direction, so that in "D" the stomach lies almost directly over the œsophagus (figs. 8 and 13, oe and s). The partition, which in "C" separated the cavities of these two structures, has disappeared in "D," and the œsophageal cavity opens into that of the stomach. There is present, then, in "D" the definitive alimentary canal of the adult ophiurid.

The "cellular mass," which in "B" and "C" was being divided into two parts by the constriction separating the archenteron into enterocœle and stomach, is to be found, in sections of "D," in the cavities of both the above structures (figs. 11, 12, 13, and 14 cp).

Lying immediately above, or aboral to, the stomach is to be found the epigastric enterocœle. It has enlarged considerably during the interval between "C" and "D," but is not yet of sufficient size for its walls to touch those of the hypogastric cœlom, and hence in this stage no circular aboral mesentery is to be found.

Stage "E," 66 Hours Old.

(Figures 15–21.)

The thickening of the ventral ectoderm which was begun in "D" has continued during the six hours which intervene between "D" and "E" and has spread to the sides of the larva (figs. 15 and 19–21).

Near the edge of this thickened oral disk are to be found five groups of rounded elevations of the ectoderm (fig. 15, I, II, III, IV, and V). The three elevations, of which each group consists, form the angles of an isosceles triangle the apex of which points away from the mouth of the larva (fig. 15). These elevations or evaginated papillæ lie immediately below and inclose the tips of those branches of the radial water canals which form the rudiments of the end tentacle and first pair of foot tentacles of each arm (figs. 19 and 21). In this way each tentacle grows into its ectoderm, the latter closing around it as it pushes out.

The function of these tentacles in the adult being mainly a sensory one, it is interesting to note that they receive their ectoderm from part of the same thickened oral area which gives rise later to the adult nervous system.

The ciliated bands in "E" do not differ in appearance and position from those in "D," but since they were not figured in the earlier stage it may be well to refer to them again in connection with figs. 15 and 16, cb 1, 2, 3, and 4. The first or most anterior band surrounds the larval organ quite near its tip.

Near the first band, and parallel to it, runs the second one also around the larval organ. The third ciliated band is separated from the second by a much wider space than that which separates the first and second bands. Were it not interrupted on the oral disk the third ciliated band would lie in the line separating the bivium and trivium—that is, between arms I and II on the one side and IV and V on the other. The fourth band, passing just posterior to the group of ectodermal elevations lying under the branches of the third radial water tube, surrounds the posterior end of the larva.

In "E" the cavities of the œsophagus and stomach have become obliterated, and the two structures appear in section as one solid mass of cells (fig. 20, st and oe). No degeneration in their size, however, is to be observed, and their outer walls remain well defined, the œsophagus retaining its connection with the ectoderm. As will be seen later, their lumen reappear and they become the definitive alimentary organs of the adult ophiurid.

Returning to the consideration of the water system, we find in "E" instead of one pair of tentacles on each radial canal, as in "D," there are two pairs present (fig. 17, t1 and t2), the second pair having grown out of the radial canal between the first pair and the water ring. The second pair is much smaller than those which were first to be formed, and, contrary to what one would expect, this discrepancy in size does not disappear as time goes on. This is also true in the sea-urchins, in which the primary tube feet in the larva are enormously larger than those which are subsequently formed. The primary tube feet in this case gradually diminish in size after the adult form is reached.

As a rule, among echinoderms the tube feet or tentacles are formed *centrifugally* from the radial canals; that is, between the end tentacle and the last pair of tube feet or tentacles already formed. This process keeps the undifferentiated growing point of each arm at its tip, but in this ophiuran, and the same is true of Antedon, the formation of the tentacles *begins* in a centripetal manner; that is, the second pair of tentacles appears, not between the end tentacle and the first pair, but between the first pair and the ring canal.

This second pair of tentacles is the rudiment of the buccal tentacles, and although differing in both function and position in the adult from that of the foot tentacles, is nevertheless entirely homologous with the latter. This homology is shown by their origin and the fact that for a time after forming they are directed away from the mouth toward the end of the arm just as is the case with the foot tentacles. After a time, however, as will be seen later, they turn back and point toward the mouth, thus showing that in this second pair of outgrowths from the radial canals we have to do with the first pair of buccal tentacles of the adult. After budding, as we see, from the radial canals, they migrate to a position on the ring canal, with which we find them connected in the adult.

In "E" the buccal tentacles have no ectoderm nor rudiment of such, the ectoderm under their tips being as yet undifferentiated from the oral disk.

The hypogastric enterocœle has assumed a more pentagonal shape than in "D," it having grown out over the radial water canals (fig. 17, he). These projections of the hypogastric enterocœle will continue to grow with the growth of the arms and become the brachial extensions of the body cœlom.

The interradial pouches of the hypogastric enterocœle, which were beginning to form in "D," have pushed down further and further between the radial canals until, coming in contact with the ventral ectoderm, they bend over, inserting themselves between the ring canal and the oral disk (figs. 17–21, hip 1–2, 2–3, 3–4, and 4–5). In the same way the pouch from the anterior enterocœle in the stone canal interradius has grown under the water ring. In these five interradial enterocœlic outgrowths, as has been mentioned before, we have the rudiments of the outer perihæmal sinus of the adult. The process by which this perihæmal sinus is formed in *Ophiura brevispina* agrees in every detail with its method of origin in *Asterina gibbosa* as described by McBride (10).

The epigastric enterocœle is in much the same condition as that in which we left it in "D," it being as yet too small to meet and form a mesentery with the dorsal edges of the hypogastric cœlom (fig. 19, ee).

The stone and pore canals, too, have changed very little during the interval between "D" and "E." From the ring canal at a point to the left of the origin of radial canal 1 the stone canal passes upward and opens into the right postero-dorsal part of the anterior enterocœle. The pore canal begins at the same point where the stone canal ends, the two canals thus having a common opening into the anterior enterocœle or ampullæ. The pore canal extends from the enterocœle to the dorsal surface of the larva, where it empties through the dorsal pore at a point a little to the right of the median sagittal plane. These two canals, although extending in the same direction, do not lie in the same straight line, the pore canal being set a little anterior to and to the right of the stone canal (figs. 17, 18, and 21, st and pc; also fig. 11).

STAGE "F," 5 DAYS OLD.

(Figures 22-30.)

Although "F" is separated from the stage last described by a considerable space of time, the changes in the larva which have been brought about are easy to follow.

The larva is considerably larger than in "E," and has reached its full development. From this time on the larval organ gradually degenerates and is finally completely absorbed by the developing star (Compare figs. 22 and 31 lo.)

The external form of the larva has been changed by the appearance of a number of elevations and depressions in its outer surface, the ciliated bands being elevated upon circular ridges (fig. 22, cb 1, 2, 3, and 4), while at points on the sides of the disk beyond the end tentacles projections in the ectoderm have made their appearance, these being the rudiments of the ophiuran arms (fig. 22, I, II, III, IV, and V).

The larval organ is cylindrical, but the disk has continued its dorso-ventral flattening. (Compare figs. 22 and 26.)

The first and second ciliated bands are situated in the same places as in "E." The third, while retaining its old position, has grown in upon the ventral disk toward the mouth (fig. 22, cb 3). On the ventral side of the larva the fourth band has shifted from its old position behind the third radial canal to one on the interradii between arms II and III and III and IV. It has also become interrupted on the oral disk in a manner similar to the third ciliated band (fig. 22, cb 4).

The depressions before referred to are caused by the invagination of the nervous system, which structure has been forming since "D" in the thickened oral disk of ectoderm. Immediately below the water ring and radial water canals the thickening has increased more rapidly than at other points, thus producing a ring-shaped internal ridge, from which extend five radial thickened ridges. These rudiments of the nerve ring and radial nerves bulge inwardly, no evidence of their presence being apparent on the outside. When the thickening process has been completed the whole nervous system gradually sinks in, leaving a circular groove from which five radial grooves pass out. This is the stage in the formation of the nervous system which has been reached in "F" (fig. 22, cg and rg). The invagination process begins at the ends of the radial nerves, just inside of the curved tips of the end tentacles, the nerve ring being invaginated last of all. (Compare figs. 23-27.) As development goes on the edges of the grooves gradually close over the nerves, the closure taking place in the same order as the invagination proceeded—that is, first over the ends of the radial nerves, then finally, after gradually traveling up the radial nerves, closing over the nerve ring.

By the meeting and subsequent fusion of the edges of the grooves, part of their cavity becomes cut off from the exterior and is left below the nervous system as the subneural space. But this will be referred to again in an older larva, in which the process of its formation is more nearly completed, it having begun in a few only of the most advanced larvæ of Stage "F."

The nervous system shows a differentiation into two distinct layers, a fibrous one nearest the water system and a cellular layer lying below the fibers (figs. 23-29). The nuclei of the cellular layer are oval, with their long diameter perpendicular to the fibrous layer.

Above the nervous system, separating it from the water system, is to be found the outer perihæmal space (figs. 23-30, opr). Recalling the condition of the perihæmal system in Stage "E," we see that the ends of the interradial projections from the hypogastric and anterior enterocœles have grown out over the nervous system, spreading in both directions until the outgrowths of each interradial pouch meet those of its adjacent fellows in the radii over the origins of the radial nerves; here the ends of the pouches fuse, and together they grow out over the radial nerves as the radial perihæmal sinuses.

In the starfishes, where the formation of this perihæmal system has been observed, it is said that no fusion takes place between the diverticula of the interradial pouches of the hypogastric and anterior enterocœles when they meet in the radii, but that a mesentery is formed at the points where the diverticula come in contact. This mesentery is described as continuing to the end of the arms, separating the radial spaces into two parallel cavities.

Nowhere could I find such a mesentery in sections of the larvæ of *O. brevispina*, nor could I feel sure that it exists in the adult ophiuran.

McBRIDE (10) and GOTO (5) both agree that in starfishes the *inner* perihæmal ring sinus arises from the anterior enterocœle, although they differ as to the method of its formation. In none of the larvæ I have is the structure in question fully formed, but in Stage "F" a cavity is arising, as an outgrowth from the anterior enterocœle in the stone canal interradius, which I take to be the rudiment of the inner perihæmal ring space. It lies to the left of the stone canal near the median sagittal plane of the larva. From the posterior side of the ventral end of the anterior enterocœle the outgrowth takes its origin, then extending posteriorly until past the water ring it bends over and grows down until its end reaches the nerve ring at a point inside the outer perihæmal sinus. Here the end of the pouch in question begins to spread under the nerve ring in both directions, parallel to the outer perihæmal ring (figs. 24 and 26, ips). This coincides exactly with its method of origin in *Asterina gibbosa* as described by McBRIDE.

Although the outer perihæmal ring is entirely cut off from the body cavities at this stage, there still remain traces of the interradial pouches which gave rise to it (fig. 29, hip 1-2 and 4-5).

The hypogastric enterocœle itself has changed very little since Stage "E," but the epigastric has enlarged to such an extent that its edges now meet the edges of the hypogastric and a circular aboral mesentery is formed (figs. 23-29, cm).

In the water system considerable growth is to be noted in the tentacles, the end and first pair of foot tentacles being capable of protrusion considerably beyond the disk. By means of these tentacles the larvæ are able to cling tenaciously to the surfaces of foreign bodies, it requiring a strong jet of water from a pipette to detach them. Special notice was taken to be sure that it was the tentacles and not the larval organ which was used as a means of attachment.

The second pair of tentacles (buccal tentacles) have acquired their ectoderm in this stage and they protrude, like the other tentacles, over the radial nerves into the radial grooves (figs. 22 and 26, t 2).

The axial sinus or ampulla is present in "F," it being that part of the anterior enterocœle which remains after the pouches have been cut off, which will form the inner perihæmal and part of the outer perihæmal systems (figs. 24, 25, and 26, ax sin).

It will be noted that beside the ampulla, which is situated anteriorly to the stone canal, there are two other cavities near the stone canal to be accounted for (fig. 26, sin a and sin b). I can not be sure of their origin, but I believe that they also come from the anterior enterocœle. I have distinguished them by the letters a and b, as they are probably the same cavities as those so lettered by McBRIDE (10) in his figures of Amphiura.

The cavity McBRIDE has lettered b′, and which he thinks represents the degenerated *right* hydrocœle, I have been unable to find in any of my sections.

The stomach and œsophagus are in a condition the same as we found them in "E;" that is, without lumen.

STAGE "G," 5½ DAYS OLD.

(Figures 31 and 32.)

Larvæ a few hours older than "F" show a decided degeneration in the larval organ (fig. 31, lo), but otherwise the external appearance of the two stages is about the same.

The grooves caused by the invagination of the nervous system have begun to disappear by the growing together of their edges, and instead of the deep furrows we find a slightly depressed line where the edges of the grooves have met (fig. 28, rg).

In the nervous system a pair of tentacle nerves has been formed from each radial nerve (fig. 31, nl). They grow out laterally from the radial nerves at points proximal to the first pair of foot tentacles, around which latter they grow and to which they belong. No nerves as yet have appeared to supply the buccal tentacles.

In "F" the buccal tentacles had only begun to curve away from the end of the arm; but in "G" this proximal bending has continued until they curve over the nerve ring and point toward the mouth.

Beside this change in the water vascular system we find in "G" the first appearance of the rudiments of the polian vesicles. They are four in number and are in the form of small interradial pouches growing distally from the convex wall of the water ring (figs. 31 and 32, pv). There is no polian vesicle present in this species in the stone canal interradius.

As no perceptible change has taken place since "F" in the organs not referred to above, the description of them given in the previous chapter will serve equally as well for "G" as for "F," and the figures of these organs in "G" may be examined in connection with their description in "F."

STAGE "H," 8 DAYS OLD.

(Figures 33 and 34.)

In the oldest larvæ I have, the metamorphosis has been almost completed. The larval organ has nearly disappeared, that part of it which yet remains being found sticking to the edge of the aboral disk of the young pentagonal star.

When living the little ophiurids clung to the bottom and sides of the aquaria dishes. Although the ciliated bands were still evident on the disk their free swimming habits had been wholly given up.

The pore canal still opens on the aboral surface, but with the growth of the latter it is traveling toward the edge of the disk, and by a continuation of this process the oral surface will ultimately be reached.

As the closure of the grooves over the nervous system took place, circular areas below the tips of the tentacles were left open, the tentacle pores, and through these the tentacles, were able to protrude and withdraw themselves.

The subneural sinuses which had begun to be formed in "F" have been completed in the eight-day larva (figs. 31 and 34 ss). In "H," then, the nervous system is cushioned below by the subneural sinus and above by the outer perihæmal ring.

The stomach, which for so long a period has been at a standstill in its development, has begun to grow, its sides pushing out between the epigastric and hypogastric body cavities. The lumen of both stomach and œsophagus have reappeared (fig. 34 s). The glandular structure which makes the walls of the stomach so complicated in the adult has not begun to form in "H," the walls being simple and one cell in thickness.

No figure of "H" as a whole object has been made for the reason that the skeletal plates should be included, and material adequate to a complete study of them is at present not in my possession.

RELATION OF LARVA TO ADULT.

The hydrocœle is the first organ to show radial symmetry in the developing larva of *Ophiura brevispina*, and from the time when this organ has completed its rotation about the œsophagus it shows a definite relation to the plane of bilateral symmetry of the larva.

The hydrocœle is not only radially symmetrical, but bilaterally symmetrical, since it is divided into symmetrical halves by the plane which passes through radial canal 3 and through the interradius of the stone canal. This plane coincides with the plane of bilateral symmetry of the larva. The other parts of the star are built about the water vascular system; hence it, as a whole, bears a similar relation to the larva as was initiated by the hydrocœle.

No secondary twisting of the various parts of the star occurs, and its relation to the larva remains constant as it began, and throughout the life history of the species the following statements hold true: Ventral and dorsal in the larva are equivalent to oral and aboral in the adult. Although no physiological differentiation exists, if we regard that part of the adult as anterior which was anteriorly directed in the free swimming larva, the trivium is anterior, the bivium is posterior.

In the foregoing I have confirmed, in an ophiurid, the conclusions drawn by GOTO from his studies on a starfish. In his work on the development of *Asterias pallida* GOTO (5) thought he was able to prove the coincidence of bilateral symmetry, which obtains in the adult starfish, with the plane of bilateral symmetry of the bipinnarian and brachiolarian larvæ.

The study of the relation of larva to adult in the starfishes is made most difficult, however, by the independent origin and subsequent twisting of the parts of the star. At the time of their origin no two parts of the star bear the same relation to the larva. The relation of each part to the larva also changes as metamorphosis proceeds.

The facts just enumerated admit of other conclusions than those deduced by GOTO, and no two investigators have reached the same conclusion. The point of view from which the subject has been approached is not the same in all cases, but the results obtained by those who have studied the question admit of being reduced to the same basis; that is, the relation of the planes of bilateral symmetry in larva and adult.

Cuénot (4) in his latest work denies the existence of any known relation between them.

Semon (13), working on a holothurian, found the two planes in question to coincide, but his conclusion is based on the supposition that the dorsal mesentery of the adult is the same as that of the auricularia larva, which supposition Bury has since shown to be incorrect.

Bury (3), after working on members of all the groups of echinoderms, concluded that the plane of bilateral symmetry of the larval form coincides not with the plane dividing the adult form into two symmetrical halves, but with the plane of radial symmetry.

McBride's (10) observation on a starfish, *Asterina gibbosa*, led him to adopt about the same view as that of Bury. He found that the plane of radial symmetry of the star makes an angle of 70° plus with the frontal plane of the larva, but may, without error, be considered as 90°. This is equivalent to saying that the plane of radial symmetry of the star is parallel with the sagittal plane or the plane of bilateral symmetry of the larva, and is also reducible to the statement that the planes of bilateral symmetry of the larva and adult are at right angles to one another. Thus right and left in the larva become aboral and oral in the adult.

The difference in results arrived at by Goto and McBride are due almost wholly to the stages in the metamorphosis selected in each case for the study of the question, Goto selecting a very late stage, when the larval body had all but disappeared, while the stage chosen by McBride is an early one, in which the rudiments of the star are just appearing.

If the five groups of echinoderms have sprung from a common stem after radial symmetry had been established, then in the metamorphosis which is found in all the groups there should be discoverable a unity of relation between larva and adult. It is hard to conceive of the radial symmetry of echinoderms as having been independently acquired by each group, although it is easy to see how secondary changes may have arisen in the metamorphosis since the groups separated.

The five groups of echinoderms stand isolated from one another almost as completely as does the echinoderm phylum from the other phyla of the animal kingdom, and it is not my intention at this time to enter into a discussion of the interrelationships of echinoderms. I wish, however, to point out an interesting series of facts presented by members of the Asterid, Crinoid, and Ophiurid groups which may have a bearing upon the subject, and in the same connection I wish to call attention to how well McBride's hypothetical ancestor of the Asterids and Crinoids (10, fig. —), when details are not too closely compared, fits into the facts of the larva of *Ophiura brevispina*.

In one of the Asterids Goto has shown that toward the end of metamorphosis the almost complete star sits as a cap at the posterior end of the larva, with its aboral end posterior, its oral surface anterior, the bivium dorsal, and the trivium ventral.

In Antedon, like the starfish, the rotation brings the developing crinoid head to the posterior end of the larva, but differing diametrically from the starfish in that the oral instead of the aboral surface of the crinoid is posterior; but this difference does not in any way affect the homologies between the two groups as has been supposed.

In *Ophiura brevispina* the relation of larva and adult at the time of metamorphosis is approximately the same as is shown in Stage "F" (fig. 22), in which ventral in the larva is ventral (oral) in the adult.

Now, if we take an ophiuran larva at Stage "F," and imagine the disk to rotate in such a way as to bring its oral surface away from the larval organ or preoral lobe, it fairly represents that which takes place in the metamorphosis of Antedon, but if we think of it as rotating in the opposite way, bringing the aboral surface away from the preoral lobe, then it more nearly illustrates the starfish metamorphosis.

In Antedon, as metamorphosis proceeds, the stem is carried on to the aboral surface, while in the starfish the preoral lobe finally disappears on the oral surface. In *O. brevispina* the place of disappearance of the larval organ more nearly recalls the crinoid than any other echinoderm, the larval organ being found in some of my oldest specimens as a small knob near the edge of the *aboral* surface between arms I and V.

COMPARISON OF THE LARVA OF ANTEDON ROSACEA WITH THAT OF OPHIURA BREVISPINA.

While I was studying the larva of *Ophiura brevispina*, characters were constantly being found which reminded me of the larva of Antedon as described by BURY (1). Some of these points of resemblance are no doubt only superficial, but others are such as to make it worth the while to devote a short chapter to the similarities of the two larvæ.

The entire ciliation of the very young larvæ gives place in both to a series of transverse ciliated bands, five in Antedon, four in Ophiura. The band nearest the anterior end of the Antedon larva, however, is small and incomplete. Two bands only in each case surround that part of the larva from which the disk is formed.

The blastopore in both larvæ, after shifting from a posterior position to one on the ventral surface, closes and the archenteron loses its connection with the ectoderm and lies free in the body cavity.

In the seven-day embryo of Antedon and Stage "C" of Ophiura the hydrocœle is a horseshoe-shaped structure lying in the posterior ventral part of the larvæ with the open end directed anteriorly, and in each case the plane of radial symmetry of the hydrocœle is at right angles to the plane of bilateral symmetry of the larvæ.

In the formation of the paired tentacles from the radial water canals the process is *begun* centripetally in both larvæ, the second pair of tentacles appearing between the first pair and the water ring instead of between the first pair and the end tentacle, as is the case in the other groups of echinoderms.

In the five-day Antedon larva and those stages represented by "D" to "F" in Ophiura the stalk and larval organ are strikingly similar, both in shape and position, the two structures being anteriorly directed in swimming.

The stem of the Antedon larva, as a result of metamorphosis, comes to be an aboral structure, and just before the disappearance of the larval organ from the ophiuran larva it is to be found as a small knob, not in the *center* of the aboral disk, it is true, but on its edge. In the starfishes it may be recalled that the preoral lobe disappears on the *oral* surface of the metamorphosing star.

To the above larval characteristics may be added the similarity which exists in the disposition of the alimentary and cœlomic systems in the adult forms.

In both Crinoids and Ophiurans the digestive apparatus is confined to the disk.

The body cavity is continued into and to the ends of the arms. When a transverse section of a pinnule of Antedon is compared with a transverse section of an ophiurid arm, the following striking correspondence is found in the parts: Aborally, segmentally arranged calcarious ossicles and muscles are present; a continuation of the body cœlom runs between and oral to the muscles; connected with and on each side of this central brachial body cavity are two other cavities, the subtentacular canals of Antedon. These latter in the Ophiurans are connected with perihæmal space in each vertebral segment.

The radial water tube lies between the subtentacular canals, and in each segment sends out a pair of tentacles. The tentacles in both the Crinoids and Ophiurids are devoid of the terminal suckers, which are so characteristic of the other echinoderms.

Separating the radial water tube from the nerve cord is to be found the radial perihæmal sinus.

In ophiurans a subneural space is present which is not represented in the crinoid arm. This is due to the fact that in Antedon the nervous system is superficial, while in Ophiura it has been invaginated, and with its invagination a space has also been carried in below it.

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EXPLANATION OF PLATES.

The figures illustrating this paper were drawn to the same scale of magnification, 330 diameters, and were reduced one-half in reproduction.

Figs. 1, 2, 4, 6, 7, 9, 17, 31, and 32 were reconstructed from series of transverse and sagittal sections.

In all cases the part of the figure which is nearest the top of the plate is either anterior or else ventral in the larva.

ABBREVIATIONS USED.

ael	Left anterior enterocœle.
aer	Right anterior enterocœle.
ap	Apical plate.
ax sin	Axial Sinus.
b	Blastopore.
cb 1, 2, 3, and 4	Ciliated bands.
cg	Circular groove.
cm	Circular mesentery.
cp	Cellular plug.
d	Dorsal pore.
ee	Epigastric enterocœle.
et	End tentacle.
hc	Canal connecting posterior enterocœle and hydrocœle.
he	Hypogastric enterocœle.
hip 1–2, 2–3, 3–4, 4–5	Interradial pouches of the hypogastric enterocœle.
hy	Hydrocœle.
ips	Inner perihæmal sinus.
ipax 5 1	Interradial pouch of axial sinus.
lo	Larval organ.
m	Mouth.
mes	Mesenchyme.
n1	First pair tentacle nerves.
nr	Nerve ring.
oe	Œsophagus.
od	Oral disk.
opr	Outer perihæmal ring.
pc	Pore canal.
pe	Posterior enterocœles.
pv	Polian vesicle.
rad n	Radial nerves.
rg	Radial grooves.
rps	Radial perihæmal space.
sin a	Sinus "a".
sin b	Sinus "b".
st	Stone canal.
ss	Subneural sinus.
s	Stomach.
t1	First pair foot tentacles.
t2	Buccal tentacles.
wvr	Water vascular ring.
I, II, III, IV, V	Arm rudiments.
1, 2, 3, 4, 5	Radial water canals.

PLATE I.

FIG. 1. Larva in Stage "A," seen from the right side, the right half of the ectoderm removed and the mesenchyme omitted.

FIG. 2. The same larva, seen from the ventral side as a transparent object.

FIG. 3. Median longitudinal section of a larva in Stage "A."

FIG. 4. A larva in Stage "B," viewed from the ventral side as a transparent object.

FIG. 5. Transverse section of a larva in Stage "B" in a plane halfway between the blastopore and the point where the hydrocele is connected with the archenteron.

FIG. 6. Larva in Stage "C," seen from the ventral side, the ventral half of the ectoderm, the mesenchyme, and part of the œsophagus removed.

FIG. 7. The left half of the same larva.

FIG. 8. Transverse section through Stage "C" in a plane indicated on fig. 6 by the letters *a–b*.

FIG. 9. The reconstructed internal anatomy of a larva in Stage "D," the ventral ectoderm removed and with it part of the œsophagus.

FIG. 10. An outline drawing of fig. 9, on which are indicated by lines the planes of the sections which follow in figures 11, 12, 13, and 14.

FIG. 11. Longitudinal section taken through a larva in Stage "D" in the plane indicated on fig. 10 by the line *m–n*.

FIGS. 12, 13, and fig. 14 of Plate II. Transverse sections taken through Stage "D" in planes indicated on fig. 10 by the lines *a–b*, *c–d*, and *e–f*.

PLATE II.

FIG. 15. Ventral view of a larva in Stage "E," to show ciliated bands and first appearance of the arm rudiments.

FIG. 16. Dorsal view of Stage "E," showing the ciliated bands.

FIG. 17. A reconstruction of the anatomy of a larva in stage "E," the ventral ectoderm removed.

FIG. 18. An outline drawing of fig. 17, on which are indicated by lines the planes of the sections shown in figs. 19, 20, and 21.

FIGS. 19, 20, and 21. Transverse sections taken through larva in Stage "E" in planes indicated on fig. 18 by the lines *r–s*, *t–u*, and *v–w*.

FIG. 31. Reconstruction of the anatomy of a larva in Stage "G." In this case as in all the other reconstructions the ventral surface is up and the ventral ectoderm removed.

FIG. 32. An outline drawing of the water vascular system of a larva in Stage "G," seen from the ventral surface.

FIG. 33. Transverse section of Stage "H," taken through the region of the stone canal.

FIG. 34. Transverse section of a larva in Stage "H," taken through the stomach.

PLATE III.

FIG. 22. Ventral view of the fully developed larva before metamorphosis has begun. Stage "F."

FIG. 23. Outline drawing of fig. 22. The lines indicate the planes of the sections, which have been drawn to show the anatomy of a larva in Stage "F."

FIGS. 24, 25, 26, and 27. Longitudinal sections of a larva in Stage "F," the planes of which are indicated on fig. 23 by the lines *a–b*, *c–d*, *m–n*, and *x–y*.

FIGS. 28, 29, and 30. Transverse sections of a larva in Stage "F," the planes of which are indicated on fig. 23 by the lines *c–o*, *d–o* and *e–o*.

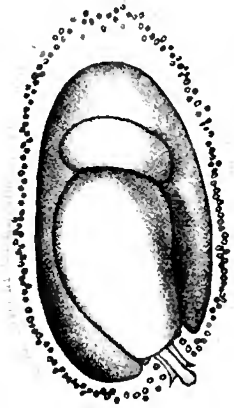
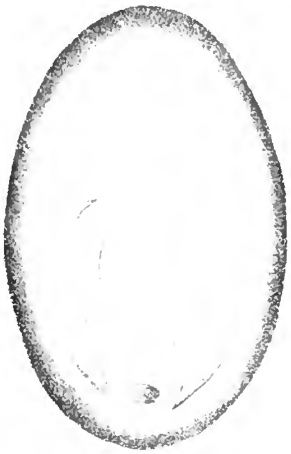


Fig. 1.



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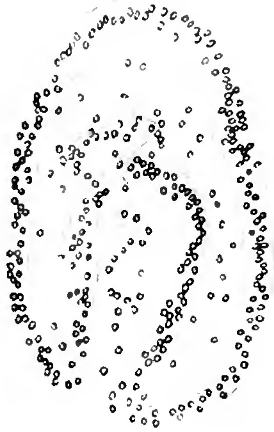
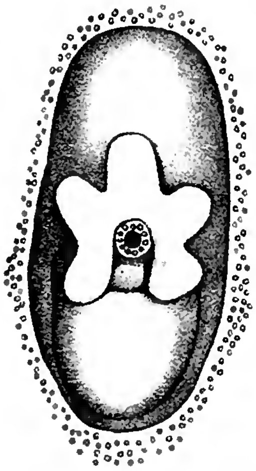


Fig. 3.

Fig. 4.

Fig. 5.



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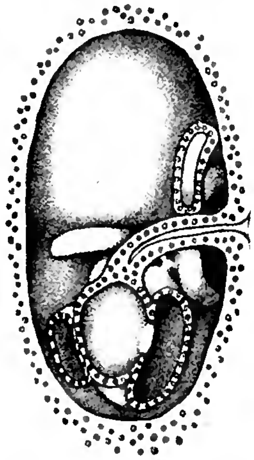

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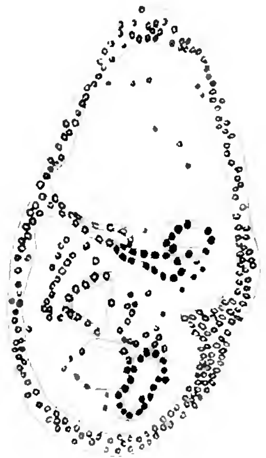

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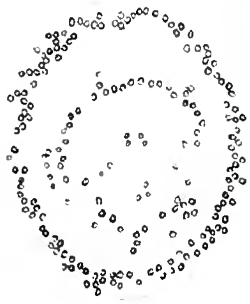

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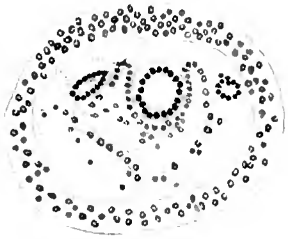

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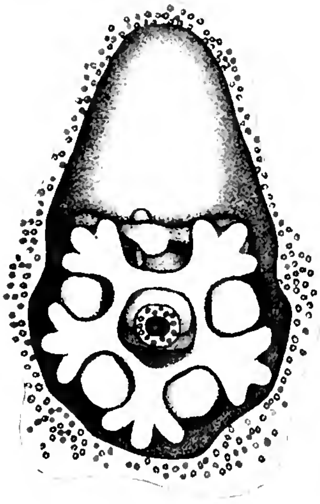

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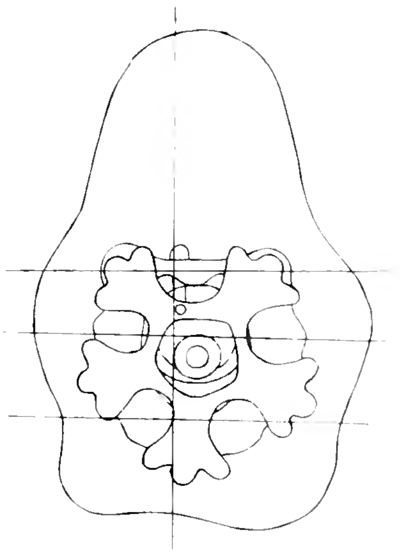
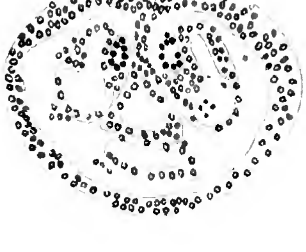


Fig. 10



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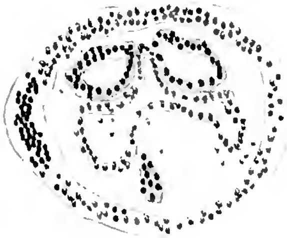
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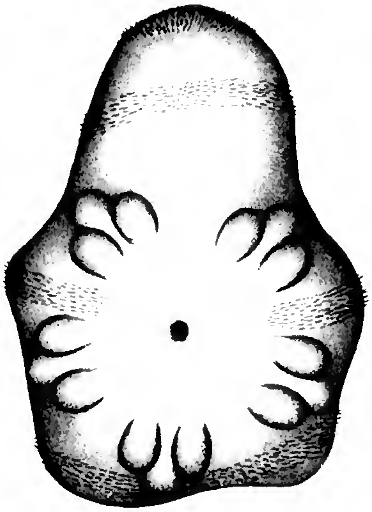
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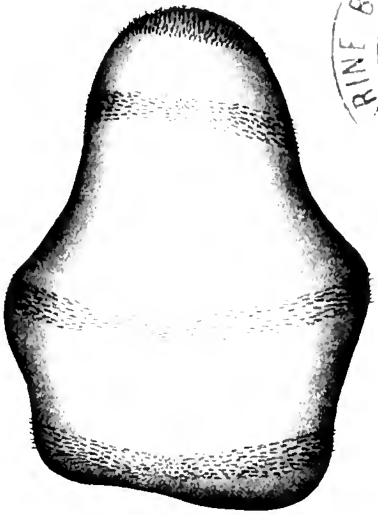
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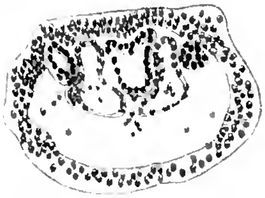
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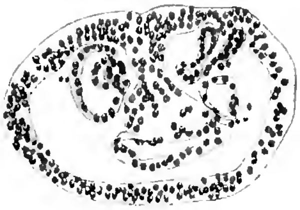
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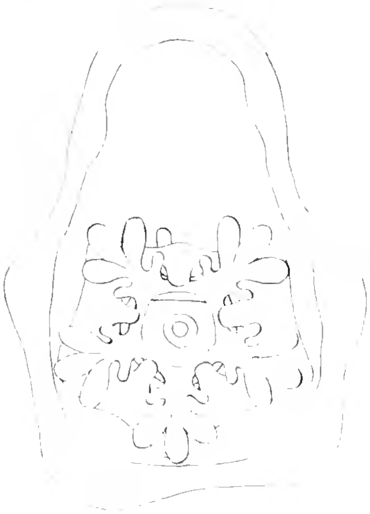
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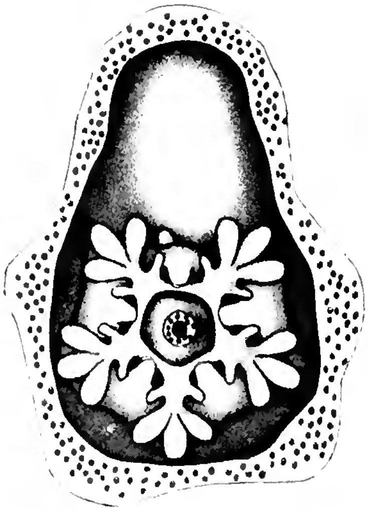
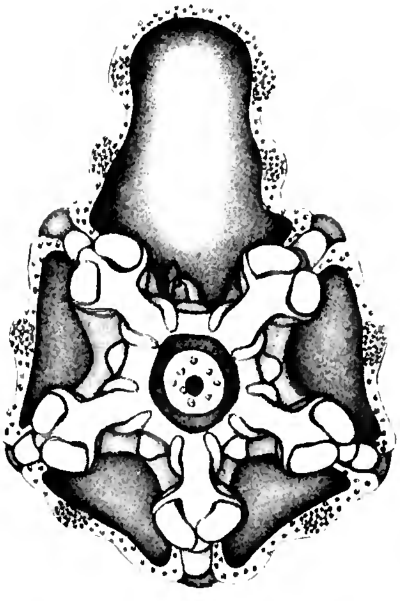


Fig. 17.


Fig. 21.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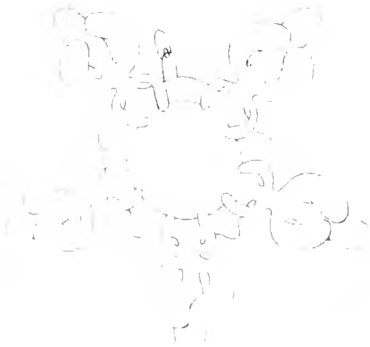
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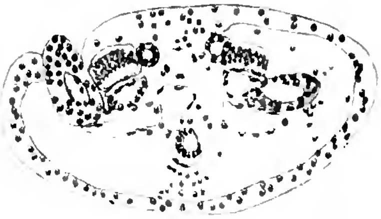


Fig. 33.


Fig. 34.

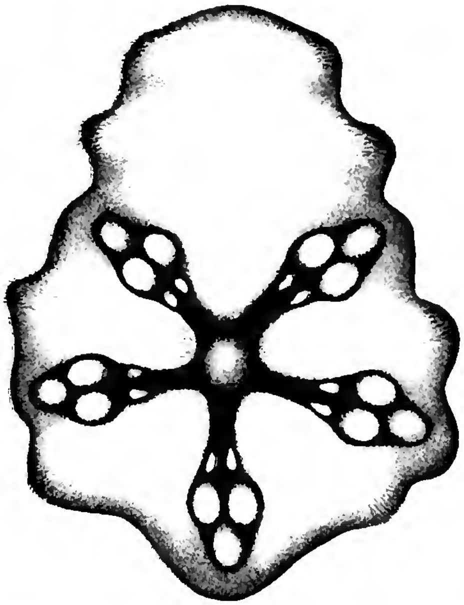


Fig. 22.

Fig. 24.

Fig. 25.

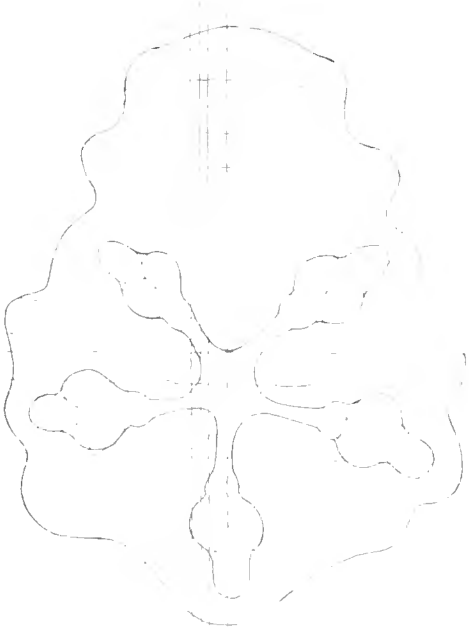
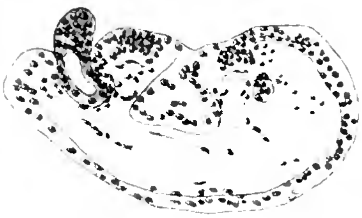


Fig. 23.

Fig. 26.

Fig. 27.

Fig. 28.



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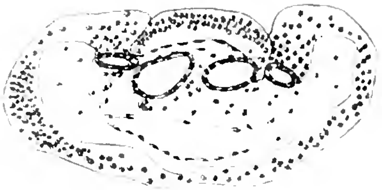

Fig. 30.