QL
384
A8G32
++

CORNELL
UNIVERSITY
LIBRARY

ZOOLOGY

Cornell University Library
QL 384.A8G32

The development of the starfish Solaster

3 1924 002 803 520 mann

Cornell University Library

The original of this book is in
the Cornell University Library.

There are no known copyright restrictions in
the United States on the use of the text.

<http://www.archive.org/details/cu31924002803520>

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY OF LONDON.

- I. *The Development of the Starfish Solaster endeca Forbes.* By JAMES F. GEMMILL,
M.A., M.D., D.Sc., F.Z.S., Lecturer in Embryology, Glasgow University, and in
Zoology, Glasgow Provincial Training College.

(Received and read November 29, 1910.)

[PLATES I.-V.]

CONTENTS.

	Page
I. STRUCTURE AND POSITION	3
II. OVARIES AND OVA	4
Arrangement and structure of the egg-tubes, 4; muscular tissue and sinus-spaces in their walls, 4; relation of the latter to genital sinuses and hæmal tissue, 5; growth of the ova, 6; accumulation of yolk-granules, 6; yolk-nuclei, 7; follicle-cells, 7; egg-ducts, 8.	
III. MATURATION, SPAWNING, FERTILIZATION, &c.	9
Time of maturation, 9; season, &c. of spawning, 9; the ova in water, 10; membrane of fertilisation, 11; cross-fertilisation, 11; early and later segmentation, 11; formation of blastula by egression and of gastrula by invagination, 12; appearance of cilia, 12; movements of blastula and gastrula, 13; hypenchyme, 13; chronology, 13.	
IV. EXTERNAL CHARACTERS, MOVEMENTS, &c. DURING THE FREE-SWIMMING PERIOD	14
Elongation of gastrula, 14; formation of arms and of sucker, 14; preoral lobe and body of larva, 14; formation of hydropore, 14; closure of blastopore, 15; movements of the larvæ, 15; ciliation at anterior and posterior ends and over general surface, 15; commencement of flexion and torsion of the preoral lobe, 16; first appearance extern- ally of hydrocœle lobes and of aboral arm rudiments, 17; chronology, 17.	

V. GENERAL HISTORY AND EXTERNAL CHARACTERS DURING AND AFTER METAMORPHOSIS	Page 17
Mode and site of attachment by the larval sucker, 17; fate of preoral lobe, and formation of oral and aboral surfaces, 19; the hydrocœle pouches and order of their development, 20; numbering of pouches, 21; the aboral arm rudiments and their adjustment to the pouches, 22; attachment by first-formed sucker-feet, 22; appearance of the eyes, the mouth, the anus, and the spines, 23; constant position of anus in specimens with normal and abnormal numbers of rays, and in <i>S. papposa</i> , 23; movements &c. of the Starfish before and after formation of mouth, 24; surface-crawling, 24; chronology, 25.	
VI. DEVELOPMENT OF CAVITIES AND ORGANS	25
Formation of (1) anterior and (2) posterior cœlom, and of (3) middle chamber or enteron, 25.	
(1) <i>Anterior Cœlom and its Derivatives</i>	26
Formation of right and left lateral diverticula, 26; hydroporic canal, 26; preoral cœlom, 26; epiderm of preoral lobe partly incorporated with oral surface of Starfish, 27; separation of the right lateral diverticulum from axial cœlom, 27; the hydrocœle groove, 28; formation of first five radial pouches, 28; formation of succeeding radial pouches, 28; relation of stalk of preoral cœlom to hydrocœle ring, 29; relation of pouch I to posterior cœlom, 29; the dorsal sac, 29; axial part of anterior cœlom, 29; internal oral circular sinus, 30; axial organ, 30; stone-canal, 31; relation of madreporic pores to stone-canal and axial sinus, 31; pouch IX/I of external oral circular sinus, 31.	
(2) <i>Posterior Cœlom and its Derivatives</i>	32
Dorsal and ventral horns, 32; extension of the horns, and the part played by them in separating preoral cœlom from axial and epigastric cœloms, 32; septum in madreporic interradius enclosing axial complex, 32; interbrachial septa, 33; extension of hypogastric cœlom on oral and aboral surfaces of enteron, 33; circular epigastric mesentery, 33; aboral ligaments of stomach and paired cœca, 34; formation and extension of pharyngeal cœlom, 34; the circular hypogastric mesentery, 35; hypogastric ligaments of stomach, 35; formation and subsequent growth of pouches of external oral circular sinus, 35; genital rachis, &c., 36.	
(3) <i>The Enteron</i>	36
Radial lobes of stomach, 38; mouth, 39; anus, 39; paired radial cœca, 40; rectal cœca, 40.	
VII. DEVELOPMENT OF THE SKELETON	41
Sequence in appearance of ambulacral and adambulacral plates, 41; plates of central and marginal parts of disc, 41; terminals double, 42; transition to adult reticulum, 42; development and grouping of spines, 43; the denticles, 43.	
VIII. HISTOLOGY	43
<i>Mesenchyme and Yolk</i> , 43; intracellular digestion of yolk, 44; reserve store retained in the mesenchyme, &c., 44; a more highly-yolked Starfish egg, 44; the hypenchyme, 45; yolk-granules in the enteron wall, 45.	
<i>A Statolith-like Body</i> in the posterior cœlom, 46; statocysts in <i>Synapta</i> , 46.	
<i>Nervous System</i> of larva, 46; relation to that of adult, 47; larval nervous system in other Echinoderms, 47.	

	Page
<i>Origin of Muscle-fibrillæ</i> in larva, 47; muscle causing flexion &c. of preoral lobe, 47.	
<i>Ciliation</i> , 48.	
IX. MODE OF OBTAINING AND REARING THE LARVÆ	48
Spawning in the tanks at the Millport Marine Station, 48; arrangement to retain the ova and to keep the larvæ healthy in aquaria with sea-water circulation, and in smaller aquaria under aeration, 48; larvæ obtained in tow-netting, &c., 49.	
X. SUMMARY, &c.	50
External characters, 50; development of cavities, 51; development of skeleton, 52; general comparison with <i>Cribrella</i> , 52; relations with development of other Starfish, 53.	
REFERENCES	53
EXPLANATION OF PLATES	55

I. STRUCTURE AND POSITION.

IN the classification of Perrier (21) the Solasteridæ form a Family of the Spinulosæ, one of the five Orders into which this author divides Starfishes. *Asterina* and *Cribrella*, the development of which has been carefully investigated (12, 15, 18), come within the same Order, but are in different Families, viz., the Echinasteridæ and the Asterinidæ respectively.

The system of Sladen (23) makes the Solasteridæ one of the ten Families belonging to the Cryptozonia, the second of his two great Orders of Starfish. *Cribrella* falls within the same Order as a member of the Echinasteridæ, but the Asterinidæ are included in the other Order, namely the Phanerozonia.

As regards *Solaster endeca*, the following characters should be noted at this stage, other points of minor importance being referred to later as occasion arises:—

The normal number of rays is nine, but occasionally there are one or two more or less. The madreporite is single, no matter what may be the number of rays. The aboral skeleton forms a fine reticulum made up of small plates, many of which carry bunches of spines. Gills are present everywhere in the interspaces of this reticulum in groups of two or three. There are no pedicellariæ. The tube-feet in each ray form a double row. The mouth-armature is, on the whole, of the adambulacral type, but the first ambulacrals are relatively prominent. The globular part of the stomach shows folded radial lobes; above it the usual radial cæca are given off from the pyloric sac, each pair arising by a long common duct. There are two small bunches of rectal cæca. The anus, though very close to the middle of the aboral surface, is slightly excentric in the direction of the interradius which on developmental grounds must be entitled V-VI (pp. 20, 23). Strong perforated interbrachial septa are present in all the interradii.

II. OVARIES AND OVA.

The gonads are in pairs, interradially placed, and confined to the disc. Each consists of a bunch of short tubes, whitish in the male and orange-coloured in the female. These are attached to the inner aspect of the body-wall close to the mid-interradial line, a short distance upwards from the margin on the aboral side. Here the body-wall is pierced by the egg-ducts.

In full-grown specimens the number of egg-tubes in each gonad may amount to several hundreds. These are somewhat indistinctly divided into a few (5-7) main groups, which in turn are capable of subdivision into small ultimate clusters of three to seven tubes. The tubes in each of these clusters join together at their attached ends to open into the same terminal branch of the egg-duct. While the majority are cylindrical or sausage-like in shape, simple branching may occur, characterized usually by a single dichotomous division near the free end, and occasionally also by the presence of one or two short lateral branches on the stem.

The wall of the egg-tubes consists of outer and inner layers separated by irregular spaces. The outer layer, which is considerably the stronger, is made up of connective and muscular tissue, the fibres of the latter being arranged chiefly in a circular direction. It is covered superficially by cubical ciliated cells, and during life the ciliary movement is such that currents of coelomic fluid pass along the surface of the tubes from their attached to their free extremities. The inner layer is thinner and consists almost entirely of connective tissue, but I find that in addition it contains a number of muscular fibres which are longitudinal in direction and occur chiefly towards the attached ends of the tubes.

The spaces between the outer and inner layers of the gonad-wall are best developed near the attached ends of the tubes. Here they open into an irregular cavity which almost surrounds the commencement of the egg-ducts, and which in its turn is continuous with one of the genital branches of the aboral circular perihæmal sinus. An open communication is thus established between the aboral sinus and the spaces in the gonad-walls. Along this line of communication occur strands of the tissue interpreted by Ludwig and others as blood vascular or hæmal. These strands arise from the hæmal tissue within the aboral circular sinus and end by spreading out within the spaces between the inner and outer layers of the gonad-walls as fine branches attached to the inner of these two layers. No open communication exists between the interior of the egg-tubes and the genital sinuses or between either and the cavities of the hæmal strands. In the adult *Solaster endeca* I cannot find definite cellular remains of the genital rachis either in the circular or in the genital sinuses; but in a young *Solaster papposa* of an inch and a half in diameter the rachis was still represented, in both these cavities, by a thin solid cord of characteristic cells.

to be usual, or at least not to be generally recognized. Ludwig (13, p. 599) and Delage (5, pp. 62-63) speak as if the layer in question consisted entirely of fibrous connective tissue. In the case of *Asterias vulgaris*, Field (7, p. 106) states that the muscular fibres of the egg-tube walls run in various directions, the outer and inner fibres being at right angles to one another. He makes no mention of spaces between the layers, nor are such spaces indicated in his illustration.

In Starfish anatomy it seems to be the rule that in hollow structures with muscular walls the longitudinal fibres lie internal to the circular ones, as, for example, in the walls of the tube-feet and of the disc itself, as well as in the peristome and the œsophagus and stomach. *Note*.—In this connection attention may be called to the statement in Bronn's 'Klassen' (13, p. 580), that in the œsophagus the circular layer is internal to the longitudinal one. This appears to be an error, as it is also said that these layers are the continuations of corresponding layers in the peristome, and the relative position of the circular and longitudinal muscles is correctly given on the page before.

The statement made above, to the effect that in *Solaster endeca* the spaces between the inner and outer layers of the egg-tube wall are continuous with the genital sinus, was based on a careful examination of serial sections through four gonads in an adult *Solaster* of large size, and I have not the slightest doubt as to its correctness for this particular species.

In Ludwig's view the spaces in question are lacunar in character (13, pp. 599 & 613), being terminal expansions of the hæmal vessels within the genital sinuses. Hamann, quoted in Ludwig (13, p. 599), described the spaces as having an endothelium-like lining and as communicating both with the genital sinuses and with the cavities of the hæmal tissue.

According to Cuénot (3, p. 88) the spaces in question belong to the perihæmal sinus system, while the cavities of the hæmal vessels lead directly into the interior of the egg-tubes. Macbride (15, p. 377, fig. 122) showed that in *Asterina* the spaces between the inner and outer layers of the gonad-walls arise as expansions at the ends of the genital branches of the aboral perihæmal sinus, but apparently in later development these spaces become completely shut off, owing to the formation of the septum through which the growing egg-ducts burrow their way to the outside. However, the same author (16, p. 449) describes the genital branches of the aboral sinus as swelling out at their blind ends so as to enclose the gonad cell-masses.

In my series of sections referred to above a distinct cellular lining was present in the larger spaces occurring around the roots and proximal parts of the egg-tubes, but further along the tubes it became less definite and finally ceased to be recognizable.

This is not the only instance in which a perihæmal sinus-cavity divides into branches which lose themselves within the mesoderm. I find in the adult *Solaster* that there is a branch extending aborally into each interbrachial septum from the corresponding segment of the external oral circular sinus. This branch soon divides into slit-like spaces, which cease to be recognizable when traced further upwards in the septum (8 a).

In development the branch in question is not difficult to follow (p. 36), and indeed I was first led to look for it in the adult from having noted it in a specimen of the age of four months.

Contents of the Egg-Tubes.—The egg-tubes contain: (1) ova in various stages of growth; (2) follicle-cells, both covering the ova and lining such parts of the gonad-wall as are free from ova; (3) irregular cells, free in the lumen of the tube, mostly rounded and loaded with fat-granules, but sometimes smaller and resembling leucocytes in form.

Ova.—These rest directly against the inner wall of the egg-tubes without the intervention of follicle-cells. Quite young ova may occur anywhere along the length of the egg-tubes, but as a rule the youngest are most abundant towards the free ends of the tubes. The nucleus or germinal vesicle contains a single large nucleolus, and exhibits in general the characters which are usually found in the nuclei of highly yolked ova. That is to say, it is large from an early stage, and it increases with the growth of the egg; its membrane is definite and resistant; there is a delicate achromatic reticulum; the chromatin is diffuse and difficult to stain; and the fluid nucleoplasm is abundant and coagulates in shreds.

The cell-contents stain readily with hæmatoxylin, are finely punctate in character, and have a rich orange colour which dissolves out readily in alcohol and other reagents. These facts indicate the early presence of deutoplasmic granules; but this first deutoplasm is free from ordinary fatty yolk, being quite unaffected by treatment with osmic acid. Indeed, the growth of the ovum may be divided into two periods: the first up till the earliest appearance of the yolk-granules which are fatty in character, and the second till full size is reached and the egg is ready to undergo the changes of maturation. At the end of the first stage the egg has reached a diameter of .15 mm., a third of this measurement being occupied by the nucleus.

Fatty yolk-granules now begin to gather closely round the nucleus, forming a zone which is at first thin and loose, but afterwards becomes thicker and more crowded, the additions taking place on the outside of the zone (Pl. III. fig. 35). Throughout this zone only a small amount of protoplasm remains, forming a reticulum between the granules. Outside of the zone in question there is a layer of protoplasm gradually increasing in size during the active growth of the egg, but gradually also being

invaded by the yolk, until in the end there remains under the egg-membrane only the thinnest possible yolk-free layer.

It should be noted that while the gross aggregation of yolk takes place from the nucleus outwards, as above described, stray granules may be observed in all stages at lesser depths, or even close under the egg-membrane. Similar granules along with many coarser ones occur within the follicle-cells, and it seems not improbable that during growth the former are transferred through the vitelline membrane to the ovum, where they congregate round the germinal vesicle, the stray granules above mentioned being on their passage inwards from the periphery. A remarkable instance of transference of the granules is given on p. 45.

The yolk-granules on their first appearance are small, rounded, and uniform in size. As growth proceeds they become slightly larger everywhere, the increase in the full-sized egg being least at the very surface close under the vitelline membrane.

In the middle and later stages of growth, bodies resembling the so-called yolk-nuclei are very evident. Their substance is finely punctate. They stain well in hæmalum, but with a characteristic reddish tinge. They are by no means regular in number, size, and position, though the largest are always found quite close to the germinal vesicle. They have no definite boundary, but merge at their periphery into the protoplasmic reticulum in which the yolk-granules lie. They disappear when the egg has reached full size and maturity. It seems probable that they are formed by the activity of the nucleus (germinal vesicle), and that migrating outwards from it they become broken up through contributing to the general protoplasmic meshwork of the cell. Chubb (2, p. 384) describes the yolk-nucleus in *Antedon* as formed by the throwing-out of small globules from the nucleolus.

A vitelline membrane is recognizable from a very early stage. In larger ova it remains thin, but is moderately tough, though not comparable in this respect with the membranes of many other ova of similar size. It seemed to be perforated by numerous fine pores, and may accordingly be termed a "zona radiata."

Apart from distortion and facetting due to pressure, the shape of the ova within the egg-tubes is already that of a spheroid with marked flattening at two opposite poles, one of which is on the side of the ovum next the gonad-wall. This, the future upper pole of the egg is bright orange in colour. The lower or yolk pole looks towards the lumen of the egg-tube and is distinctly paler than the first. The transition between the two colours is gradual, and occurs at the equator or widest part of the egg. The diameter in the equatorial plane averages 1 mm., while the vertical diameter is approximately .8 mm.

Follicle-Cells.—The follicle-cells give a covering to the eggs, except where the latter are attached to the gonad-wall, and also line such parts of the wall as have no ova resting against them. Here, in places, they are folded inwards in the form of

villus-like tufts, on the surface of which they assume an elongated form, many of them being crowded with granules or globules of fatty nature, while others have a large proportion of clear mucoid contents.

The larger villi rest on a fold of the inner layer of the egg tube-wall, and this fold may contain an extension from the spaces previously described as existing between the inner and outer layers of the gonad-wall.

The follicle-cells surrounding young and half-grown ova are cubical or polygonal in shape, and provide a covering several layers thick. As growth nears completion, these become reduced to a single layer made up of cubical or flattened cells. Still later they seem to undergo complete degeneration, the eggs when shed being destitute of a cellular covering.

Practically all the follicle-cells contain fatty granules, mostly small and resembling those within the eggs, but often larger and comparable with ordinary fat-globules. As was indicated above, it is possible that the smaller granules are transferred directly through the vitelline membrane into the ovum during growth.

There is no definite lumen within the egg-tube, the spaces between the eggs being occupied by follicle-cells, and by a small amount of fluid containing some irregular cells which are probably of leucocytic origin. In some cases masses may be noted which look like the débris of degenerating ova. These masses are without definite outline and consist of densely crowded fine yolk-granules, with small nuclei here and there among them. Round the nuclei a certain grouping of the yolk-granules is observable, as if each nucleus was establishing a cell-territory. The nuclei are probably of leucocytic nature.

Egg-Ducts.—The walls of the egg-ducts contain inner and outer layers corresponding in structure with those of the gonad-tubes, but the gonad sinus-spaces are not continued into the depth of the body-wall. The ducts are lined with ciliated cylindrical epithelium rising into folds and having many cells with clear mucoid contents. The transition between the germinal cells of the egg-tubes and the epithelium of the ducts is quite sudden, and even in immature specimens there is no septum intervening between the contents of the tubes and the lumen of the ducts.

It is difficult to determine macroscopically the exact number of external genital openings. During active spawning, however, as many as four eggs emerged at the same time, but discretely, from a single interradius. Serial sections of an interradius in the adult showed that each of the gonads had two slit-like terminal ducts formed by the union of several tributary ducts, some of which joined the terminal one within the thickness of the body-wall. In *Solaster papposa*, according to Müller and Troschel (quoted from Ludwig, 13, p. 592) and Cuénot (4, p. 623), each gonad has a number of ducts which pierce the body-wall independently, but close together, the small area on which they open being thus sieve-like in character.

My own observations on *S. papposa*, made from serial sections of an interradius in a half-grown specimen, showed only two external apertures (one for each gonad). Each of these led to a crypt-like cavity, into the bottom of which several egg-ducts opened. Eversion of this cavity may occur during later growth or at the periods of ripeness, thus producing the condition described by the authors above named. For a further discussion of these points, see under reference 8 *a*.

III. MATURATION, SPAWNING, FERTILIZATION, &c.

Maturation.—Preparation for the maturation-changes begins after the egg has reached full size, and while it is still attached to the gonad-wall. The germinal vesicle elongates radially and migrates towards the attached side of the egg until one of its poles lies close under the surface. The nucleolus becomes vacuolated, ceases to react actively to stains, and finally disappears. Meantime the membrane of the germinal vesicle has broken down. The contents remaining in position help to form a tract or plug, which is free from fatty yolk-granules and extends right to the centre of the egg. This tract comes to the surface in the middle of what will afterwards be recognizable as the upper pole of the egg. Here it expands into a small circular disc. After the eggs are shed this disc appears under reflected light as an area slightly darker than the rest of the surface, no doubt owing to its greater transparency and freedom from yolk.

In the ova examined, the formation of the first polar body was in active progress at the time of shedding. An egg fixed immediately after extrusion showed the first of the spindles lying obliquely within the disc above mentioned and close under the surface. In eggs fixed three hours after extrusion both polar bodies were found extruded and adherent to the surface, while the small female pro-nucleus, now difficult to detect, lay some distance below. No doubt the pro-nucleus next migrates towards the centre of the egg.

Spawning.—Apparently the brooding-habit is absent. Spawning occurs in the end of March or the beginning of April, and extends at intervals over a week or more. For example, a specimen taken in the trawl off the Marine Station at Millport on March 22nd, 1910, gave out ova on the 25th, on the 30th of the same month, and again on April 2nd. No further spawning took place, although the specimen was kept under observation for the next four weeks. The number of eggs on the first occasion is not known approximately, but on the second it amounted to over three thousand, and on the third to between two and three hundred. On the second occasion (March 30th) the period of most active spawning lasted about two hours. During this time the Starfish was attached to one side of the tank near the surface, the body and arms being strongly arched so that only the tips of the latter were adherent. The ova could be seen emerging as many as four at a time from the genital

apertures in each of several interradii. The same Starfish, when spawning on April 2nd, took up a somewhat different position, viz., on one side of the tank right at the surface, with the uppermost arms unattached, bent over, and separated so as to expose the interradiial angles. The ova were emitted chiefly from these interradii, but also from one or two others, sometimes singly, sometimes two or three together, at short intervals, for two and a half hours. Some years ago I observed a specimen of *Solaster papposa* in the act of spawning. The process was almost exactly identical with that which has been last described.

At the time of shedding, the eggs may be compressed in any direction, but they very quickly assume their proper form, that of an "oblate spheroid" (p. 7). Being rather lighter than sea-water, they rise gently to the surface and remain there when undisturbed. As was indicated previously, they float with the equator of the spheroid horizontal. The upper pole is of a rich orange-colour, and has in its centre the small area free from fatty yolk. The lower pole is paler in colour and of distinctly greater specific gravity, so that the egg rights itself almost at once, should its balance be disturbed.

The vitelline membrane is closely applied to the surface of the egg all round. In the eggs shed on the first two occasions it was quite thin, transparent, and smooth on the surface, but in those which were shed last there was an additional outer covering, somewhat frayed on the surface, and with minute granular débris adherent. The difference is probably caused by the addition to the true egg-membrane of a mucous coat formed within the ovary itself.

Two other specimens of *S. endeca* were kept in the same tank as the one which spawned, and fortunately one of these proved to be a ripe male. On March 30th, while ova were being shed by the female, the male was observed resting in an ordinary position on the side of the tank about two feet distant, and sending out thin streams of sperm from five or six interradii. On this occasion practically all the ova were fertilized, although in the end only a few of them developed quite normally beyond the gastrula stage. On the next occasion of spawning (April 2nd) the emission of sperm by the male was not obvious. All the eggs were, however, fertilized, and a very large proportion of them underwent normal development.

The eggs of *Solaster* are much too large and opaque to allow the process of fertilization to be watched under the microscope. It can readily be seen, however, that they attract the sperm strongly as soon as they are shed, and therefore a considerable time before the maturation-changes are completed. No doubt the disc at the upper pole and the stalk leading from it down to the centre of the egg serve as a track of entrance and guidance to the spermatozoon, which would find difficulty in boring a way through the densely crowded mass of fatty yolk-granules present everywhere else.

Segmentation and Gastrulation (Pl. I. figs. 1-6; Pl. III. figs. 24, 25).—In from three to three and a half hours after they were shed the eggs began to separate off their vitelline membranes as “membranes of fertilisation”*. The process was complete in from four to five hours. The width of the clear space left between membrane and egg varied considerably, but was on an average equal to about a seventh of the diameter of the egg itself. This membrane persists throughout segmentation and until the blastula is beginning to rotate within it—that is, till about the fifth day after fertilisation.

Segmentation all through is total and equal, the first and second cleavage-planes (Pl. I. figs. 1-2) being vertical and at right angles to one another, while the third is horizontal. The succeeding divisions follow with regularity and give rise to a solid “morula” (figs. 3-4) made up of very numerous cells which are practically equal in size. As many as three hundred such cells may be counted in a median section. The flattening at the poles becomes less marked, but the mass floats as before, and the under half is still paler in colour than the upper. It should be stated that while equality of segmentation is certainly the normal condition, a slight degree of

* *Note on Cross-Fertilisation.*—To the membrane of fertilisation is usually ascribed the function of keeping out other sperms after the entrance of the one which is to fertilise the egg. The sperms crowd actively round the ova immediately the latter are shed, and yet, as we have seen above, it was not till three hours afterwards that the membrane even began to separate. This might seem to give ample time, were no other factors at work, for the occurrence of polyspermy or even for the entrance of sperms of mixed origin.

As is well known, cross-fertilisation may occur between widely different echinoderms. In this connection a series of experiments I made some time ago affords the following results with reference to *Solaster*:—The ova of *Solaster endeca* are strongly attractive to the spermatozoa of *Solaster papposa* and are fertilised by them.

Segmentation, though often very unequal, was sometimes quite regular and led to a very considerable degree of further development. Blastula, gastrula, and early larval stages were easy to obtain. Later, the larvæ tended to die off after showing various abnormalities of growth, such as malformation or loss of the larval arms and vesiculation of parts of the larval body. Serial sections of the larvæ showed very marked irregularity in the internal cavities, the typical arrangement being interfered with in many ways, though there was evidently an attempt at the formation of all the characteristic coeloms. The presence of several ciliated canals leading to the surface from one or other of the internal cavities was a common deviation. Some of the hybrid larvæ lived for over two months, but none of them entered on the stage of sucker fixation which leads to metamorphosis.

The ova of *Solaster papposa* are also strongly attractive to the spermatozoa of *S. endeca* and are fertilised by them. The resulting segmentation showed greater irregularity than in the converse experiment, but unfortunately I had not the opportunity in this case of carrying the observations to later stages.

In my experiments, the sperm of *Solaster endeca* was also tried with the ova of *Echinus esculentus* L., *Asterias rubens* L., *Uraster glacialis* O. F. M., *Cribrella oculata* Penn., *Brissopsis lyrifera* Forb., *Echinocardium cordatum* Penn., and *Synapta digitata* Mont. The results as regards fertilisation were negative in every instance, and the eggs of the sea-urchin alone exhibited the power of attracting the sperm.

On the other hand, the ova of *Solaster papposa* attracted the sperm of *Asterias rubens*, and underwent irregular segmentation under their influence. The same ova neither attracted nor were fertilised by the sperm of the other species mentioned above.

subequality may also be present in healthy ova. One also comes across cases in which the early segmentation is very markedly unequal. Such ova may seem to develop normally during the gastrula and the early larval stages, but none of them which I isolated entered on the later larval stages or underwent metamorphosis.

Blastula and Gastrula.—The process of blastula and gastrula formation presents those remarkable features which were first carefully described by Masterman (18, pp. 378–381) as occurring in the ova of *Cribrella*.

A rudimentary primary blastocœle in the form of narrow slit-like spaces develops within the cell-mass. Numerous small furrows running into one another next appear all over the external surface, producing a finely lobulated appearance almost as if the egg were reverting to its middle segmentation-stages. Soon the furrows become fewer but better marked. This takes place through the levelling up of some and the confluence and deepening of others. The surface pattern now becomes simpler, simulating an earlier stage in segmentation. The resemblance is often very striking, even as far downwards as the 16-, the 8-, and the 4-celled condition. Usually, however, instead of the knobby segmentation pattern, there is an appearance as of lobes running together, which may best be described as resembling the convoluted surface of a cerebral hemisphere. In the end, all the furrows disappear, and the surface becomes perfectly smooth, at least as seen from above. Sections of eggs at the time when the furrows first appear show the two following peculiarities: (1) the superficial cells are elongating and arranging themselves in a single layer at the surfaces between the furrows; (2) at the same time the deeper cells of the blastula are undergoing a similar rearrangement with reference to the sides and bottoms of the furrows. It is obvious that the result will be to produce, out of the originally almost solid cell-mass, a single greatly folded layer of columnar cells (Pl. I. fig. 5) enclosing an irregular and slit-like central space which may be called the definite blastocœle. A few cells, not falling into line with the others, remain within this cavity and form the earliest mesenchyme. The disappearance of the first furrows and the consequent simplification of the surface pattern is accompanied by further narrowing and elongation of the individual cells. In this way the blastula-wall, although it is losing in superficial extent, is still able to accommodate all the cells which first entered into its formation. There is now also a slight increase in the size of the blastula as compared with the unsegmented egg, the difference amounting to something like one-eighth of the diameter of the latter.

It is worthy of note that during all these changes the paler colour of the lower pole is preserved. Cilia make their appearance on the surface about the same time as the first blastula-furrows, causing currents within the membrane of fertilisation which still persists. [This membrane now disappears and the blastula begins to perform irregular rotary movements in the water,] its paler side always remaining underneath.

Gastrulation.—Gastrulation takes place by invagination and commences before the last surface-furrows have straightened out. Indeed, it may be described as beginning by

the widening and deepening of a large central furrow in the under pole. Accordingly at first the blastoporic opening is often slit-like in shape. The final smoothing of the surface-wrinkles advances with the progress of gastrulation, the opening out of surface provided by the former process compensating in part for that portion of the blastoderm which is invaginated. The blastopore now becomes a large circular opening in the middle of the distinctly flattened under surface, while the upper aspect of the gastrula is rounded or dome-like in shape. The invagination does not involve the whole of the pale area at the lower pole. In the fully formed gastrula the line of colour-transition is found outside the lip of the blastopore, at about a third of the distance between this and the centre of the dome.

The movement of the gastrula now becomes one of smooth rotation round a vertical axis, accompanied by slight intermittent horizontal progression, giving a somewhat epicyclic character to the whole. In the specimens under observation, as a rule, the direction of movement was dextral * as observed from above, but reversal took place from time to time, and in the course of a few days there seemed to be longer duration of the sinistral † than of the dextral periods. Probably the changes occur rhythmically in nature, though I had evidence that they were hastened by stimulation.

[In healthy specimens the archenteron (Pl. I. fig. 6) is a large cavity lined by columnar ciliated hypoblast and separated from the epiblast by a very narrow space containing stellate mesenchymal cells. The cavity is empty, except for stray yolk-granules and occasional cells (see p. 45).]

In *Cribrella*, according to Masterman (18, p. 382), the archenteron becomes completely filled up at this stage by a network of "hypenchyme" cells which are thrown off from the primitive hypoblast. This does not occur in *Solaster*, at least not in healthy specimens, but at a slightly later stage a certain number of cells are budded off into the anterior and posterior cœloms of the young larva. In the latter cavity they frequently give rise to a homogeneous spherical body, the appearance of which strongly suggests that it may function as a statolith during the middle and later free-swimming stages (p. 46).

Chronology.—The following details regarding the progress of the above changes in examples of a set of ova under observation will be of interest:—

At time of shedding.....	The first maturation-spindle lying close under the upper pole of the egg.
3 hours after shedding...	Both polar bodies extruded.
5 " " ...	The membrane of fertilisation completely separated.
9 " " ...	The yolk-free disc at the upper pole becomes oval and then dumb-bell in shape (10 hours); it next divides into two, while the first cleavage-furrow begins to form (11 hours).

* Same as that of the hands of a clock.

† Opposite to that of the hands of a clock.

13 hours after shedding ...	The first cleavage completed.
15 " " ...	The second cleavages completed.
18 " " ...	The third cleavages completed.
20 " " ...	Egg divided into about 16 cells.
28 " " ...	" " " 64 "
2½ days after shedding...	Segmentation completed ; a solid "morula" stage made up of quite small cells.
4 " " ...	Blastula showing numerous furrows externally.
5 " " ...	Only a few furrows now visible ; gastrulation beginning.
6 " " ...	Gastrulation complete.

(For later chronology, see pp. 17, 25.)

IV. EXTERNAL CHARACTERS, MOVEMENTS, &c. DURING THE FREE-SWIMMING PERIOD.

(Pl. I. figs. 12-14 ; Pl. II. figs. 15-20.)

In describing the succeeding stages in the development of *Solaster* I think it right to make use of the terms *larva* and *larval* (as Masterman does for *Cribrella*), although a larval mouth is never formed and the store of food contained in the egg has to last until the end of metamorphosis. Comparison with other forms, particularly with *Asterina* and *Cribrella*, enables one already to fix the anterior and posterior ends of the larva. The former is indicated by the summit of the gastrula-dome and the latter by the blastoporic opening.

The dome-shaped gastrula gradually elongates to form a cone, the base of which is perforated by the blastopore (Pl. II. fig. 15). The apex of the cone (anterior end of the larva) next makes a slight bend towards what is to be the ventral aspect (fig. 16). A ventral concavity or dimple is thus formed near the junction of the anterior and middle thirds of the cone. All the larval planes and surfaces can now be readily identified (see p. 37). The three larval arms next begin to grow out around the dimple above named. All three are directed ventrally. There is an anterior median unpaired one in front. The other two form a pair, one on each side a short distance behind the dimple. A little later the cells forming the floor of the dimple become elongated to form a disc-shaped sucker. The part of the cone which carries the arms and the sucker is recognizable afterwards as the preoral lobe of the larva.

Meantime certain changes have become manifest in the posterior part of the cone, which may now be called the body of the larva. This part becomes flattened from side to side and correspondingly extended in the sagittal plane (figs. 16-18). The blastopore lessens in size and the base of the cone becomes slightly oblique (p. 37). Dorsally on the right side, a little behind the junction of the preoral lobe and the body of the larva, a pit makes its appearance, at the bottom of which the hydroporic opening is formed. As will be seen later (p. 26), this takes place through the sinking in of a short ectodermal funnel to meet a hollow outgrowth from the anterior cœlom.

Shortly afterwards the blastopore closes, and the larval body becomes marked off from the preoral lobe by a groove which passes transversely across the back of what may be called the neck of the larva. This groove is produced in part by dorsal flexion of the head on the body, and partly through further expansion of the body in the sagittal plane. The hydroporic opening on the right side is the first, and for a time the only, departure from the external bilateral symmetry of the larva.

The arms are hollow outgrowths and contain prolongations from the anterior coelom. They are at first short, blunt, and ciliated uniformly with the rest of the body. Later they lengthen and acquire small glandular ridges at the tips, over which the cilia become reduced. They are then able, acting either singly or together, to cause the larva to adhere lightly to smooth surfaces. They have also become muscular, so that they can perform movements of (1) simple shortening or retraction and lengthening or protrusion, (2) spreading apart so as to expose the sucker, (3) closing together so as to hide the sucker (Pl. II. figs. 18, 19). The cilia are now reduced over the glandular ridges, though still present in the intervening furrows.

The sucker develops as a round, slightly elevated disc of much elongated cells in the bottom of the concavity between the larval arms. The cells are ciliated at first, but afterwards lose their cilia.

While the larvæ are elongating and becoming cone-like in shape, they remain upright in the water, performing circular movements exactly like those of the gastrulæ, though the direction of movement was now sinistral* as seen from above in the majority examined.

After they have reached full length, one begins to find them from time to time in an oblique position in the water, the anterior end, however, being still always higher than the posterior. In this position they are rotating round their own antero-posterior axis as before, and in addition they are progressing slowly along a straight line in the direction towards which the anterior end points. Reversal of this latter movement can occur, especially under stimulation, but it is rare and lasts only for a short time.

During the first two or three days of the free-swimming stage the larvæ are rather lighter than the sea-water and tend to remain without effort near the surface. Later their specific gravity gradually comes to equal and finally to exceed slightly that of the water. When this stage has been reached the movement of progression with the anterior end first will keep them from sinking helplessly to the bottom, while reversal will ensure that they need not remain continually at the surface. The characteristic position of the larva in the water indicates that the original difference in weight between the anterior and posterior ends of the larva has been retained in some degree throughout the whole free-swimming stage.

The whole surface of the larva is richly ciliated, excepting the sucker and the

* See note on p. 13.

glandular ridges at the tips of the arms. During life, the action of the cilia can readily be observed under the microscope by keeping the larvæ on the stage in a suitable cell and using strong oblique illumination. While ciliation is fairly uniform all over, it was noted during the first week that the cilia which covered the anterior pole seemed larger than the average. They did not, however, form a definite tuft standing out from the rest. The strongest and most persistent currents produced by the cilia pass from anterior to posterior end of the larva all along its sides, and it is this ciliary action which causes the forward progression of the larva. More than once while I was watching this action under the microscope, the direction of movement quickly became reversed; streams of particles began to flow over the anterior end, and had the larva been free to swim about, it would undoubtedly have moved with the posterior end in advance. Reversals of this kind occurred with relatively greater frequency in the specimens I was working with on the stage of the microscope than in those which remained undisturbed in the aquaria.

At the posterior end of the early larva, external to the blastopore, there is a narrow annular area of cilia which lash in an outward direction. The current thus produced, taken along with the stronger currents passing backwards over the general surface of the body, results in a forward eddy of small particles towards the blastoporic opening. After the blastopore has closed, the annulus in question becomes uniform with the rest of the surface of the body.

It was stated above that the formation of the hydroporic opening on the right side is the first interference with the external bilateral symmetry of the larva. The next departure from this symmetry is a more obvious one, and results in a change in the relative position of the preoral lobe and the body of the larva (Pl. II. figs. 19, 20). Two movements are involved, namely, (1) lateral flexion of the preoral lobe towards the left side of the body, (2) torsion of the neck of this lobe in the dextral* direction as the larva is looked at from the anterior end. Both movements occur together and in a gradual manner, and both are completed only two or three days after fixation by the sucker has taken place. Meantime their result is to bring the back of the preoral lobe obliquely against the left side of the body, a very sharp angle being formed on this side in the region of the neck (fig. 20). The whole movement is of greater rapidity and acuteness than can be accounted for simply in terms of differential growth, and as a matter of fact it seems to be caused by the action of the special band of muscular fibrillæ (Pl. II. fig. 19; Pl. III. fig. 34) which is referred to further on (p. 47).

Now commences a process of much interest, whereby the walls of the preoral lobe are in part incorporated with the left body-wall of the larva (Pl. II. figs. 22, 23). But this takes place during metamorphosis and will be described later, along with the completion of the flexion and torsion of the preoral lobe (pp. 19, 27).

* See note on p. 13.

The characters of the larva at the end of the free-swimming stage may be summarized as follows:—The preoral lobe is bent sharply to the left, and twisted dextrally* through an angle of approximately 75 degrees; the arms are long, glandular at the tips, muscular, and capable of anchoring the larvæ temporarily by adhesion to smooth surfaces; the body has become disc-like in shape through expansion in the larval sagittal plane; four notches are beginning to appear on the dorsal and posterior edges of the disc marking the position of future interradii. A much larger notch bounded by prominent lips is becoming evident on the right side at the root of the preoral lobe (p. 22). The first five radial pouches of the hydrocœle in some cases appear externally before fixation, while in most they are not evident till the fixed stage has begun. It will be more convenient to include the account of their appearance under the heading of metamorphosis (p. 20).

The above changes took place as follows:—

6 days after fertilisation ...	Gastrulation complete.
7 " " ...	Gastrula elongated to form a cone.
8 " " ...	Ventral dimple present.
9 " " ...	Indication of larval arms, and of ectodermal pit for the hydropore.
10-11 " " ...	Arms longer and coming together so as to conceal the sucker; the larval body flattening in the sagittal plane; the blastopore closed.
13-18 " " ...	Body becomes disc-shaped; the characteristic flexion and torsion of the arms in progress; larvæ able to adhere by the tips of the arms.
19 " " ...	The majority of the larvæ now attached by the sucker.

(For earlier chronology, see p. 13, and for later, p. 25.)

V. GENERAL HISTORY AND EXTERNAL CHARACTERS DURING AND AFTER METAMORPHOSIS.

(Pl. I. figs. 12-14; Pl. II. figs. 22, 23.)

Under this heading two periods have to be distinguished—the one of attachment by means of the sucker whose development we have already seen in the larva (p. 14), and the other during which, the sucker having atrophied, the earliest tube-feet are the attaching-organs. It is during the first of these periods that the greatest changes take place. The second is chiefly concerned with the acquirement by the various organs of their more perfect form and of their functional activities.

Attachment by the Larval Sucker.—In order to attach themselves, the larvæ cause their arms to diverge widely, so that the sucker becomes prominent and is thus enabled to adhere readily to a suitable surface. The attachment is by true sucking action and not simply through the formation of an adhesive cement. At this stage the sucker is oval in shape with the longer diameter transverse, and, like the tips of the

* See note on p. 13.

larval arms, it is of a more vivid orange-colour than the rest of the preoral lobe. The three arms surround the sucker in tripod fashion, but the right one is now rather larger than the left, which at this stage is somewhat compressed in the angle between preoral lobe and body.

The actual site of fixation must depend more or less on chance. At any rate, in the aquaria I employed, attached specimens were found fairly uniformly over the bottom and sides alike, a slight preference being shown for a position on the sides just under the water-level. In those which settled on a vertical surface there was no strict uniformity as regards which part of the body was uppermost, but in the majority of instances an upper position was occupied by the neck or region of junction between the preoral lobe and the body.

Once the larvæ are attached they keep the same position till movement is possible by means of the tube-feet. If they are detached without injury during the first day or two after fixation, they will in many instances (five out of seven in the experiment) succeed in re-attaching themselves. They are enabled to do this by the muscular action of the arms, as well as by the action of the cilia on the surface of the body, which helps to tumble them over until the sucker finds a suitable locality for attachment. Older specimens when detached sink quickly to the bottom, and can fasten themselves anew only if they happen to fall with the sucker undermost; otherwise they are unable to right themselves, and, though capable of survival for a considerable period, they do not undergo a normal metamorphosis. The first few days of fixation by the sucker are marked by the following important external changes:—

1. Flexion and torsion of the preoral lobe are completed.
2. Much of the wall of the preoral lobe is gradually incorporated into the middle part of the left side of the larva, and assists in forming the oral surface of the Starfish. Subject to this reservation, and from the point of view of external form, the left side of the larva becomes the oral surface of the Starfish.
3. Similarly the aboral surface of the Starfish may be described as representing the right side of the larva; but this statement is also subject to the reservation that in reality the epiderm of the aboral surface is in great part derived from that which covered the posterior end of the bilateral larva.
4. The series of radial pouches of the hydrocœle comes into prominence on the oral (left *larval*) surface. The first-formed pouches acquire lateral branches for the tube-feet. The 8th radial pouch is added.
5. The aboral rudiments of the arms begin to grow out round the margin. The whole aboral surface becomes covered with small papillæ containing the developing spines.

The later period of fixation by the larval sucker is marked by further outgrowth and commencement of functional activity on the part of the tube-feet, complete

disappearance of the whole preoral lobe except the sucker, and, finally, by atrophy of the sucker itself.

The points mentioned above will now be gone over in more detail, the first three being taken together.

1, 2, 3. *Flexion &c. of Preoral Lobe, and Formation of the Oral and Aboral Surfaces.*—The commencement of the flexion and torsion of the preoral lobe was noted before the end of the free-swimming stage (p. 16).

The preoral lobe became sharply bent at the neck towards the left side of the body, and at the same time twisted in the dextral direction as seen from the anterior end. Roughly speaking, the combined movement may be compared with that which would result in the human subject from extreme overaction of the left sterno-mastoid muscle, the head representing the preoral lobe of the larva. The back of the preoral lobe is brought to begin with obliquely against the left body-wall of the larva. This is the condition at the end of the free-swimming stage. Later the movements are carried out to their fullest degree, the leftward flexion being nearly through the full half-circle of 180 degrees, while the torsion is through a right angle. At the same time, the back of the preoral lobe is taken into or incorporated with the left body-wall of the larva. As a result, the anterior or frontal larval arm comes to look outwards from near the middle of the left side of the larva, or, rather, of the oral surface of the Starfish, as this side may now be called. The sucker and the paired larval arms also look outwards from the oral surface, but are nearer that part of the margin which in the larva was at the junction between the preoral lobe and the larval body.

The changes above described are illustrated in figs. 21–23 of Pl. II. As they proceed, the preoral lobe settles down more and more on the oral surface, from which it finally ceases to project. The smoothing out of its walls involves a considerable addition to the central area on the oral surface. This is needed in connection with the very marked widening of the hydrocœle ring that is also taking place, and it provides a sufficient space, in the middle of which the mouth-opening can afterwards break through.

It will be remembered that the lower pole of the gastrula (posterior end of the larva) was paler in colour than the upper pole (anterior end of larva). The changes described above result in the massing of the richly pigmented epiderm (anterior end epiderm) into the area on the oral side of the Starfish which overlies the circle of the hydrocœle. When the radial canals of the hydrocœle grow out they are accompanied on the surface by corresponding extensions of pigmented epiderm, which are broad enough also to overlie the sucker-feet when these are formed in their turn. The purely actinal surface of the young Starfish is thus derived chiefly from the body-wall of the anterior end of the larva. Conversely, we find that the aboral surface is now covered with the pale epiderm which in the perfectly bilateral condition was confined to the posterior part of the larva. It is only in the region of the notch opposite the larval

neck that traces of the deeper pigment still exist, and even these are lost when at a later stage the notch becomes filled up.

We see accordingly that on the right side a forward sliding movement of the wall of the posterior part of the bilateral larva has taken place, and that this movement is the counterpart of the migration backwards and to the left undergone by the preoral lobe.

These facts, while they are important in the ontogeny of *Solaster* (see under Nervous System, p. 46), may also be of great importance from their bearing on general questions of asteroid phylogeny.

4. *The Hydrocœle Pouches.*—The radial pouches of the hydrocœle appear externally as an incomplete circle of lobular swellings on the oral (left larval) surface around the central area where the preoral lobe is becoming incorporated with the body-wall. The gap left in the circle is opposite to the larval neck. Four of the pouches appear practically simultaneously and are succeeded almost at once by a fifth. These form a series the members of which, for reasons that will appear later, are to be numbered in the dextral or watch-hand direction, as seen from the oral side, commencing with pouch No. I immediately to the dextral (*i. e.*, the larval dorsal) side of the preoral lobe. In the fully-formed *Solaster* the normal number of rays is nine, and accordingly four new pouches remain to be formed in addition to the five that have already appeared. These are added one by one, extending the series onwards from pouch No. V, still in the dextral direction as one looks from the oral side. There is a short pause till VI appears. VII follows after an interval of similar length. VIII is delayed relatively longer, and IX longer still. Indeed, IX is not added until the preoral lobe has almost completely disappeared, the sucker has begun to atrophy, and the larva is attaching itself by means of the first-formed tube-feet. Pouch IX at the end of the series is now adjacent to pouch I at the beginning, and nothing stands in the way of the completion between these pouches of the ring-canal of the hydrocœle.

Soon after they have made their appearance externally, the radial pouches of the hydrocœle become three-lobed in shape. This is due to the outgrowth at their sides of the first tube-feet, and at their extremities of the terminal tentacle. Later, a second pair of tube-feet is formed on each radial pouch between the first pair and the terminal tentacle.

The sequence in the formation of the tube-feet on the radial pouches corresponds with that in which the pouches themselves were developed. For example, pouches I to V are provided with two pairs of feet at a period when VIII is still in the tri-lobed condition and IX has not yet made its appearance. So long as the preoral lobe is large, pouch I of the hydrocœle, being somewhat compressed in the angle between that lobe and the disc, is not free to appear externally with as great prominence as the next three pouches in the series; but after the preoral lobe disappears, the pouch in question, being no longer hidden or compressed, shows in all respects quite as

advanced a degree of development as the succeeding members of the series, thus offering the sharpest contrast with pouches VIII and IX, which are still lagging far behind.

Although the details fall to be given later (p. 27), it may be stated here that the ring-canal of the water vascular system is completed in such a way that the cavity of the preoral lobe occasionally remains in continuity, though for a very short time, with the axial sinus cœlom by means of a stalk, which, as in *Asterina* (Macbride, 15), is encompassed by the hydrocœle ring. Soon, however, the cavity of the preoral lobe disappears, and the sucker atrophies, migrating at the same time outwards beyond the circle of the ring-canal. The last remnant of it is to be looked for as a stalked papilla attached a short distance from the margin on the oral surface (Pl. I. fig. 13). In four cases out of five this papilla lies in interradius IX/I, while in the others it either lies just outside of pouch IX or in the interradius between that and pouch VIII. The variation is of no importance, and probably occurs in connection with the adjustment that has to take place between the hydrocœle rays and the aboral arm-rudiments (p. 22).

The stone-canal opens into the ring-canal of the hydrocœle between the origins of radial pouches I and II (p. 31).

Considering the manner in which the radial pouches of the hydrocœle are developed, and in particular the perfectly definite sequence in which the last four of them appear, one can have no hesitation in numbering the series by the method adopted above—that is, by commencing it with pouch I on the dextral * side of the preoral lobe as one looks at the *oral* surface, and continuing in the same direction from that point.

Leaving out of count such methods of numbering the rays of Asteroids as are based on other than developmental grounds, we have to distinguish two systems. In one of these the numbering proceeds as described above (*e. g.*, Macbride for *Asterina*), while in the other the order is precisely the converse—that is to say, it begins with ray I on the sinistral side of the preoral lobe as one looks at the oral surface, and continues the series counterclockwise from this point (Ludwig, 12, and Goto, 10 *a*, for *Asterina*; Goto for *Asterias pallida*, 9, 10; Masterman for *Cribrella*, 18). The order of development in *Solaster* establishes a presumption that the former of the two systems of numbering is the right one for Starfish in general.

The short pause between the formation of the first five radial pouches and that of the sixth is an indication that the *Solaster* family was derived from a five-rayed ancestor. Further evidence on this point will appear in connection with the development of the anus. I am indebted to Prof. J. W. Gregory for the note that an apparently authentic member of the family, *Solaster moretonis* Forbes, occurs as far back as the Oolite (Forbes in Mem. Geol. Surv. U. K. 1856, dec. v. pp. 1–3).

* See footnote on p. 13.

Formation of Aboral Arm-Rudiments.—The aboral surface is now somewhat disc-like in shape, with four or five shallow indentations at the margin, and one deep notch—the nuchal notch—bounded by two prominent lips or lobes, which are at first a considerable distance apart but afterwards draw closely together. The shallow indentations separate corresponding aboral arm-rudiments as these grow out, but the notch (Pl. II. figs. 21–23) is produced in consequence of the sharp leftward flexion of the preoral lobe, and the subsequent rapid reduction of the walls and internal cavity of this lobe (see also on p. 27). In a cleared specimen at this stage, viewed from the aboral side (Pl. I. fig. 7), the series of hydrocœle-pouches is seen to commence with pouch I lying underneath the sinistral (*larval* dorsal) lip or lobe of the notch. But this lip will afterwards be associated with pouch II of the hydrocœle in the formation of ray II of the Starfish. Meantime accordingly it may be designated aboral arm-rudiment No. 2. Since, to begin with, it overlies pouch I, it must undergo a sliding movement in the sinistral direction as viewed from the aboral side. This movement is approximately through an angle of 30 degrees.

The other lip or lobe bounding the notch is the ventral one, with reference to larval orientation. It must be called arm-rudiment No. 1, since in the end it comes into relation with pouch I of the hydrocœle to form the corresponding ray of the Starfish. Before doing this it performs an angular movement in the same direction as arm-rudiment 2 but of greater extent, since in order to reach its final position it has to travel over the area formerly occupied on the right side by the neck of the preoral lobe. The full range of angular movement undergone by aboral arm-rudiment 1 may be put down as something like 60–65 degrees.

The shallow indentations, referred to above, separate other less prominent arm-rudiments, which appear to the number of three or four just after fixation has begun. These arm-rudiments are to be enumerated in accordance with the numbering of the hydrocœle-pouches with which they afterwards come into relation. Those which now appear are 3 to 5. They have to undergo a certain amount of angular movement in the same direction as arm-rudiments 1 and 2, but the amount is less than that of 2, and it diminishes as one goes down the series. The remaining arm-rudiments—*i. e.*, 6 to 9—appear in the same sequence as the hydrocœle-pouches with which they are to become associated, and each is a little later than its corresponding pouch.

Attachment by the first-formed Sucker-Feet.—Even after the sucker has atrophied there still remain a number of external changes to be noted before metamorphosis is at an end. Some of these changes consist in the completion of processes already begun, and others in the acquirement of new characters or structures.

The former category includes :—Formation of pouch IX of the hydrocœle and of aboral arm-rudiments 8 and 9 ; partial filling up of the notch between arm-rudiments 1 and 2 to form interradius I/II—the madreporic interradius ; complete disappearance by absorption of the larval sucker and arms ; increase in the size and number of the spines.

These points hardly require further description. Emphasis may, however, again be laid on the fact that while the larval sucker and arms are actively absorbed, much of the preoral lobe epiderm is not destroyed, but is incorporated with the oral surface of the Starfish.

The most important new structures that appear externally during this period are the eye-spots, the mouth, and the anus.

The Eyes.—In the first seven rays the eyes appear as bright reddish spots at the base of the terminal tentacles several days before the formation of the mouth. In rays VIII and IX they appear respectively along with and a little later than this opening. After death their pigment is extremely soluble and readily washes out, so that they may easily be overlooked in their earliest stages unless they have been observed in the living condition.

Formation of the Mouth.—The ring-canal of the hydrocœle now encloses a relatively large central area on the oral surface. The mouth appears in the middle of this area, usually in the form of a triradiate fissure (Pl. I. fig. 13), the angles of which point approximately in the direction of interradii II/III, V/VI, VIII/IX. Later, the opening becomes circular with slightly crenated edges. That part of the body-wall which lies between it and the ring-canal forms the soft membrane of the peristome. Still later, the first pair of adambulacral ossicles in each interradius comes to project inwards towards the centre of the mouth, carrying spines of larger than average size. The mouth-armature is accordingly of the adambulacral type, although the first pairs of ambulacra do not recede so markedly as in the better-marked examples of this type.

Formation of the Anus.—The formation of the anus takes place several days after that of the mouth. The opening is small, and is to be found near the centre of the aboral surface, in the interradius which is designated V/VI according to our system of numbering. It will be remembered that in the ordinary five-rayed Starfish the anus, when present, falls within interradius V/I according to the same system. We can say, then, that the anal interradius of *Solaster* corresponds with that of an ordinary Starfish, on the assumption, which we have already seen to be well grounded, that rays VI to IX are later additions or interpolations.

In this connection it is worthy of note that in *Solaster papposa*, which has a greater number of rays than our *Solaster*, the anus is still to be found in the same interradius, namely V/VI. Equally striking is the fact, which I have been able to establish for both species, that in any individual, no matter whether the number of rays is greater or less than the normal, the anus still occurs in that interradius, which, according to our method of numbering, is the normal one (8*a*). The principle that parts forming a serial succession are specially liable to variation in number may perhaps serve to throw light on the very great variability of both species, and particularly of *S. papposa* (17), in the number of their arms.

For mesenteric relations of rectum and anus, see p. 39.

In the weeks that succeed the formation of the mouth and anus, the most marked

new feature in the external appearance of the young Starfish is that the spines become relatively very numerous and very prominent. The length of a single spine may amount to about one-eighth of the diameter of the whole Starfish including the arms. The spines now tend to become grouped in twos or threes, the members of each group being united by an arching fold of integument which reaches about halfway up their sides. It should also be noted that meantime a distinct notch has made its appearance at the tip of each arm outgrowth, and that in these regions the spines become disposed in two sets. It will be seen afterwards (p. 42) that in *Solaster* the skeletal plates occupying the position of terminals are double from the first, the members of each pair being an appreciable distance apart (Pl. I. fig. 8).

Movements.—The young Starfish may begin to move about with the help of its first-formed sucker-feet during the sixth week, and therefore prior to the formation of the mouth. In one of the small aquaria I had with me in Glasgow I marked the position of eight of them at this period by pencilling circles on the outside of the glass. Two days afterwards all but three had shifted their position, some of them by as much as two and a half inches. The young Starfish are now able to right themselves after being turned upside down exactly in the manner of the adult. They cling tightly to suitable surfaces, and if sucked up into a pipette or tube must be released at once, as it will be difficult to get them out alive and uninjured should they succeed in taking hold inside.

After the mouth is formed the young Starfish wander about freely over the sides and bottom of the tanks; but perhaps the most interesting point to be noticed in their habits is the facility with which they can "swim" in any direction just under the surface of the water. Movement is fairly rapid, especially where there happens to be a fine powdering of dust on the surface by which the surface-tension is increased. The rate, as measured in half a dozen specimens of the age of six months and 2.75 mm. in diameter, varied from 25 mm. in ten minutes downwards. The young Starfish floats by keeping the tips of a number of its tube-feet protruded slightly above the surface. Some of these are continually being withdrawn, advanced, and again protruded. Withdrawal is effected by means of a sharp muscular twitch, which pulls the tip at once below the surface-level. On the other hand, in protrusion, the surface-film seemed to shed off naturally from the tips of the gently extended feet.

The tube-feet cause progression not by taking a sucker-like hold of the surface-film as in ordinary movement over solid surfaces, but rather by elbowing the body along, advantage being taken of the resistance due to surface-tension. At any given time the tips of a considerable number of feet are protruded, and these have no difficulty in keeping the Starfish afloat; but as its specific gravity is now much greater than that of water, owing to the formation of the skeletal plates, the animal will sink very rapidly to the bottom if once it be depressed ever so little below the surface. To begin with, it must have launched itself by crawling up the side of the tank, then

bending the uppermost arms and the body outwards on the surface of the water, as grown-up Starfish do when seeking a new attachment. It is difficult, however, to see how a young *Solaster* in its natural surroundings could ever have the opportunity of practising the trick of surface-floating which I have described above. The same faculty has been observed in other very young Echinoderms.

Chronology.—The following details regarding time supplement those given on pp. 13, 17:—

4-5 weeks		Larval sucker no longer functional; attachment by the first-formed tube-feet.
6-7	„	Formation of mouth; formation of radial pouch IX of the hydrocœle.
7-8	„	Formation of anus; appearance of aboral arm-rudiments 8 and 9; diameter of disc and arms about 1·8 mm.
12	„	Three pairs of sucker-feet on each ray; arm-rudiments 8 and 9 still a little smaller than the rest; diameter about 2·2 mm.
5 months		Five pairs of sucker-feet; arms all alike; diameter about 2·6 mm.
7	„	A sixth pair of sucker-feet beginning to appear; diameter 3 mm.

VI. DEVELOPMENT OF CAVITIES AND ORGANS. (Pls. III.-V. figs. 24-56.)

The mode of formation of the gastrula has already been described. At the end of gastrulation the archenteron is a dome-shaped cavity with a uniform lining of columnar ciliated cells. For the next few days this cavity follows in general the shape of the growing larva (see p. 14), becoming elongated as the larva lengthens, sending out hollow processes into the arms as they develop, and flattening from side to side in its posterior half like what we have called the body of the larva. At the same time the cavity becomes gradually marked out into three regions, although there is no external indication that such a change is taking place. The regions are respectively anterior, middle, and posterior, the anterior being much the largest, while the posterior opens on the external surface by the blastopore (Pl. IV. fig. 36). The middle region is the smallest and is much compressed from side to side. It is at first ill-defined, appearing rather as an isthmus between the other two than as a distinct region. Its mode of separation is described in detail under the heading "Enteron" on p. 37. The division is completed by the tenth day. The first and third of the chambers constitute respectively the anterior and posterior cœloms of the *Solaster* larva, while the middle one becomes the enteron or gut.

In the further description under this heading I shall give as far as possible a consecutive history of each of these cavities and its derivatives, both in the larval condition and throughout metamorphosis. It is hoped that such difficulties as may arise through having to speak of the later development of one set of structures much in advance of others may be minimised by the cross-references throughout the text, as well as by the illustrations, and the general summary on pp. 50-52.

(1) *Anterior Cœlom and its Derivatives.*

As the anterior cœlom expands, its lining epithelium for the most part decreases in height in order to flatten out over the larger surface. In front the cavity of the cœlom extends into the three larval arms, and posteriorly it grows backward on either side of the middle chamber in the form of left and right lateral diverticula, which become evident a considerable time before the cœlom itself is separated from the enteron. The anterior cœlom, as a whole, now rests saddlewise on the middle chamber, and in the course of time the parts forming the flaps of the saddle, *i. e.* the two diverticula, extend backwards so far that they completely overlap the enteron on either side.

An opening to the exterior—the hydropore—is acquired by the anterior cœlom, on the right side of the larva in the position already described (p. 14), at about the tenth day of development. A short funnel-like invagination of the ectoderm meets and fuses with a similar but longer pouch from the anterior cœlom, rupture of the fused walls afterwards taking place. The anterior cœlom contributes much more than the ectoderm to the length of the hydroporic canal. The hydropore is situated from the first on the right side of the body, but the internal opening of its canal is, to begin with, a little to the left of the mid-dorsal line. So far as I can make out, the dorsal sac, or madreporic vesicle (right hydrocœle of Macbride), is budded off from the anterior cœlom dorsally a little to the right of the middle line almost in the angle formed in that region between the right lateral diverticulum and the cœlom itself. It separates from the anterior cœlom shortly after the latter has become finally closed off from the gut. Its development is difficult to follow, since it remains for only a very brief period in open communication with its parent cavity. By this time the junction of the preoral lobe with the body of the larva is indicated by the transverse dorsal furrow referred to on p. 15.

The following parts may now be distinguished as derivatives of the anterior cœlom of the larva: (1) the fore part of the cœlom forming the cavity of the preoral lobe (preoral cœlom); (2) the central part (axial cœlom) receiving the internal opening of the hydroporic canal and communicating behind with the two following; (3) the right lateral diverticulum, and (4) the left lateral diverticulum; (5) the dorsal sac, or madreporic vesicle. The further development of each of these will now be described.

Preoral Cœlom.—The general history of the preoral cœlom resembles that of the corresponding cœlom in *Asterina* (15) and *Cribrella* (18). It reaches its greatest development in the later free-swimming stages, though it has begun to diminish a day or two before fixation actually takes place. During the torsion and flexion of the preoral lobe the cavity is constricted at the neck (pp. 16, 19) and becomes gradually separated from the central part of the anterior cœlom, which, being included within the body of the Starfish at metamorphosis, remains as the axial sinus. The preoral

cavity, now isolated, grows rapidly smaller and finally disappears. In this process its lumen becomes filled up with wandering cells.

As Macbride rightly stated in connection with the development of *Asterina* (15), it is a point of great importance to determine whether, when the hydrocœle ring completes itself, the stalk of the preoral cœlom is encircled by this ring or remains outside. According to Macbride, the former condition occurs quite definitely in the case of *Asterina*. In most of my *Solaster* specimens, owing probably to the relatively later period at which the hydrocœle ring completes itself, the line of the stalk-cavity was obliterated at the time of closure of the hydrocœle ring. It happens, however, that variations in the degree of development of different parts occur in different examples, and in one or two instances I was able to ascertain with certainty the existence, for a short time at least, of a communication on the oral side of the completed hydrocœle ring, between the cavity of the preoral lobe and that of the axial sinus.

As the relative lateness of closure of the hydrocœle ring in *Solaster* is readily explicable on the ground that other four arms are, so to speak, intercalated after the five primary ones, we may conclude that the stalk of the preoral lobe has the same morphological relation to the hydrocœle ring in *Solaster* as in *Asterina*.

Meantime the sucker and the tips of the larval arms are actively absorbed, but normally a large part of the preoral-lobe epiderm is incorporated with that of the oral surface (p. 19). This brings the cells of the larval apical field into the position where the ring-nerve is developing, and makes it possible that the nervous system of the larva should take some part in the formation of that of the adult (see further, pp. 46–47).

Sometimes the preoral lobe fails to apply itself so closely to the left body-wall as to allow the incorporation of the epiderm with the left body-wall to be fully carried on as described above. Such cases, if partial, may in the end develop all right, the redundant tissue being ultimately absorbed. For a time the area (oral field) enclosed by the hydrocœle is smaller than normal, but this gradually rights itself, though there is some delay in the formation of the mouth-opening.

Right Lateral Diverticulum of the Anterior Cœlom.—The right lateral diverticulum becomes separated from its parent cavity on the third or fourth day after fixation, giving rise to the so-called epigastric cœlom of the Starfish. Two chief factors are at work in causing the separation. One is the gradual extension of the dorsal and ventral horns of the posterior cœlom in the larval sagittal plane (pp. 32–33), until in the end they meet back to back at the madreporic interradius, enclosing between their layers the various structures of the axial complex to be afterwards described (pp. 29–31). The other factor is the sharp flexion and torsion of the preoral lobe and the subsequent atrophy of the stalk-cavity. The notch produced externally on the disc (pp. 17, 22) by these processes cuts deep into the neck between right lateral diverticulum and anterior cœlom, reducing this to a V-shaped cleft (Pl. IV. fig. 49; Pl. V. fig. 55). The cleft is

next obliterated altogether during the process whereby aboral arm-rudiment 1 travels right across the region where the neck existed in order to reach its final position over the first radial pouch of the hydrocœle. The internal cavity of arm-rudiment 1 is thus derived from the tip of the (larval) ventral horn of the posterior cœlom (p. 32).

Left Lateral Diverticulum of Anterior Cœlom.—The bottom and sides of the left lateral diverticulum give rise to the hydrocœle and to part of the internal oral circular sinus, while the central portion of the diverticulum becoming obliterated assists in providing the area on which the mouth afterwards opens. The development of the hydrocœle will now be described, but that of the internal oral circular sinus is better taken under the heading of the axial cœlom (p. 29).

While at an early stage in growth the cells lining the greater part of the anterior cœlom and its derivatives become flattened, those which form the bottom of the left lateral diverticulum remain cylindrical and crowded together. This part of the diverticulum may be called the hydrocœle groove. It is in the form of a crescent with dorsal and ventral horns, the convexity being directed backwards. The concave side looks forward into the main cavity of the left lateral diverticulum. The dorsal horn of the crescent ends with a definite tip raised a little from the cœlomic lining and bending slightly to the right of the plane in which the rest of the crescent lies.

The wall of the hydrocœle crescent and that of the posterior cœlom (p. 32) along with the intervening mesenchyme form a somewhat thick mesentery attaching the gut to the left body-wall. The radial pouches appear as hollow outgrowths on the convex side of the hydrocœle groove, and push their way into the tissue of this mesentery. Increasing in size they project into the posterior cœlom covered by a lining from it, and keeping as close as they can to the left body-wall. Five radial pouches appear on the hydrocœle crescent at practically the same time. One end of this series is at the tip of the dorsal horn of the crescent, and here, as was stated previously, our numbering of the series begins. The other end falls short of the tip of the ventral horn, and it is to this region that the later-formed pouches are added.

To begin with, the third and fourth rather outgrow the others. Next come the second and fifth, while the first lags a little behind, probably because it has less freedom to expand by reason of its position with reference to the preoral lobe and the body (p. 29).

After the formation of the first five pouches there is a short pause before the sixth makes its appearance. It does so just beyond the fifth on the ventral horn of the crescent, and is succeeded after a similar delay by pouch VII. By this time the free-swimming stage is at an end, so that pouches VIII and IX remain to be added during the course of metamorphosis.

Meantime the hydrocœle groove in the region of pouches III and IV has become nipped off from the rest of the left lateral diverticulum, forming a short canal open at both ends and gradually extending dorsally and ventrally along the crescent. At the time of fixation, conversion of the groove into a canal is not quite complete for the whole of the dorsal horn, and for the ventral horn is accomplished only as far as the

origin of pouch VI. The further extension of the canal follows the development of the later-formed pouches, and it is only after the preoral cœlom has almost entirely disappeared that the tips of the dorsal and the ventral horns of the hydrocœle crescent meet in interradius IX/I, thus completing the ring-canal of the water vascular system. The remains of the stalk of connection of the preoral cœlom with the axial sinus are traceable as passing oralwards within the completed ring (p. 27). In preparation for their meeting, both ends of the crescent, but particularly the dorsal one, curve slightly to the aboral (right larval) side. This bending to the right is evident in the dorsal horn during the middle free-swimming stage, but in the ventral horn only at the commencement of metamorphosis.

It should be stated that for a time pouch I of the hydrocœle does not have the chance of projecting into the posterior cœlom. To begin with, this pouch pushes out into the somewhat thickened mesenchyme of the anterior cœlomic wall, to which is added afterwards the tissue produced in this region through the reduction of the preoral cœlom. Finally, the ventral horn of the posterior cœlom extends round to the madreporic interradius, displacing the tissue in question. By this time radial canal I is embedded in the oral wall of ray I, but the ampullæ belonging to the tube-feet of this ray can project freely into the cœlomic cavity now provided.

Dorsal Sac or Madreporic Vesicle.—The origin of the dorsal sac or madreporic vesicle has already been noted (p. 26). Almost immediately after its separation the cells lining it become much flattened. In the larva it lies on the ventral side of the hydroporic canal, and in the young Starfish just after metamorphosis it will be found close under the surface, slightly nearer the centre of the disc than the hydropore and somewhat to the dextral * side of that opening as one looks from the aboral side. This also is the position it occupies in the adult with reference to the axial cœlom and the madreporic plate. In early metamorphosis its outer wall, *i. e.* that adjacent to the axial cœlom, becomes invaginated by a fold containing a group of cells continuous with those forming the axial organ within the axial cœlom. Later, the tissue thus folded in the dorsal sac acquires a highly vesicular appearance. At the very end of metamorphosis a new element is added to the interior of the fold. This is an ingrowth from the posterior cœlom of the kind of cells which Macbride has described in *Asterina* as giving rise to the genital rachis (see under posterior cœlom, p. 36).

It will be seen that the place of origin of the madreporic vesicle would suit a homology with the hydrocœle. In no instance, however, that I came across did it actually develop a hydrocœle-like structure as in the examples of *Asterina* put on record by Macbride. Once I found it provided with an external opening on the dorsal side close to the hydropore, but this was in a specimen which showed various other abnormalities. No enantiomorphic specimens were recognised.

Axial or Central Part of Anterior Cœlom.—It remains now to give an account of the axial or central part of the cœlom, *i. e.* that part which remains after the separation of

* See note on p. 13.

the hydrocœle, the dorsal sac, the epigastric cœlom, and the preoral cœlom. The structures whose development we have thus to describe are: the internal oral circular sinus, the perihæmal pouch of interradius IX/I, the axial organ, and the stone-canal. We have also to indicate what are the final relations of the axial cœlom and the stone-canal to the pores of the madreporic plate.

Internal Oral Circular Sinus.—This sinus is derived partly from the axial cœlom and partly from the left lateral diverticulum. It will be remembered that the hydrocœle ring is nipped off from the bottom of this diverticulum, the rest of the diverticulum being still unappropriated and opening widely into the axial cœlom. From the latter cavity, indeed, it is now no longer to be sharply distinguished, since at the commencement of the fixed stage, while the preoral lobe is settling back on the left (larval) side, the axial part of the anterior cœlom also undergoes a certain amount of migration backwards and to the left. At a later stage in metamorphosis the wall of the enteron lays itself against that of the oral surface in preparation for the formation of the mouth. In this process the remainder of the left lateral diverticulum undergoes obliteration of the central part of its cavity, as well as of that segment of its periphery which is in the neighbourhood of radial pouches III or IV and V of the hydrocœle. The rest goes to aid the axial cœlom in forming the internal oral circular sinus, which at this stage is naturally incomplete in the region of the pouches just named. The completion takes place later by extension of the sinus-cavity from either side, and this extension seems to be aided by the fact that two or three small lacunæ have been left along its track during the process of obliteration referred to above. The internal oral circular sinus now forms an annular cavity surrounding the mouth inside the ring-canal of the hydrocœle. A ribbon of hæmal tissue comes to grow round it in the manner described below under "Axial Organ."

The Axial Organ.—The axial organ forms a fold of the wall of the axial cœlom running parallel with the stone-canal on the dextral* side of the latter, as one looks from the aboral aspect. As stated above, the cells invaginated into the dorsal sac are continuous with those of the axial organ. The first appearance of the organ is due to proliferation *in situ* of a strip of cells belonging to the lining of the axial cœlom. A ridge is thus formed consisting of cells rich in protoplasm, rounded or polygonal in shape, and with very little intercellular substance. The organ is relatively large in the middle or later stages of metamorphosis, and even then can be traced oralwards into a ribbon of similar tissue extending for some distance along the wall of the internal oral circular sinus in the sinistral* direction as viewed from the oral side. This ribbon afterwards becomes the circular hæmal vessel, which in the adult lies in the septum between the internal and the external oral circular sinuses.

The genital rachis grows through the upper part of the axial organ (p. 36), extending downwards at the same time for a short distance, but not nearly reaching to the internal oral ring.

* See note on p. 13.

The Stone-Canal.—The stone-canal takes origin as a groove beginning on the hydrocœle, opposite the origin of radial pouch II and passing to the right on the posterior wall of the axial cœlom. The outer end of this groove next seems, so far as I could make out, to leave the surface, and burrowing a way underneath the epithelium in the same direction emerges again in the axial cœlom close to the inner opening of the hydroporic canal. The final conversion of the original groove into a canal takes place about the same time as the conversion into a canal of the dorsal end of the hydrocœle groove itself, *i. e.*, a day or two after fixation. By this time also the opening of the stone-canal into the hydrocœle has become shifted to its permanent position in the interspace between radial pouches I and II of the hydrocœle.

There is still divergence of opinion as to whether in adult Starfish the stone-canal and the axial sinus communicate with one another or are completely separated. However, the weight of opinion and evidence is strongly gathering in favour of the latter view (Macbride, 15, p. 351; 16, p. 441; Durham, 6, p. 330; Goto, 9, p. 273; Perrier, 20, p. 1146; Hamann, 14). I have given elsewhere in detail the results of an examination of a series of sections through the madreporic interradius of a large adult *S. endeca* (8 a). The pore-canals number about four hundred and may roughly be divided into a set occupying the middle area of the madreporite and a set around the margin, the two sets being approximately equal in total number. The canals of the middle set join in small groups to form collecting-spaces opening into a central chamber within the madreporite, which I have called the ampullary part of the axial sinus and which is continued directly into the stone-canal. The marginal set also join a system of collecting-spaces which, on the one hand, lead into the aboral end of the axial sinus and, on the other, are connected by a number of apertures with the central chamber mentioned above. Taking into account both development and adult structure, none of the pore-canals should, strictly speaking, be described as opening into the stone-canal, and the term *ampullary part of axial sinus* should be substituted for *ampulla of stone-canal*.

Perihæmal Pouch IX/I.—The last derivative of the anterior cœlom that falls to be referred to here is the pouch forming that segment of the external oral circular sinus which belongs to interradius IX/I. The origin of the segment in question is difficult to follow, but I believe I have traced it to an outgrowth from the axial cœlom immediately in front of the first radial pouch of the hydrocœle occurring towards the end of the free-swimming stage. Much later, in one instance, a small outgrowth from near the tip of the (larval) ventral horn of the posterior cœlom came to open into the cavity of this perihæmal segment, and thus presumably to contribute a little to its extension. I could not find that this occurred in other cases, but if it does it might go some way towards reconciling *Solaster* on the one hand, and *Asterina* and *Cribrella* on the other, in regard to the mode of origin of their oral perihæmal pouches. See page 35.

(2) Posterior Cœlom and its Derivatives.

The posterior cœlom is at first hardly to be distinguished from the middle chamber or enteron. The detailed account of its mode of separation is given on p. 37. It soon begins to extend in the sagittal plane, giving rise to dorsal and ventral horns. The ventral horn grows with slightly greater rapidity than the dorsal one, and partly for this reason the opening of this cœlom into the enteron undergoes some degree of ventral displacement.

The two horns continue to grow forward, insinuating themselves between the body-wall and the gut, and keeping still in the sagittal plane, except that the ventral one, which is also the longer, swerves a little to the right side of the middle line.

The dorsal horn extends forward as far as the dorso-anterior angle of the larval body, where it is brought to a stop meantime by abutting against the central part of the anterior cœlom, into which the hydroporic canal opens. The ventral horn on its part grows forward as far as it can, and then bends dorsalwards in front of the enteron in the direction of the hydropore.

During the early stages of metamorphosis, the growth of the ventral horn, aided by the flexion and torsion of the preoral lobe, plays a chief part in separating the right larval (or epigastric) and the axial regions of the anterior cœlom from one another, and also in obliterating the stalk of the preoral cœlom. In doing this the tip of the ventral horn may be described as bifurcating temporarily into right and left processes. The right process is the smaller, and abuts against the neck of the right lateral diverticulum, which it helps to occlude (p. 27). It then disappears as a distinct process by merging with the main cavity of the ventral horn.

The other process of the tip of the ventral horn swerves to the left or oral side, expanding as it does so. This brings it against the stalk between the preoral and axial cœlom, which it helps to occlude. After occlusion is effected it extends across the position of the larval neck towards the madreporic interradius, excavating the tissue in front of it and reaching its final position over the first radial pouch of the hydrocœle. It now ceases to be recognizable as a distinct process by merging with the general cavity of the ventral horn.

The manner in which these changes occur and the part played by the ventral horn will be better understood if one refers to what was said on page 22 about the adjustment of the disc-arm rudiments to the radial pouches of the hydrocœle. The tip of the ventral horn of the posterior cœlom is contained within the (larval) ventral lip of the nuchal notch on the disc. This lip or lobe has to travel across the region of the neck in order to reach its final position over pouch I of the hydrocœle.

The walls of the dorsal and ventral horns now approach back to back in the madreporic interradius to form a thickened mesentery or septum stretching from the enteron outwards to the body-wall. Within this septum are contained the structures forming the axial complex, the development of which has already been described (pp. 29-31).

A great decrease in size on the part of the axial cœlom, with consequent narrowing of the septum, takes place in the later stages of metamorphosis. Next occurs breaking down of the part of the septum which stretches between the enteron and the axial cœlom, so that this cœlom is now attached only to the body-wall.

As the whole body expands in growth, the body-wall leaves a deep inward prolongation or septum (interbrachial septum) in each interradius. The inner portions of the septa become thickened and develop calcareous plates, while the outer portions seem to disappear, leaving the inner ones as isolated pillars or arches stretching across the body-cavity from the oral to the aboral surface. The skeletal plate at the oral end of each pillar forms the so-called odontophore. The axial cœlom, with its contained structures, is attached to the inner edge of the interbrachial septum belonging to the madreporic interradius.

The perforation of the outer portions of the septa referred to above had not taken place in my oldest sectioned specimens, which were six months old.

The posterior cœlom gives origin to the following derivatives:—(1) the general hypogastric cœlom; (2) the pharyngeal cœlom; (3) all the segments of the external oral circular sinus except that of interradius IX/I; (4) the aboral circular sinus and the genital rachis.

Hypogastric Cœlom.—By far the greater part of the cavity which in the adult surrounds the enteron and its diverticula is derived from the posterior cœlom of the larva. As the two horns of the latter grow round the enteron in the sagittal plane towards the madreporic interradius, they, as well as their parent cavity, begin to invade the right and left sides of the larva so far as other structures allow. However, the early condition here (Pl. III. figs. 28–33) does not warrant our speaking of right and left horns of the posterior cœlom as Masterman does in the case of *Cribrella*. On the right side the extension of the posterior cœlom is checked by the right lateral diverticulum of the anterior cœlom (the future epigastric cœlom), and on the left side by the left lateral diverticulum, the bottom of which, as we saw before, gives rise to the hydrocœle.

The walls of the posterior cœlom, meeting back to back with the walls of these diverticula, form right and left mesenteries for the enteron, both of which, to begin with, extend dorso-ventrally and are crescent-shaped, with the convexity directed backwards. On the right side the crescent becomes a circle when, during metamorphosis, the epigastric cœlom is cut off from its parent cavity, and the horns of the posterior cœlom meet at the madreporic interradius. At first the epigastric cœlom is of sufficient size to cover the whole of the right face of the enteron. In the later stages of metamorphosis the enteron expands in the (Starfish) horizontal plane so much that the epigastric cœlom no longer covers the whole of its aboral surface, but is confined to a central area around which there is a gradually increasing margin which is covered by an aboral extension of the posterior cœlom. As the paired radial

diverticula of the enteron grow out, pockets from the epigastric cœlom extend outwards along their aboral aspect, and these pockets bifurcate as the diverticula themselves become divided into two. The adjacent walls of the epigastric and hypogastric cavities now form a circular sheet with paired radial extensions, which, as it stretches between the enteron and the aboral body-wall, may be called the epigastric mesentery. Later, the circular part of this mesentery disappears as a continuous structure, being broken up into very numerous strands of fibrous tissue which serve as dorsal suspensory ligaments to the walls of the stomach, and leave passages, chiefly interrarial in position, through which the epigastric cœlom communicates with the rest of the perivisceral cavity. The so-called interrarial cœca grow out among these fibrous strands, but do not extend beyond them. On the other hand, the paired radial extensions of the mesentery above named do not become broken up into fibres, but remain as the boundary-walls of the epigastric cœlomic pockets, which in the adult lie above the paired radial diverticula of the stomach (p. 40).

On the left side in the young larva, as was stated above, the wall of the posterior cœlom meets that of the hydrocœle groove to form a mesentery, which, to begin with, is crescent-shaped and extends dorso-ventrally, with the convexity directed backwards. This mesentery is somewhat thickened, and it receives the radial pouches of the hydrocœle as they first grow out. These pouches, in further growth, keep as close as they can to the left body-wall, and, accordingly, an angular space is left between the hydrocœle and the enteron, which is occupied by a leftward extension of the posterior cœlom. This is the first indication of the tendency, afterwards very fully carried out, for the oral (left larval) aspect of the enteron to be covered by a lining derived from the posterior cœlom of the larva.

The hydrocœle (p. 28) becomes nipped off from the bottom of the left lateral diverticulum. The left mesentery then separates the posterior cœlom from the remainder of this diverticulum and from the anterior cœlom. The mesentery in question has a broad attachment to the wall of the enteron, and later this area of attachment becomes greatly increased through secondary obliteration of part of the left lateral diverticulum (p. 30).

From a comparatively early stage (three or four days before fixation of the larva) the tissue in question begins to be excavated by pockets from the posterior cœlom, which, passing for a short distance towards the middle of the left side of the larva, then elongate in the larval sagittal plane concentrically with the curve of the posterior cœlom and its horns, but naturally forming parts of a much smaller circle. So far as I can make out, the constant pockets are two in number and originate one from the dorsal and one from the ventral horn of the posterior cœlom. That from the dorsal horn comes off quite close to the tip of the horn in the neighbourhood of the second radial pouch, while that from the ventral horn arises near the tip at a time when the latter is just beginning to extend dorsalwards in front of the enteron

(see p. 32). I must, however, leave these points in some doubt meantime, as certain discrepancies appear in my different series. The pockets or diverticula in question give rise to the so-called pharyngeal cœlom which, in the adult, surrounds the lower portion of the gastric wall.

During early metamorphosis the stalks of origin of these diverticula seem to become obliterated, but they themselves, extending in the manner previously described, have already met and united on the side away from the madreporic interradius. Later they complete the circle of the pharyngeal cœlom by becoming continuous also over the region of the madreporic interradius. The sheet of tissue which now separates the pharyngeal and hypogastric cœloms may be called the circular hypogastric mesentery. This mesentery becomes perforated in each interradius, leaving a flat band or ligament connecting the stomach-wall with the floor of each of the rays. Still later, these connecting bands or ligaments also become perforated, each in its mid-radial line. The hypogastric and the pharyngeal cœloms now communicate with one another both by radial and by interradiial apertures. The remaining parts of the circular hypogastric mesentery then break up into more or less isolated ribbons, forming the numerous ligamentous strands which in the adult pass downwards and outwards from the stomach-walls to an attachment over the junction of the ambulacral and the adambulacral sets of ossicles.

The External Oral Circular Sinus.—The external oral circular sinus or circular oral canal of the perihæmal system, together with its extensions along the rays, is formed, as Macbride first described for *Asterina*, from a series of small diverticula, all but one of which arise from the posterior cœlom, and which interdigitate with the radial pouches of the hydrocœle. Of these, the first three in *Solaster*, *i. e.* those between pouches I and II, II and III, and III and IV, become evident two or three days before fixation; the fourth soon follows, while the rest are delayed in correspondence with the later formation of the pouches between which they lie. Thus, at a stage in metamorphosis when the larval sucker is no longer functional, the perihæmal diverticula between pouches VII and VIII and between VIII and IX are still in course of being budded off from the ventral horn (Pl. IV. fig. 45).

The origin of perihæmal pouch IX/I from the anterior cœlom has been referred to on p. 31, and also the possible contribution to this pouch on the part of the posterior cœlom. In the case of pouch I/II, which in *Solaster* undoubtedly is to be described as arising from the posterior cœlom, I have noted an instance (towards the very end of the free-swimming stage) of a fine canal connecting the pouch in question with the dorsal angle of the axial cœlom, but believe that this condition is exceptional.

In *Asterina* (Macbride, 15) and *Cribrella* (Masterman, 18), by the same method of numbering, pouch I/II arises from the anterior cœlom, while all the others (including pouch V/I, which corresponds, in position at least, with IX/I of *Solaster*) arise from the posterior cœlom. The differences are thus sharp, but are, perhaps,

rendered less unaccountable when one considers the secondary communications which in all three species make their appearance normally or otherwise between the anterior cœlom and the tips of the dorsal or ventral horns of the posterior cœlom.

The subsequent history of these diverticula is similar to that which Macbride has described in the case of *Asterina* (15). They become constricted off from the posterior cœlom as small cavities lying one in each interradius between the oral (left larval) body-wall and the hydrocœle ring. They next become U-shaped, the basal part of each U being turned towards the centre of the oral surface, while the limbs stretch out along the rays. Each ray thus has a pair of radial perihæmal canals which are derived from adjacent diverticula. In each pair the radial perihæmal canals lie close together on the deep side of the radial nerve-tract. Deeper still, and separated by a layer of intervening tissue, is the radial canal of the hydrocœle.

The basal parts of the perihæmal diverticula lengthen out, and, abutting on one another, form, as was shown by Macbride, the series of segments of a circle which constitutes the external oral circular sinus. They are at first closed off from one another, and remain thus for the first three months or so. In the adult their radial extensions communicate with each other between successive pairs of sucker-feet, and also proximally to the first pair.

Some time after the fourth month, a short vertical branch from each of the perihæmal pouches appears, passing aborally in the tissue of what will afterwards be the interbrachial septum, and apparently ending in the tissue-spaces there. In the adult *S. endeca* I have described the occurrence of such a perihæmal branch in each of the interradii. It is unaccompanied by hæmal tissue (8 a).

Genital Rachis and Aboral Perihæmal Ring.—A small pocket, the bottom of which is lined by primitive germ-cells, forms during the middle stages of metamorphosis from the tip of the dorsal horn of the posterior cœlom and pushes its way between the madreporic vesicle and the axial sinus in the Starfish horizontal plane. The germ-cells grow also downwards a short distance in the core of the axial organ, but the cavity of the pocket does not accompany this extension. The pocket seems to become the aboral perihæmal sinus, as described by Macbride in *Asterina*; but I was unable to trace it, even in my oldest specimens, across the madreporic interradius, and, indeed, in these specimens it was only just beginning to extend, together with the contained genital rachis, on to the body-wall beyond the axial complex towards the sinistral side as viewed from the aboral aspect, *i. e.* towards ray II. In the adult *S. endeca* there occurs an interruption of the aboral perihæmal sinus in the madreporic interradius (8 a).

(3) *The Enteron.*

It is the middle chamber of the young *Solaster* larva which gives rise to the enteron. The mode of separation of this chamber presents certain peculiarities,

a detailed description of which will be of interest in view of the remarkable manner in which the larval coelomic cavities are disposed.

Separation of Enteron from Anterior and Posterior Cœlom (Pl. III. figs. 25–33).—As the gastrula elongates, the cells lining the archenteric cavity become diminished in size, partly owing to the fact that they are now spread over a larger area, but chiefly because a considerable amount of mesenchyme has already been formed at their expense. Even in the early cone stage the diminution in size of these cells may be seen to be unequal in amount in different places, a zone of larger cells being left rather less than halfway up the archenteric wall. For purposes of description we may divide the zone into two bands, an anterior marked A A in figs. 25–27 and a posterior marked B B; and it may be stated here that the anterior band contains the tissue which gives origin to the right and left lateral diverticula of the anterior cœlom, while the posterior will form the walls of the middle chamber or enteron. Even at this early stage flattening from side to side of the posterior part of the elongating gastrular cone is beginning to take place. Usually, also, the base of the cone is slightly bevelled, in such a way that a rather acuter angle is formed on its postero-ventral than on its postero-dorsal side. With the help of these indications it is often possible to recognise the different aspects of the larva from a very early stage. By turning over the cleared larvæ under the microscope one can make out (1) that the whole thickened zone (including both A and B bands) is more definite at the sides than dorsally; (2) that the want of definiteness seems best marked a little to the right of the mid-dorsal line; (3) that there is also some slight deficiency of the zone towards the mid-ventral line.

At a somewhat later stage, when the length of the cone is double its breadth and the ventral dimple is appearing, the following further points may be made out:—(1) the posterior part of the larva is more distinctly flattened from side to side; (2) the band marked B B of the archenteric wall is projecting inwards at the sides but not dorsally or ventrally, thus forming two ridges within the archenteron which may be called respectively the right and left enteric folds; (3) dorsally the gap between these folds lies a little to the right of the middle line; (4) ventrally the corresponding junction lies a little to the left of the middle line; (5) in optical section the right fold seems to be rather larger than the left, though the apparent size varies somewhat according to the side from which they are seen, and examination of serial sections is required to bring out the differences with exactness. The latter method shows that towards their dorsal junction the right fold is distinctly the larger, though the less prominent. Ventrally the opposite condition is found, though here the differences are less. Near the middle the right fold has still a slight predominance over the left.

The archenteron now shows anterior and posterior chambers with an isthmus between. The isthmus is short from before backwards, narrow from side to side, but elongated dorso-ventrally. The right and left enteric folds forming its opposite sides

present convex surfaces to each other. These surfaces now flatten, at the same time increasing in area. Next they become slightly concave, so that, in each, anterior and posterior lips can be distinguished. The two posterior lips now unite across the isthmus, the fusion advancing from the dorsal towards the ventral side. The two anterior lips also unite, but in this case the fusion begins ventrally.

Dorsally the greater size of the right enteric fold causes its anterior lip slightly to overarch the corresponding lip of the left fold. The opening between the middle and the anterior chamber is thus gradually reduced to a slit situated dorsally and looking to the left. On the other hand, the slit to which the opening between the middle chamber and the posterior cœlom gradually becomes reduced is situated ventrally, but the early predominance in this region of the left enteric fold is not sufficiently well maintained to cause this opening to be deflected towards the right, and accordingly it remains practically in the middle line.

The processes above described convert the enteric isthmus into a short flattened canal leading ventrally and posteriorly, with a slight inclination to the right, from the anterior to the posterior cœlom (Pl. V. fig. 49). The canal now separates itself off completely from the cavities in front and behind, the anterior aperture remaining open slightly longer than the other. On the whole, the right gastric fold contributes more than the left one to the total area of the enteron. One expression of the difference is seen in the slight pouching to the right of the wall of the enteron, which is indicated in Pl. III. figs. 31 & 32. This pouching is much better marked at a corresponding stage in the development of *S. papposa*, and for purposes of comparison a drawing from such a stage is given in Pl. III. fig. 33.

After the separation of the enteron is complete, it is no longer possible to locate its former junctions with the anterior and posterior cœloms, so as to be able to trace their position during and after metamorphosis. The growth of the posterior cœlom with its two horns induces the enteron to assume the form of a crescent lying within that of the cœlom in question. Dorsal and ventral horns may accordingly be distinguished, and the tips of these, like the corresponding parts of the posterior cœlom in the course of metamorphosis, come to project into the disc arm-rudiments which we have numbered 1 and 2 (p. 22). The shape of the enteron as seen from the side is now that of a disc with a deep notch opposite the region of the preoral lobe, *i. e.* between arm-rudiments 1 and 2. In course of time this notch becomes filled out, owing to continued expansion of the enteron and to reduction in size of the structures (axial complex) occupying the notch, in much the same way as the similar notch in the epigastric cœlom (p. 27) gradually disappears.

By this time the enteron shows six or seven short outgrowths into the arm-rudiments. The two largest of these are constituted by the tips of the horns of the enteron, which have been already referred to as entering arm-rudiments 1 and 2. The others are in connection with succeeding arm-rudiments. The last two (8 and 9) are latest in formation, like the rays to which they belong. All these outgrowths are lobes of

what will afterwards be recognisable as the stomach of the Starfish, and must not be confused with the paired radial cæca, which are of still later development (see below).

The Mouth.—The formation of the mouth has already been referred to (p. 23) as taking place in the centre of the oral surface shortly after the sixth week of development. In this region the wall of the enteron fuses with the body-wall and both become thinner. The mouth-opening then breaks through, and at first the pharynx is triradiate in cross-section. The angles point approximately to interradii II/III, V/VI, and VIII/IX. There is no stomodæum.

The Anus.—The anus is formed during the seventh or eighth week, in interradius V/VI. An outgrowth from the enteron fuses with the body-wall, the actual opening arising afterwards by rupture as in the case of the mouth. The anus is now connected by a short canal—the rectum—with the pyloric sac, the junction of the two being not exactly in the middle of the roof of the sac, but slightly excentric in the direction of interradius V/VI (Pl. I. fig. 11).

The mesenteric relations during these changes require separate description. The rectum grows up between the layers of the epigastric mesentery (p. 33) in interradius V/VI, and has accordingly a sinistral and a dextral wing of mesentery when viewed aborally, the former wing stretching towards radius VI and the latter towards radius V. In the progress of the rectum towards the middle of the aboral surface the sinistral wing of mesentery seems to lead the way, by means of a small thickened part close to the rectum and anus. This part is soon recognisable as a short stout band, containing muscular fibres, which connects the junction between the rectum and the pyloric sac with the central knot of the aboral radial musculature. The muscular fibres of this band are early and definite in their appearance, and the band itself, still more shortened, remains in the adult, where it must play an important part in slinging the rectum and pyloric sac to the aboral body-wall. It may also, in conjunction with the fibrous fold to be next described, serve as a sphincter between the rectum and the pyloric sac, besides aiding in the evacuation of fæces from the rectum.

(In the development of *Asterina*, Macbride (15, p. 368) calls attention to a remarkable group of epithelio-muscular cells in the lining of the epigastric coelom on the inner aspect of the body-wall, for which he is at a loss to find a function, unless it be that of giving origin to the muscular fibres which dilate the anus. I would venture the suggestion that this group of cells has to do with the formation of suspensory muscular tissue corresponding with the band described above, and perhaps also with the formation of the central knot of the aboral radial musculature.)

The dextral wing of the original mesentery of the rectum, *i. e.* that towards radius V, does not shorten so much, but remains in part, and in the adult forms a fold chiefly if not entirely fibrous in character, which stretches from the outer aspect of the junction between the rectum and the pyloric sac to the aboral radial muscle of ray V, joining this about half an inch out from the centre of the disc (8 a).

Paired Radial Cæca.—The paired radial diverticula appear as folds on the roof of the stomach which converge towards a central point, but, owing to the positions of the anus and the axial complex, they are not disposed in a perfectly symmetrical manner. The outer extremities of the folds, which, to begin with, fall some distance short of the ends of the stomach-lobes mentioned above, become elevated from the surface and grow out as blind pouches into the rays. Closure of the lips of each fold in its outer part now occurs. The stalks of the pouches are lengthened thereby, and their openings are all brought together into a small chamber—the pyloric sac—in the roof the stomach. This chamber is U-shaped, the concavity of the U being occupied by the anus (Pl. I. fig. 11). The position of the madreporic interradius is marked by an indentation near the middle of the convex side of the U. This indentation causes the roots of the radial diverticula to fall into two groups, one consisting of four pouches belonging to rays II to V inclusive, and the other of five pouches belonging to the rest of the rays, viz. VI to IX and I. Fig. 11 illustrates the relation of the roots of the various pouches to one another in a *Solaster* aged six months. These relations remain practically the same in the adult, if one allows for differences in the proportionate size of parts.

During the fourth month the radial diverticula begin to broaden at their outer ends. This is followed by bifurcation at these ends, with accompanying division of their suspensory mesenteries and of the pockets of epigastric cœlom contained therein (p. 34).

Interradial or Rectal Cæca.—The so-called rectal cæca are late in development. They may, however, be recognised during the fifth month. In the six months' specimen from which fig. 11 was taken they are represented by two outgrowths. Of these the larger shows division into three lobes, and originates, as nearly as one might judge, opposite interradius VI/VII. The other arises opposite interradius II/III, and, though it has a somewhat crenated margin, is not yet divided into distinct lobes. In the adult *Solaster* the cæca in question also come off by two roots occupying positions similar to those just indicated. That which corresponds with the outgrowth last described usually gives off five slightly lobulated cæca, 1 cm. in length, which lie respectively in interradii IX/I, I/II, II/III, III/IV, IV/V, while the other gives origin to similar cæca for interradii V/VI, VI/VII, and VII/VIII. The remaining interradius, namely VIII/IX, is oftenest left unprovided with a cæcum. Apparently the larger of the roots in the young *Solaster* is afterwards outstripped in growth by the smaller, since it is the latter which provides five out of the total of eight cæca.

It may be of some theoretical interest to point out that the distribution of this set of five cæca is such that they might be considered as representing a set belonging to the five-rayed ancestor of *Solaster*, leaving the rest as interpolations, like the four later-formed rays. However, it would be manifestly unsafe to lay stress on the relations of parts so variable in Starfish morphology as are the rectal cæca. Of much greater

interest and importance is the constant position of the anus alike in *S. endeca* and *S. papposa* (p. 23).

VII. DEVELOPMENT OF THE SKELETON. (Pl. I. figs. 8, 9, 12; Pl. II. figs. 19 & 20.)

Representatives of three sets of skeletal elements, namely the ambulacral plates, the plates of the dermal reticulum, and the spines, make their appearance independently two or three days before the end of the free-swimming stage.

Ambulacral Plates.—The ambulacral plates develop in the mesoderm of the left side of the larval body, where they form a crescent similar in curvature to the hydrocœle, and, like the hydrocœle, having the gap between its horns opposite to the neck of the larva. As in other Starfish, the innermost or proximal elements in each ray are first laid down, the sequence in *Solaster* corresponding with that in which the radial pouches themselves are formed. Five pairs thus appear almost simultaneously in connection with pouches I to V of the hydrocœle, there being, however, delay in the formation of the first plate of the first pair in the series, *i. e.*, that adjacent to the larval neck. A sixth pair appears at the time of fixation, but the ninth is only added after the mouth has formed. The first ambulacrals are, of course, to the oral side of the first tube-feet.

A second pair of ambulacrals appears in each ray shortly after the ray has acquired its second pair of sucker-feet, and so on with succeeding pairs, the formation of the ossicles being later than that of the correspondingly numbered feet. Thus in a specimen four months old there were three pairs of ambulacrals, and at seven months the number had increased to five. The bodies of the first and second ossicles in each row have united together by the fourth month.

The first pair of adambulacrals appears in each interradius at much the same time as the second ambulacrals in the adjacent rays. Succeeding adambulacrals appear in similar sequence. The first pairs are much larger than the others, and they form the teeth. Small groups of spines early become associated with each of the adambulacrals. Those associated with the first pair are longer and stronger than the others, and two or more of these in each interradius project horizontally inwards towards the centre of the mouth. These form what may be called the denticles, and their development is slightly different from that of ordinary spines (p. 43).

Dermal Reticular Skeleton.—The plates of the dermal reticular skeleton develop in the deeper mesodermic layer of the aboral body-wall. Towards the end of the free-swimming stage on the right side of the larva one finds a middle area with many such plates in process of formation. This area overlies the right lateral diverticulum of the anterior cœlom (future epigastric cœlom). It is separated by a narrow plateless interval from a marginal area overlying the posterior cœlom (future hypogastric cœlom), in which five or six pairs of small plates may be made out. Comparison with later stages shows that these pairs are destined to be carried outwards at the tips of

the various aboral arm-rudiments. So far accordingly they correspond with the single terminal ossicle in the typical Starfish ray. The first pairs to appear belong to rays II to V. That of ray I, which lies in the (larval) ventral lip of the nuchal notch, follows almost immediately. The remainder arise in the same series as the arm-rudiments to which they belong.

In a five-rayed Starfish such as *Asterina* the terminals on the one hand, and the central and primary interradials on the other, develop over cavities corresponding respectively to the posterior and the right lateral (epigastric) cœloms of *Solaster*. In *Solaster* the central and the primary interradials are represented by the plates of the middle area above mentioned, but I was unable to discover any such orderly arrangement of these plates as would make it possible to recognise among them the homologues of the typical series. They numbered 25 or 30 in all at the time when there were five pairs of terminals.

Similar plates now begin to appear all over the marginal area, and a plateless interval can no longer be made out. Just prior to the formation of the mouth the total number of plates in the whole aboral body-wall may be put down as over a hundred. They are uniformly distributed and of practically uniform size, but still sufficiently small to leave much uncalcified space between them. Meantime the aboral surface of the disc has been enlarging with greater rapidity than the oral one, so that the former now curls round at the margin, particularly in the interradial and along the sides of the rays. This brings the marginally situated plates into contiguity with the adambulacrals, when these develop in their turn.

All the plates now increase in size at a rate out of proportion to the general growth of the disc, so that the adjacent edges tend to meet or overlap, the interspaces left being few and small. It is in one of these interspaces that the anus opens.

The plates are now disc-like as seen from above, and their margins, instead of showing numerous sharp projecting points as during the earlier period of active growth, are for the most part smooth and adapted for movement against or over one another.

Still later (fifth month) larger interspaces begin again to appear on the disc and arms, but before these have reached any considerable size a secondary plate develops in each which, by gradually increasing in size, particularly in one direction, comes to bridge across the space and finally to subdivide it, thus giving rise to the first meshes of the skeletal reticulum. No doubt succeeding meshes are added in a similar fashion, as the area of the aboral body-wall continues to increase.

In the adult the form of the plates has changed. Many of them (doubtless including all the original, as well as the earlier secondary plates) have developed four or five angular processes for articulation with their neighbours, and form principal nodes in the skeletal network. The rest, much more numerous and no doubt including the more recently formed elements, remain somewhat rod-like in shape, since they have only

to lie along the strands or at less nodal points of the meshwork. In cleared tissues the former stand out as being slightly larger, more angular, and more densely calcified than the rest, as well as associated with larger rosettes of spines. They occur all over the surface, as well as roughly in radial and interradial rows. Sometimes also they form a ring about halfway between the centre and the margin of the disc. Possibly this ring has some relation to the former boundary between the right lateral and the posterior cœloms.

To the dermal skeletal system of plates belong also the plates with which the interbranchial septa are strengthened. The lowest of these lies between the first two adambulacrals forming the so-called odontophore.

The Spines.—The spines appear as small nodules in the superficial mesodermic layer of the aboral body-wall. At first they are uniformly distributed, and twice or thrice as numerous as the dermal plates of the deeper layer (Pl. I. fig. 8). By the time of fixation their position is marked by small papillæ standing out everywhere from the aboral surface.

Later, the papillæ increase in length (Pl. I. figs. 12, 14), and the jagged tips of the spines stick out from their summits. New papillæ also appear in the body-wall wherever space allows. In the fourth and succeeding months the spines form a very prominent feature in the external appearance of the young Starfish (p. 24, Pl. I. fig. 14).

Meantime, the inner ends of the spines tend to cluster together in twos and threes, and each cluster becomes associated with one of the deeper plates, the latter developing a rounded knob for its support. During later growth new clusters appear and new spines are added to existing clusters. In the adult the clusters over the main nodal plates contain from 7 to 9 spines, while over the rest the number is less or the clusters are absent altogether.

The mode of development of the plates and of the spines closely resembles that described in other Starfish, *e. g.*, by Ludwig in *Asterina* (12), and need not be repeated here. It may be noted, however, that those which project horizontally oralwards from the first adambulacrals are flattened slightly in the horizontal plane, and in their first appearance resemble an ordinary dermal plate rather than the little closed star or cartwheel which forms the base of the typical spine.

VIII. HISTOLOGY.

A number of points may perhaps be most conveniently grouped together under the heading of Histology. These are: the mesenchyme and the disposal of the yolk; the statolith(?); the central nervous system; the larval muscular system; ciliation of internal cavities.

Mesenchyme and Yolk.—It will be remembered that during segmentation the whole of the ovum is divided up into cells, and that the cell-contents at the upper and lower

poles retain the peculiarity of colouring which marked these poles in the egg itself. As development proceeds, the yolk-granules undergo gradual intracellular digestion. The process continues for a remarkably long time, which it will be convenient to divide into two periods: (*a*) up till the beginning of metamorphosis and (*b*) during the middle and later stages of metamorphosis.

(*a*) At the end of the free-swimming stage many granules may be demonstrated with the help of osmic acid in all the tissue-cells except the epidermal ones forming the sucker and the adhesive tips of the larval arms. On the whole, they are most numerous in parts which have as yet undergone little growth, or in which much growth has still to take place—*e. g.*, lining of enteron, of hydrocoele, of portions of posterior cœlom, and epiderm over posterior part of body. But it is within the mesenchymal cells, particularly those of the disappearing preoral lobe, that the yolk-granules are now to be found in greatest abundance, and here their size and staining capacity is still practically undiminished. During the course of metamorphosis, the granules disappear from the cells of the tissues generally, but in the case of the mesenchyme this does not take place till the very end of metamorphosis after the mouth-opening has formed. The enteron also shows certain striking peculiarities in this respect which are referred to below.

The mesenchyme thus serves an important function in the development of the highly-yolked *Solaster* egg, by retaining for the later stages a reserve store of nutrition. The diffuse distribution of this tissue will render its store of nutriment accessible to the cells of the various actively-growing structures. As regards the origin of the mesenchyme, it will be remembered that at the end of gastrulation only a very small amount of this tissue is present between the epiblast and the primitive hypoblast. The amount increases very rapidly during the early differentiation of the three chambers into which the archenteron becomes divided. The increase takes place through budding from the basal aspect of the cells lining these chambers. It occurs earliest and most abundantly from the lining of the anterior cœlom, and partly accounts for the flattening of the walls of this cavity. Less abundant and later is the production of mesenchyme from the lining of the posterior cœlom. Little is contributed by the enteron, as might be expected considering the small original size of the chamber and the very great expansion which it afterwards undergoes. The contents of the young mesenchyme-cells consist in chief part of large-sized yolk-granules. In this connection it is interesting to compare with *Solaster* the very heavily-yolked Starfish eggs from the Franklin Islands described by E. H. Henderson (11). These specimens were in metamorphosis, and the type of development corresponded exactly to that shown in *Asterina* as described by Macbride, the chief difference being that the embryos under discussion were much larger, and had all the interstices of the body gorged with yolk to such a degree that it formed nine-tenths of the whole bulk. The yolk was made up chiefly of large globular or irregularly-

shaped masses not contained within cells, but penetrating everywhere between the layers and compressing all the cavities and organs.

Probably the hypenchyme-cells which Masterman (18) describes as being budded off from the hypoblast into the archenteron of *Cribrella*, and completely filling up that cavity for a time, are loaded with yolk-granules. They may indeed be a means of withdrawing a certain amount of yolk from tissues which would be hampered in their activities by its presence in undue amount, the yolk thus segregated being in a position where it can readily be digested and absorbed later on. In *Solaster* there is a slight but apparently constant production of hypenchyme-cells during the period when the archenteron is dividing into its three chambers. A few such cells may usually be found both in the anterior and the posterior coeloms.

There is, however, another method by which in *Solaster* a certain small amount of surplus yolk may find its way into the interior of the archenteron. It seems to be the rule in the re-arrangement of cells accompanying blastula formation that some yolk-granules should escape to the free surface. At first I thought the condition was abnormal, but the high proportion of cases in which it occurred convinced me that, at any rate, it is not inconsistent with perfectly normal later development. At first the granules are retained within the membrane of fertilisation which still surrounds the egg, and one may watch them eddying hither and thither under the action of the cilia. As gastrulation proceeds they are swept into the widely open blastopore, at the mouth of which they remain for a considerable time as a kind of plug which is usually devoid of cellular structure, but sometimes contains a few nuclei evidently belonging to cells that, like the granules, have been extruded from the surface.

(b) *The Yolk-Granules in Middle and Later Metamorphosis.*—During this period perhaps the most remarkable change in the proportionate size of permanent parts is that undergone by the walls of the enteron. It will be remembered how narrow in early development was the isthmus between the anterior and the posterior coeloms which gave origin to the gut. In the middle and later free-swimming stages the gut still remains small, and is lined by columnar epithelium of no great height. Afterwards, it expands enormously, forming not only the sac-like stomach but also the nine pairs of radial cæca, and much the greater part of this large cavity is lined by high columnar epithelium. On staining deeply with osmic acid, the surprising fact emerges that the whole of this epithelium now contains yolk-granules in profusion. Roughly speaking, just prior to the formation of the mouth, one-half of the total yolk still present may be put down as being contained within the cells of the enteron. A gradual transference of granules from the mesenchyme to the hypoblast cells must have been taking place, as it is quite impossible that the amount of yolk present in the small enteron of the swimming larva could suffice for spreading out over the larger enteron at metamorphosis. I cannot say where the yolk-granules finally persist longest, not having applied the necessary methods to old enough stages of *Solaster*. But in *Asterias*

mulleri Sars I find it to be within the radial cæca that the yolk-granules occur in greatest abundance during and after metamorphosis. In *Asterina*, from sections which Prof. Macbride kindly showed me, I should judge that a good proportion of the yolk was aggregated within the cells of the enteron as far back as the gastrula stage. Indeed, *Asterina* and *Solaster* stand in sharp contrast to one another as regards the relative prominence of the enteron in early stages. In *Solaster* the development of this part may be said to be post-dated not only with reference to its broad features of form and size, but also in the more intimate detail of the accumulation of yolk-granules within its cells.

A Statolith-like Body.—An interesting modification of the hypenchyme within the posterior cœlom now falls to be mentioned. This is a spherical, almost homogeneous body, about .075 mm. in diameter, which occurs free in the cavity of the posterior cœlom, in a large proportion of cases, during the middle and later free-swimming stages (Pl. I, fig. 10; Pl. III, fig. 32). As far as I could make out, it takes origin from a small mass of hypenchyme which gradually loses its cellular character, the cell-contents becoming massed together to form the body which has just been described. I venture to suggest that this body may function as a statolith. In the hinder wall of the posterior cœlom there is found at this stage an area often pocketed outwards, where the cells are more elongated than over the rest of the cœlom-wall (Pl. I, fig. 10). This may possibly be a sensitive area or pit in connection with the body above described. The changes in the direction of movement which the larva can exhibit, while itself retaining a definite position in the water, and the long duration of the free-swimming stage, are circumstances that seem to emphasise the advantage to the larva of possessing some kind of balancing mechanism.

It is true that, in general, statoliths and statocysts are of ectodermal origin. But in the case of an echinoderm larva it must be remembered that the greater part, if not the whole, of the muscular tissue is developed from cœlomic epithelium, while in the adult it seems to be certain that this epithelium can give rise to nerve-structures such as those which form the entoneural system.

Synapta provides us with at least one example of an echinoderm larva possessing statocysts and statoliths. Here it would seem that they are of ectodermal origin (Semon, 22), although their development is not fully known.

In the *Synapta* itself the presence of "otocysts" has long been recognized (Thomson, 1862, 24, p. 136). More recently they have been found also in various other genera and families of Holothurians, and their function as statocysts has been ascertained (Becker, 1).

Nervous System.—In the larva perhaps the most definite indication of a nerve-structure is to be found in a network of fine horizontal fibrils lying between the inner ends of the elongated sucker-cells, but superficial to the basement-membrane. These fibrils disappear altogether during the atrophy of the sucker.

It will be remembered that in the young larva the cilia are longer and lash more vigorously on a small area at the anterior pole than over the general surface of the body (p. 15). This condition is transient. More important is the fact that the epidermal cells of the area in question are distinctly longer than those which cover the rest of the preoral lobe (Pl. I. fig. 10; Pl. III. figs. 33, 34), and that they remain so throughout the whole of larval life. It is the basal parts of the cells which are elongated, and between them a few fine horizontal strands like nerve-fibrils may be detected, though not in such numbers as under the sucker. The area in question may be called the apical field or plate. During metamorphosis the walls of the anterior end of the larva are incorporated in great part with the oral surface of the young Starfish, the actual epiblast-cells retaining their individuality throughout. What we have called the apical field of the larva is carried to a position near the centre of the oral face in the region of the earlier-formed hydrocœle-pouches. Here the tissue of the field is at any rate brought very near to the site of formation of a considerable segment of the oral nerve-ring, which by extension at the two ends completes the ring. Certain it is that, like practically all the other structures, the nervous system is differentiated latest in the last-formed rays.

A nervous system more or less well developed has been described for larvæ belonging to all the five main divisions of Echinoderms.

Thus in *Asterias vulgaris* Packard, Field (7, p. 113) noted the presence, at the apex of the frontal field, of an area carrying elongated ciliated cylindrical cells with what seemed to be nerve-fibres at their bases, and this area he compared with an apical plate.

Macbride (15, p. 353) found underneath the "larval organ" of *Asterina* a layer of fibrillæ which he considered to be nervous in character.

The larvæ of *Antedon* and *Synapta* possess well-marked nerve-structures which, in the case of the latter, help to form the nervous system of the adult. Nerve-tissues have also been described in the echinid pluteus (Mortensen, 19; Macbride, 16 a) and in the larval *Amphiura* (Russo, quoted from Bronn's 'Klassen,' II. 3, iii. p. 868). They are said to be recognisable in the latter as far back as the gastrula stage, and to give rise to the nervous system of the adult.

Solaster, however, furnishes an example in which a larval nervous system of the apical type comes very near to being carried over during metamorphosis into the central nervous system of the adult.

Muscular Tissue of Larva.—The larval muscular tissue is developed from the lining of the various cœlomic cavities, particularly from that of the anterior cœlom. The latter gives rise to the fibres which are in connection with the larval arms and with the sucker, and to the oblique band which was referred to on p. 16 as in all probability exercising a gubernacular action in effecting the flexion and torsion of the preoral lobe. The band in question is illustrated in Pl. III. fig. 34.

This band of fibrillæ takes origin from the lining of the left side of the anterior

cœlom, as well as from the lining of the hydrocœle, particularly in the neighbourhood of pouches III and IV. Its general course is indicated by the line on Pl. II. fig. 20. Anteriorly it can be traced to a little in front of the groove which marks off the preoral lobe from the body of the larva. At a slightly later stage one finds that the fibrillæ are short and somewhat matted, as might now be expected. One finds also that they become connected anteriorly with fibrillæ which, passing to the right side of the body-wall and joining others coming from the region of the sucker, probably have something to do with the production of the deep nuchal notch which is found in early metamorphosis on the aboral side of the disc, and which afterwards in great part becomes filled up to form the madreporic interradius (pp. 22, 27).

Ciliation.—In the adult the whole of the inner lining of the body-cavity, as well as of the digestive sac and its appendages, carries cilia on its free surface. It was noted on p. 13 that the primitive hypoblast of the gastrula is ciliated like the epiblast. In the latter this condition is carried through and beyond metamorphosis. In the former, however, it is difficult to trace continuity of ciliation, particularly in the case of the middle chamber or enteron, but I believe that it occurs.

IX. MODE OF OBTAINING AND REARING THE LARVÆ.

The best way to secure material for the study of *Solaster* development is to keep healthy adults through the spawning-season and to have the water circulation so arranged that any ova that may be shed will not be swept away in the outflow. As the eggs are lighter than water, this can readily be effected by drawing the outflow from the bottom of the tank. In the end of March last (1910) three small tanks at the Millport Marine Station were set apart for my use and fitted up in the manner required. The outflow was effected by means of syphon-tubes, the inner ends of which dipped down to the bottom, while, to prevent the possibility of excessive emptying, the outer ends in each case dipped into a vessel the water-level in which could not fall more than a few inches below that of the top of the tank.

To begin with, all the available *Solaster endeca* were kept in the first of these tanks. On March 30th one of the Starfish shed a large number of eggs, which were duly fertilised in the manner previously described (pp. 9–10). All the Starfish were then transferred to the second of the tanks, and on April 2nd the same female again extruded a number of eggs which were fertilised in their turn. The Starfish were then put into the third tank, but no further shedding of ova took place.

It is impossible, so far as I know, from the external characters, to tell with certainty whether a specimen is male or female. Hence it is advisable to keep a number together, in order to make sure that both sexes are represented. As happens in other Echinoderms, a male is stimulated to emit sperm by the presence in the same tank, even at some distance away, of a spawning female. Failing this effect, artificial

ertilisation can be induced without difficulty if specimens are available from which portions of testis can be removed and shredded into the vessel containing the ova.

It is not satisfactory, however, to cut out portions of the female gonad for obtaining ova. A great deal of waste material is introduced into the hatching-vessel, and, worse than that, the eggs hardly ever come out clean, but are still surrounded by follicle-cells and other débris.

In calm weather, in certain localities near the Millport Station, one may come across floating larvæ of *Solaster* towards the middle and end of April. I have gathered them on three occasions in the channel between the Station and the Fairlie shore. I failed, however, entirely to induce these larvæ to undergo metamorphosis. This circumstance, along with the fact that many of them when taken showed minor abnormalities of growth, would lead to the inference that it is chiefly unhealthy larvæ which come to the surface of the sea. They are soft and readily break up against the cloth of a tow-net. In gathering them from the surface the best way is to lift them one by one with some water in a dipper.

The two sets of fertilised eggs obtained in the manner previously described were kept, all through, in their original tanks, specimens being taken from time to time for examination and preservation. In a week or so, as I had to return to Glasgow, about twenty were put into each of two small glass aquaria which I took up with me to the Embryology Laboratory at the University. Throughout the succeeding months an easy circulation of sea-water was maintained in the hatching-tanks at the Station, the incoming current being filtered by tying over the nozzle a bag of fine-meshed cloth, which was cleaned out from time to time. It soon became necessary to guard against escape of the young larvæ, when they began to leave the surface and swim throughout the tank. One had accordingly to furnish the inner end of the syphon with a filtering surface, offering no bar to the outflow, but rendering the current so weak that the larvæ would not be injured by being sucked against the cloth. This was done by attaching a very large filter-funnel to the end of the syphon, the mouth of the funnel having tied over it a piece of tow-netting material of moderate mesh. Many larvæ came to rest against this surface, but a little disturbance of the water near them from time to time sufficed to clear them off without injury. I cannot speak too highly of the care and attention paid to the brood all through by Mr. John Peden, the Laboratory Attendant at the Station.

The tanks employed were of the enamelled fireclay kind, which have proved so useful since they were fitted up in the Millport Station about ten years ago. Their contents remained sweet all through, and their smooth surfaces gave suitable attachment to the larvæ when they reached the fixation stage, besides being excellent ground for the young Starfish to travel over after metamorphosis was finished.

Now, at the beginning of November 1910, four * specimens are still alive and

* The last of these survived till February 1911.

apparently healthy. Since the end of metamorphosis, however, their growth has been very slow. Probably the tanks do not afford them the proper kind of food, all that is available being the fine growths of algæ present on the sides and some granular débris which has settled to the bottom. I hope later to have the opportunity of making experiments with a view to finding out what their natural food may be, and of rearing them through further stages in early growth.

So far I have been quite unable, in examining material dredged up from likely *Solaster* ground at Millport, to come across examples either in metamorphosis or in the stages that immediately succeed it.

Of the two glass vessels containing young larvæ which I took with me to Glasgow, one had a capacity of half a gallon and the other rather less. Both were shaded and kept under gentle continuous aeration by means of an aerating apparatus (8) devised by me in connection with an earlier attempt at the rearing of *Solaster*. From time to time a little fresh water was added to make up for the loss caused by evaporation. Development proceeded in a perfectly normal manner, but with somewhat greater rapidity than at the Station, owing no doubt to the difference in temperature of the laboratory in Glasgow and the sea-water at Millport. The living specimens in these aquaria, being always at hand, proved of the greatest use for purposes of general observation.

I am much indebted to the Superintendent, Mr. Richard Elmhirst, and the Staff of the Millport Station for the ready and careful manner in which they assisted me all through in the work of obtaining and rearing the larvæ. My best thanks are also due to Mr. Alex. Gray, formerly Curator of the Station, with whose good help a first and practically successful attempt at the work was made several years ago. Acknowledgment is also due to Mr. Jas. A. Boyle, Art Master at Hillhead High School, Glasgow, for much expert assistance in the finishing of the Plates.

X. SUMMARY OF CHIEF FEATURES IN DEVELOPMENT OF *SOLASTER*.

(For paging, see under CONTENTS, p. 1.)

(A) *Externally*.

Egg floating, flattened at upper and lower poles, the latter paler in colour; segmentation total, equal; blastula formed by egression of the central cells along numerous lines, and gastrula by invagination at lower pole.

Closure of blastopore; no formation of larval mouth; a long free-swimming stage; "larva" with three glandular arms and a disc-shaped sucker; for a time, perfect external symmetry except for hydropore on right side.

Flexion and torsion of preoral lobe towards left side; stage of attachment by the larval sucker; reduction in size of preoral lobe, and incorporation of much of its epiderm with the oral surface of the Starfish; metamorphosis occurring in such a way

that, while in point of external form the left side of the larva becomes the oral surface of the Starfish and the right side the aboral, in reality the epiderm of the oral surface is chiefly derived from that of the anterior part of the larva, and, conversely, the epiderm of the aboral surface originates chiefly from that of the posterior part of the larva.

Five hydrocœle-lobes appearing to begin with, the rest being added later in such a way that the whole series may properly be described as beginning in the hydroporic region and progressing thence in the watch-hand direction as seen from the oral surface.

Aboral arm-rudiments also incomplete in number for a time.

Disappearance of the preoral lobe ; atrophy of the sucker as the tube-feet become functional. Development of mouth and anus ; outgrowth of the arms and appearance of the rosettes of spines.

(B) *Internally.*

1. *In Larva.*—Archenteron divides into anterior and posterior cœloms and a middle chamber, the enteron or gut.

Anterior cœlom provides cavity of preoral lobe and a central part which gives rise to right and left lateral diverticula, as also to dorsal sac, hydroporic canal, and perihæmal pouch IX-I. Bottom of left lateral diverticulum becomes hydrocœle groove and gives rise to radial pouches ; five of the latter appear almost simultaneously, and are to be numbered in the manner indicated for the corresponding external swellings ; groove of stone-canal opens into hydrocœle groove between origins of pouches I and II ; pouches VI and VII are added ; hydrocœle groove and stone-canal groove begin to be roofed over.

Posterior cœlom sends out dorsal and ventral horns in sagittal plane, and gives rise to a series of six perihæmal pouches and to diverticula for the pharyngeal cœlom. It also tends to extend over the left side of the enteron, and in a less degree over the right.

2. *In Metamorphosis.*—Preoral cœlom disappears ; central part of anterior cœlom becomes axial sinus ; right lateral diverticulum gives rise to epigastric cœlom ; hydrocœle groove is separated off from left lateral diverticulum and extends to form ring-canal, the last two radial pouches being now added. Rest of left lateral diverticulum, along with part of axial cœlom, forms the internal oral circular sinus.

Posterior cœlom with its two horns and two pharyngeal diverticula enlarges to form hypogastric and peripharyngeal cœloms. The last two perihæmal pouches are given off, and along with the others form the external oral circular sinus. Tip of dorsal horn gives rise to pocket with special cells, the rudiments respectively of the aboral circular sinus and the genital rachis.

Enteron expands greatly and shows blunt swellings in each ray. Mouth and anus form, as well as the paired radial and the rectal cæca. The anus is in interradius V/VI.

The ambulacral and adambulacral plates appear in a typical manner; but the aboral skeleton shows numerous small uniformly distributed plates in the disc and two terminals in each arm-rudiment. Small nodules for the spines appear everywhere over the aboral surface.

The ambulacral and adambulacral plates increase in size and number; while the plates of the aboral skeleton increase in size, and at a much later stage in number also. For a time the latter fit closely with one another; afterwards interspaces, the future meshes of the skeletal reticulum, appear between them and are bridged over by new plates. The spines increase in size and form small groups, which become associated with the first-formed plates.

(C) *General.*

The development of *Solaster* agrees in very many points with that of *Cribrella* (as described by Masterman), including the remarkable mode of blastula and gastrula formation and the even more remarkable origin of the hypogastric coelom. Like that of *Cribrella*, the swimming larva of *Solaster* with its three glandular arms and sucker on the preoral lobe can readily be referred to the brachiolarian type. This is all the plainer since in *Solaster*, as I could satisfy myself by observation of living specimens, the tips of the arms lose their cilia and become capable of exercising slight and temporary adhesive functions. Their primary object, I should judge, in *Solaster* is to enable the muscular sucker to be brought into play at the proper time for initiating the stage of definite fixation.

If one were looking at *Cribrella* and *Solaster* alone among Echinoderms, nothing could have greater apparent reason in point of form than Masterman's comparison of the hydrocoele with the epigastric coelom, and it would be alike attractive and legitimate to accept the homologies he has sought to institute between the various larval cavities in *Cribrella* and *Balanoglossus*. In the case of *Solaster* it might further be argued that the posterior annulus referred to on p. 16 gave additional evidence of enteropneust affinity; while the manner in which much of the preoral lobe, including the (rudimentary) apical nervous system, became incorporated at metamorphosis with the oral surface of the Starfish indicated greater ontogenetic continuity than the more abrupt changes occurring in the metamorphosis of *Asterina* and apparently of the bipinnaria. But attractive as this hypothesis is, it seems to me that it would impose difficulties of interpretation on the development of other Starfish and of Echinoderms in general, greater than those from which it could relieve *Cribrella* or *Solaster*. The position has been stated by Macbride (15, 16, 16 a, 16 b), and I must put myself down as a supporter of his view that in *Cribrella* (and *Solaster*) we are dealing with a form of development modified from that which should be looked upon as typical and primitive in the Order.

Of course, the question, being one of evidence, may yet be reopened, *e. g.*, by the discovery of a feeding bipinnaria in which the hypogastric coelom originates wholly

or partly behind the stomach. Meantime we must suppose that in the development of the yolky *Solaster* egg the larval alimentary canal has been reduced to the stomach, and even the development of this part has been greatly post-dated, while at the same time a sliding-back of the walls of the cavity (or cavities) giving rise to the hypogastric cœlom has taken place. The peculiar foldings of the whole blastula-wall, including that part which becomes invaginated in gastrulation, may provide opportunity during their formation and disappearance for a considerable amount of rearrangement of the hypoblastic tissue; but, so far, I have not been able in the ontogeny of *Solaster* to trace adequately the steps by which the backward migration of the cœlom in question may be supposed to have taken place. Probably a hint remains in the deficiency dorsally of the thickened zone A B, referred to on p. 37, while, later, the oblique direction of the dorsal part of the enteric slit, the greater size of the right enteric fold, and the pouching to the right of the enteron wall are indications that the backward migration has been concerned—chiefly, at any rate—with a structure belonging to the left side. But if this view is accepted, one could not refuse to admit as possible the further inference that some degree of backward migration had taken place ventrally also, and that it probably affected a right-sided structure.

The posterior cœlom of *Solaster* and *Cribrella* must correspond with whatever gives rise in other Starfish to the hypogastric cœlom. This, according to the best evidence available (that of Macbride for *Asterina*, 15), is the left posterior cœlom alone, though, as is well known both in *Asterina* (10 a) and *Asterias pallida*, Goto (9, 10) states that a part is contributed from the right side.

The evidence on this point to be extracted from my account of *S. endeca* only serves to keep open the question, on which, however, further light may be expected from an exact comparison of the corresponding stages in *S. papposa* and possibly also from a fresh examination of more abundant *S. endeca* material prepared with a view to the elucidation of this special point.

Such other comparative notes as it seemed necessary to include in this paper have been introduced in connection with the structures to which they refer; *e.g.*, hydrocœle (p. 21), nervous system (p. 46), anus (p. 23), external oral perihæmal sinus, etc. (p. 35).

New points brought out in regard to the adult anatomy of *Solaster* are discussed in a separate paper (8 a).

REFERENCES.

1. BECKER, S.—Die Hörbläschen von *Leptosynapta bergensis*. Biolog. Centralblatt, xxix. p. 413.
2. CHUBB, C. C.—The Growth of the Oocyte in *Antedon*. Proc. Roy. Soc. lxxvii. p. 384.
3. CUÉNOT, L.—Formation des Organes Génitaux et Dépendances de la Gland Ovoïde chez les Astérides. Compt. Rend. vol. 104, 1887, p. 88.
4. ——. Études Morphologiques sur les Échinodermes. Arch. de Biol. vol. xi. 1891, p. 623.

5. DELAGE et HEROUARD.—Traité de Zoologie Concrète. Tome III. Les Échinodermes. 1903.
6. DURHAM, H. E.—Note on the Madreporite of *Cribrella oculata*. Proc. Roy. Soc. 1888, vol. xliii. pp. 330–332.
7. FIELD, G. W.—The Larva of *Asterias vulgaris*. Q. J. M. S. 1892, pp. 105–128.
8. GEMMILL, J. F.—An Automatic Aerating Apparatus suitable for Aquaria &c. Journ. Roy. Micr. Soc. 1910, pp. 9–13.
- 8 a. —. Notes on the Adult Anatomy of *Solaster endeca* Forbes: (1) Madreporite, etc.; (2) Anus; (3) Egg Ducts; (4) and (5) Aboral and Oral Perihæmal Sinuses. Proc. Roy. Phys. Soc. Edinb. vol. xviii. pp. 174, 191.
9. GOTO, S.—Vorläufige Mittheilung über die Entwicklung des Seesternes, *Asterias pallida*. Zool. Anz. 19, xix. pp. 271–274.
10. —. The Metamorphosis of *Asterias pallida*, with Special Reference to the Fate of the Body-Cavities. Journ. Coll. Sc. Imp. Univ. Tokyo, Japan, vol. x. pt. iii. pp. 239 *et seq.*
- 10 a. —. Some Points in the Metamorphosis of *Asterina gibbosa*. Ibid. vol. xii. pt. iii. pp. 227 *et seq.*
11. HENDERSON, E. H.—Some Observations on the Development of an Asterid with large Yolky Eggs from the Franklin Islands. Ann. & Mag. Nat. Hist. ser. 7, vol. xvi. pp. 387–392, pls. xii. & xiii.
12. LUDWIG, H.—Entwicklungsgeschichte der *Asterina gibbosa*. Zeitschr. f. wiss. Zool. vol. xxxviii. 1882, pp. 1–89.
13. — (& O. HAMANN).—Bronn's Klassen u. Ordnungen des Thierreichs, Bd. 2, Abth. 3, Buch ii. 1889.
14. HAMANN, O.—As above, p. 653.
15. MACBRIDE, E. W.—The Development of *Asterina gibbosa*. Q. J. M. S. xxxviii. pp. 339–411.
16. —. Cambridge Natural History. Vol. i. (1906) Echinoderms.
- 16 a. —. The Development of *Echinus esculentus*. Phil. Trans. Roy. Soc. vol. cxcv. 1903.
- 16 b. —. The Development of *Ophiothrix fragilis*. Q. J. M. S. vol. li. pt. 4, 1907.
17. MCINTOSH, D. C.—Meristic Variation in the Common Sun-Star (*Solaster papposa*). Proc. Roy. Phys. Soc. Edinb. vol. xvii. pp. 75–78.
18. MASTERMAN, A. T.—The Early Development of *Cribrella oculata* Forbes, with Remarks on Echinoderm Development. Trans. Roy. Soc. Edinb. vol. xl. pp. 373–417, pls. i.–v.
19. MORTENSEN, TH.—Die Echinodermenlarven der Plankton Expedition. Ergebnisse Plankton-Exped. Bd. ii. J. 1898.
20. PERRIER, E.—Recherches sur l'Organisation des Étoiles de Mer. Compt. Rend. vol. cii. 1886, pp. 1146–8.
21. —. Res. Scient. Expéd. 'Travailleur' et 'Talisman.' Échinodermes, 1894, pp. 10–15.
22. SEMON, R.—Die Entwicklung von *Synapta digitata*. Jen. Zeitschr. Bd. xxii. pp. 175 *et seq.*
23. SLADEN, W. P.—'Challenger' Reports. Zoology, vol. xxx. pp. xl–xlii and p. 452.
24. THOMSON, WYVILLE.—On the Development of *Synapta digitata* O. F. M. Q. J. M. S. n. s. ii. 1862, pp. 131–146.

EXPLANATION OF PLATES I.-V.

Lettering in all the Plates.

- I, II, III, &c. . . The hydrocœle pouches as numbered in the manner explained on p. 21.
I. 7, 13; II. 22, 23; V. 50-52, 56. In I. 11, however, the above numerals indicate the paired radial cœca.
- 1, 2, and 3, &c. . The aboral arm-rudiments associated with the hydrocœle pouches of same numbers. I. 7; II. 22, 23.
- A thickened zone of hypoblast in archenteron. III. 25-27 (p. 37).
- a.a. anterior larval arm. I. 8, 10; II. 17-23; III. 34; IV. 41, 42.
- a.c. anterior cœlom. III. 25-34.
- am. ambulacral plates belonging to the various rays. I. 8; II. 19, 20.
- an. anus. I. 11.
- arch. archenteron. I. 6.
- ax.c. axial cœlom. I. 10; III. 32-34; IV. 36-44, 46; V. 49-52.
- B thickened zone of hypoblast in archenteron. III. 25-27 (p. 37).
- bl. blastopore. I. 6; II. 15, 16; III. 25-30; IV. 36; V. 49.
- D dorsal side of larva. III. 26.
- d.h. dorsal horn of posterior cœlom. IV. 39, 40, 44; V. 50-55.
- d.s. dorsal sac, or madreporic vesicle. IV. 39, 46; V. 52-56.
- d.t. adambulacral spines forming denticles. I. 14; IV. 48.
- ep.c. epigastric cœlom (right lateral diverticulum of anterior cœlom). IV. 44-48.
- f. statolith. I. 10; III. 28; IV. 41.
- g. enteron or gut. IV. 36, 38, 40-47; V. 49, 50, 53, 56.
- g.r. genital pocket from posterior cœlom. V. 56.
- hyd. hydroporic canal. IV. 39; V. 51, 52, 56.
- hy. hydrocœle. I. 10; III. 28-34; IV. 36-48; V. 50-52, 56.
- i.ph.c. internal oral circular sinus. IV. 46-48; V. 56.
- i.r.d. rectal cœca. I. 11; IV. 48.
- L left side of larva. III. 27.
- l.a. left larval arm. I. 10; II. 17-20, 22, 23; V. 50.
- l.g. left enteric fold. III. 28-33.
- m. madreporic opening. I. 11; II. 17, 18; V. 53-55.
- meth. mouth. I. 13-14; V. 56.
- mus. special muscular bands. III. 34 (p. 47).
- n. nuchal groove or furrow on margin and aboral surface of Starfish disc.
II. 21-23; IV. 44.
- n.r. area of heightened epiderm on preoral lobe (larval nervous system). I. 10;
III. 34; IV. 41-42.
- o.ph.c. diverticula for external oral perihæmal sinus. I. 10; IV. 41, 43, 45-48;
V. 51, 56.
- p.c. posterior cœlom. I. 10; III. 25-34; IV. 36-46; V. 49-55.
- pg.c. hypogastric cœlom. IV. 46-48; V. 52-56.
- p.ph.c. diverticula for pharyngeal cœlom. IV. 44, 47, 48; V. 56.

<i>pr.c.</i>		preoral coelom.	I. 10 ; IV. 36-38, 41, 42, 44, 45 ; V. 49-55.
<i>pr.l.</i>		preoral lobe.	I. 8 ; II. 16-22 ; IV. 41, 42, 45 ; V. 56.
<i>p.st.</i>		peristome.	IV. 48.
R		right side of larva.	III. 27.
<i>r.</i>		rectum.	IV. 48.
<i>r.u.</i>		right larval arm.	I. 8 ; II. 17-18, 22, 23 ; IV. 37, 41, 45 ; V. 53.
<i>r.d.</i>		radial cæca of stomach.	I. 11 ; IV. 48 ; V. 56.
<i>r.g.</i>		right enteric fold.	III. 28-33.
<i>r.l.c.</i>		right lateral diverticulum of anterior coelom.	III. 28-33 ; IV. 36-38, 40, 42, 44-47 ; V. 53-55.
<i>r.pl.</i>		plates of the aboral reticular skeleton.	I. 8, 9.
<i>s.</i>		sucker.	I. 8, 10, 13 ; II. 17, 18, 22, 23 ; IV. 42, 44.
<i>sp.</i>		spines.	I. 8, 9.
<i>st.</i>		stomach.	I. 11.
<i>st.c.</i>		stone-canal.	IV. 46.
<i>t. 1, t. 2, &c.</i>		terminal plates (double) belonging to the various rays.	I. 8.
V		ventral side of larva.	III. 26.
<i>v.h.</i>		ventral horn of posterior coelom.	I. 10 ; IV. 39, 40, 44 ; V. 50-55.
<i>y.</i>		yolk-granules swept into archenteron.	III. 29 (p. 45).

PLATE I.

PLATE I. Figs. 1-14.

(For lettering see pp. 55-56.)

- Figs. 1-4. Stages in segmentation. (1-3, $\times 20$; 4, $\times 25$.) In fig. 4 slit-like spaces are beginning to appear in the cell-mass.
- Fig. 5. Section of advanced stage in formation of blastula by egression of central cells along many lines (p. 12). The flattening on the underside is due to commencing gastrulation. ($\times 30$.)
- Fig. 6. Vertical section of the fully-formed gastrula (p. 12). ($\times 30$.)
- Fig. 7. Diagram from right (aboral) side of larva at end of free-swimming stage, to illustrate the early relations of the hydrocœle pouches to the aboral arm-rudiments (see p. 22). The pouches are lettered with roman numerals, and the aboral arm-rudiments, with which these finally become associated to form the rays of the Starfish, are indicated by corresponding arabic numerals. ($\times 20$.)
- Fig. 8. Larva towards end of free-swimming stage cleared and looked at from right side, showing the developing skeletal elements. The spines (*sp.*) are represented by numerous small nodules all over the field (p. 43). Of the aboral plates, six pairs of terminals (*t.*) have appeared, as well as a number of the plates (*r.pl.*) which develop over the epigastric area (p. 41). Seen more faintly as at a deeper level and partly out of focus are five pairs of ambulacrals (*am.*) (p. 41). ($\times 45$.)
- Fig. 9. A few spines and plates of the aboral skeleton as seen in a specimen twelve weeks old (p. 42). ($\times 200$.)
- Fig. 10. Microphotograph of sagittal section of advanced larva, showing particularly the statolith-like body on the posterior cœlom (p. 46). The high epithelium over the crown of the preoral lobe will also be seen (p. 46, nervous system). ($\times 30$.)
- Fig. 11. Diagram from aboral side, illustrating the relations of the radial and rectal cœca, the stomach, and the anus in a specimen four and a half months old. Description on p. 40. ($\times 35$.)
- Fig. 12. Small portion of disc from aboral side in a specimen of about same age as in fig. 13, but more highly magnified. The papular appearance due to the developing spines is indicated, the latter being outlined as in a cleared specimen. ($\times 45$.)
- Fig. 13. Young *Solaster* at time of formation of mouth. The triradiate shape of the mouth will be noted (p. 23). The ninth radial pouch of the hydrocœle has just appeared. The arm-rudiments for arms VII-IX have not yet separated from one another. The sucker is now small and outside of the hydrocœle-ring (p. 21). ($\times 45$.)
- Fig. 14. Young *Solaster* about six months old, from oral side, showing characteristic appearance of spines, ambulacral grooves, denticles, etc. ($\times 45$.)

J.F.G.

DEVELOPMENT OF SOLASTER ENDECA.

PLATE II.

PLATE II. Figs. 15-23.

(For lettering see pp. 55-56.)

- Fig. 15. Gastrula beginning to elongate, the blastopore being still widely open (p. 14). ($\times 40$.)
- Fig. 16. Anterior end of cone bending to larval ventral side (p. 14). ($\times 40$.)
- Fig. 17. Young larva from right side showing the three larval arms, the position of the sucker, and the hydroporic opening (p. 14). ($\times 45$.)
- Fig. 18. Older larva from right side at a stage just prior to commencement of flexion and torsion of the preoral lobe (p. 16). ($\times 40$.)
- Fig. 19. Still older larva from left side. The preoral lobe is beginning to undergo its change of position (p. 16). Several pairs of ambulacral ossicles have now appeared, and these are shown as if in a cleared specimen (p. 41). The larval arms are represented as being drawn close together (p. 15). The line on the body indicates the direction of the muscular fibrillæ referred to on pp. 16, 47. The hydroporic pit seems larger than it should be, owing to slight shrinkage in the (preserved) specimens from which figs. 18 and 19 were drawn.
- Fig. 20. Larva from left side, towards end of free-swimming stage. The preoral lobe is much more sharply flexed on the body, which is now almost disc-like in shape. Six pairs of ambulacral ossicles are present. ($\times 40$.)
- Fig. 21. Sketch of a larva which had recently attached itself by means of the sucker to a small duck-weed. A section of this specimen, showing plant, sucker, etc., is given in Pl. IV. fig. 44. The preoral lobe, which is seen in shadow, has not yet undergone its full flexion and torsion. The edge of the disc is slightly everted at one part and shows between it and the preoral lobe two or three blunt swellings due to the hydrocœle pouches. The long groove on the disc running towards the sucker is the nuchal notch or groove (p. 22). ($\times 40$.)
- Fig. 22. Specimen detached after about three days' fixation and seen from oral side. The preoral lobe is now completely bent against the oral (left larval) surface, the remains of the anterior arm being towards the middle of this surface (p. 19). The sucker and the other two arms are nearer the margin. Six of the radial pouches of the hydrocœle appear externally and a rudiment of the seventh. ($\times 40$.)
- Fig. 23. Specimens detached after about six days' fixation and viewed from oral side. Five of the radial pouches of the hydrocœle now show swellings for the sucker-feet. Compare with fig. 22. The preoral lobe has now almost entirely disappeared. ($\times 40$.)

This series is continued in figs. 13 and 14 on Pl. I.

PLATE III.

PLATE III. Figs. 24-35.

- Fig. 24. Sketch from cleared specimen at stage in middle gastrulation with one of the large surface-furrows still present and leading into the blastopore, which is widely open. The invaginated hypoblast is seen in darker shading as a slightly folded layer within the epiblastic layer. ($\times 35$.)
- Fig. 25. Optical section of stage immediately succeeding gastrulation. The blastopore is narrow; the archenteron has expanded and shows in its lining the thickened zone A B, from which, as was explained on p. 37, the right and left lateral diverticula of the anterior coelom, as well as the walls of the enteron, will be derived. ($\times 30$.)
- Figs. 26-27. Two optical sections of a stage slightly later than the last, fig. 26 being a view from the left, and fig. 27 a view from the dorsal aspect and slightly from the right. Both show elongation of the gastrula-cone as well as commencing formation of the ventral dimple. Fig. 26 shows also the slight obliquity of the base of the cone referred to on p. 37. It will be observed that the posterior part of the cone is now somewhat narrower in the frontal than in the sagittal plane. The constriction marking the enteric folds is not apparent in the lateral view (fig. 26), since it is actually present as yet only at the sides. ($\times 30$.)
- Figs. 28-30. Three sections from a frontal series of a young larva about 24 hours older than that shown in the last two figures, but with the blastopore still open and the enteron still in the form of an isthmus between the anterior and the posterior coeloms. The sections illustrate particularly the different sizes of the right and left enteric folds dorsally, mesially, and ventrally, throughout the series. It will be observed that dorsally (fig. 28) the right fold (*r.g.*), though less prominent, is larger than the left one; ventrally (fig. 30) the condition is reversed, though with smaller differences, while mesially (fig. 29) the right fold is still slightly larger. ($\times 50$.)
- Fig. 31. Frontal section of older larva. The apertures between the middle and posterior chambers are just closing at the points which the section cuts. It will be seen that the right gastric fold is contributing rather more than the left one to the total area of the enteron, and also that there is a slight pouching to the right of the enteron-wall. ($\times 45$.)
- Fig. 32. Similar section to the last, but of a slightly older larva. The middle chamber is now quite closed off from those in front and behind. In front, however, the seam of the closure is still recognisable looking leftward. The same slight pouching to the right on the part of the enteron is seen here as in the fig. 31. ($\times 45$.)

PLATE III. (*cont.*).

- Fig. 33. Frontal section of a *S. papposa* larva at stage similar to that shown in fig. 31. The section passes to the dorsal side of the mid-frontal plane. It will be observed:—(1) That the enteron still opens widely in front into the anterior cœlom, the opening looking leftward; (2) there is a very definite pouching to the right of the posterior part of the enteron; (3) the right gastric fold contributes a good deal more than the left one to the area of the enteron. Although it does not appear in this section, the blastopore is still widely open, and the enteron still communicates with the posterior cœlom. ($\times 45$.)
- Fig. 34. From sagittal series of larva at stage when the flexion and torsion of the pre-oral lobe (p. 16) is in early progress, the section being to the left of the middle line of the body, but practically mesial at the anterior end of the frontal lobe. A good part of the length of the muscular band concerned in the movements mentioned above come into the section. Pouch IV of the hydrocœle, the sucker, and the anterior larval arm are also seen. ($\times 45$.)
- Fig. 35. Section of egg-tube of an adult *S. endeca*, after long fixation in an osmic acid mixture (Lindsay Johnston fluid). Ova in different stages of growth are illustrated with special reference to the accumulation of the yolk-granules, which have undergone an intensely black coloration (p. 6). Similar granules along with larger ones are seen in the layer of follicle-cells round each ovum, as also in the spaces between the ova within the lumen of the egg-tube. ($\times 90$.)

24

25

26

27

28

29

30

31

32

J.F.G.

33

34

35

PLATE IV.

PLATE IV. Figs. 36-48.

(Illustrative sections of specimens in larval stages and in metamorphosis, drawn with camera lucida to magnification of 25 times. The various cavities are coloured as follows:—The posterior cœlom and its derivatives are red and the enteron brown. The preoral and axial cœloms are coloured yellow, as also are the hydroporic canal and the internal oral circular sinus. The right lateral diverticulum of the anterior cœlom (epigastric cœlom) is shown in green, and the hydrocœle and dorsal sac in blue. The dull ground-colour is space filled by mesoderm.)

Fig. 36. Frontal section through larva about 8 days old. The blastopore is still open and the middle chamber or enteron still communicates with the anterior and posterior cœloms. The right and left lateral diverticula of the anterior cœlom are beginning to grow backwards over the enteron.

Fig. 37. Section similar to the last, but not perfectly frontal, through a slightly older specimen. The enteron now appears as a distinct region, not simply as a neck between the anterior and posterior cœloms.

Fig. 38. Frontal section through slightly older specimen. The anterior and posterior cœloms are completely separated from the enteron and the blastopore is closed.

Fig. 39. Transverse section of larva about middle of free-swimming stage. The section passes through the hydropore, the ventral side of the larva being uppermost. Both horns of the posterior cœlom appear in the section, as well as the dorsal sac and the first radial pouch of the hydrocœle.

Fig. 40. Transverse section through middle of body of larva at stage slightly later than that shown in fig. 38. The dorsal and ventral horns of the posterior cœlom, as well as the right and left lateral diverticula of the anterior cœlom, and the enteron appear in the section. The right lateral diverticulum in this example is very large.

Fig. 41. Sagittal but not quite median section through a larva in the later free-swimming stage. The preoral and axial sinus regions of the anterior cœlom are beginning to be marked out. Some of the perihæmal pockets (*o.ph.c.*) are separated from the posterior cœlom. The ventral horn of this cœlom is cut along a great part of its length. There is a statolith within the posterior cœlom (p. 46).

Fig. 42. Sagittal section through larva in still later free-swimming stage. Flexion of the preoral lobe has begun, and accordingly while this lobe is cut in its sagittal plane, the body of the larva is cut rather in the future oral-aboral plane, the aboral (right larval) side being underneath. This explains the position in the section of the right lateral diverticulum (epigastric cœlom) as well as the fact that the posterior cœlom is cut on

PLATE IV. (*cont.*).

opposite sides of the enteron. The sucker is fully exposed. In this section and the last the heightened epiderm (*n.r.*) over part of the preoral lobe (larval nervous system, p. 46) is indicated.

- Fig. 43. Oblique section through left side of body of larva just prior to attachment, showing a considerable number of the hydrocœle and perihæmal pouches as well as the tip of the ventral horn of the posterior cœlom. The hydrocœle groove is closed off from the left lateral diverticulum of the anterior cœlom to form a canal in the region of pouches III to V.
- Fig. 44. Vertical section through disc, sucker, leaf, etc. in the specimen illustrated in Pl. II. fig. 21. The section passes transversely across the nuchal groove (*n.*) about halfway between the margin and the middle of the disc. The epigastric cœlom (*ep.c.*) is not yet completely separated from the axial cœlom, nor the latter from the preoral cœlom. The dorsal and ventral horns of the posterior cœlom appear in the section as well as the two corresponding horns into which the enteron is drawn at this stage (p. 38).
- Fig. 45. Ventral section across disc of specimen in early metamorphosis. The section does not pass through the centre of the disc, but falls well towards the margin on which rays VII to IX will be formed. The prominence on the oral side, due to the preoral lobe, is not yet entirely lost. The perihæmal pockets for interradii VII/VIII and VIII/IX are in process of being budded off from the posterior cœlom.
- Fig. 46. Vertical section across disc about halfway between centre and margin in a specimen in middle stage of metamorphosis. The section passes across the madreporic interradius, and is to be compared with fig. 44 as regards general orientation. The epigastric cœlom is now completely separated from the axial cœlom. The latter is dividing into two horns (*i.ph.c.*) which are continued into the internal oral circular sinus. On the right side of the sketch the ring-canal of the hydrocœle is cut at its junction with the stone-canal, and on the left side between pouches VIII and IX.
- Fig. 47. Typical vertical section across disc in metamorphosis some time prior to the formation of the mouth. The enteron has expanded very markedly, and shows a flattened area on the oral side, in the middle of which the mouth will afterwards be formed. To the right the radial vessel of arm III appears, while to the left there is the shorter radial vessel of arm VII.
- Fig. 48. Vertical section across half of disc of a specimen four and a half months old. Mouth and anus have been present for a considerable time. The anal opening does not appear in the section, but some of the commencing

PLATE IV. (*cont.*).

rectal cæca are cut through. The surface prominences are due chiefly to spines, those which form the denticles being particularly large. The epigastric and hypogastric mesenteries separate the epigastric and pharyngeal cæloms respectively from the hypogastric cælom. A Tiedemann's body is closely attached to the ring-canal of the hydrocœle. The other parts of the hydrocœle in section are the ampullæ of the tube-feet.

PLATE V.

PLATE V. Figs. 49-56.

(Diagrams illustrating the moulding of the various cavities at different stages as seen from the larval left or oral (figs. 49-53) and from the larval right or aboral (figs. 54-56) sides. Magnification about 18 times. Colouring as on Pl. IV.)

Fig. 49. Diagram from left side of internal cavities in a larva about eight days old. The three primary divisions of the archenteron are becoming separated, the anterior being the largest. The posterior cœlom is beginning to send out dorsal and ventral horns.

Fig. 50. Diagram from left side of internal cavities in larva about eleven days old. The dorsal and ventral horns of the posterior cœlom have extended considerably, and the hydrocœle groove or bottom of the left lateral diverticulum of the anterior cœlom now shows the outgrowth of the first five radial pouches and partly conceals the enteron. The larval arms have also appeared.

Fig. 51. Diagram from left side of internal cavities in a larva about fifteen days old. The horns of the posterior cœlom have grown round still further. Perihæmal diverticula (*o.ph.c.*) are coming off from the posterior cœlom, while that from the anterior cœlom has already become separated. The ring-canal of the hydrocœle is beginning to be nipped off from the left lateral diverticulum. The preoral cœlom is still large.

Fig. 52. Diagram from oral (left larval) side of internal cavities in a specimen during early fixation. The dorsal and ventral horns of the posterior cœlom have grown round so far as to compress between them the structures of the axial complex. The perihæmal diverticula of the posterior cœlom are beginning to be nipped off. The stalk of the preoral cœlom is almost obliterated. The hydrocœle is represented as already forming a complete ring, and as separated all round from the anterior cœlom, but this is slightly in advance of the ordinary course of development. Fusion is taking place between the enteron and the oral body-wall in preparation for the formation of the mouth. Pouch I of the hydrocœle is represented as being cut away close to its origin.

Fig. 53. Diagram from oral side of internal cavities in a young Starfish towards end of metamorphosis. The mouth-opening (*mt.h.*) has formed. The pharyngeal cœlom (*p.ph.c.*) is not yet a complete circle, but it opens into the hypogastric cœlom (*pg.c.*) in most of the interradii. The perihæmal pouches (*o.ph.c.*) are taking on their characteristic form. The tip of the (larval) dorsal horn of the posterior cœlom is pushing in the wall of the dorsal sac, where it lies against the axial sinus, thus helping to form the genital pocket (*g.r.*). The internal oral circular sinus (*i.ph.c.*) is still a wide

PLATE V. (*cont.*).

space on the side turned towards the axial sinus, into which it freely opens. For diagrammatic purposes one or two of the structures are shown as slightly more advanced in development (*e. g.*, radial cæca of stomach, *r.d.*) and others less advanced (*e. g.*, pharyngeal cœlom) than they should be at this stage. ($\times 60$.)

- Fig. 54. Diagram of internal cavities in a stage similar to that of fig. 50, but viewed from right side of larva. From this side the hydropore (*m.*), the dorsal sac (*d.s.*), and the right lateral diverticulum of the anterior cœlom (*r.l.c.*) are seen.
- Fig. 55. Diagram from aboral (right larval) side of specimen a little younger than that from which fig. 52 was taken. The epigastric cœlom (right lateral diverticulum of anterior cœlom) (*r.l.c.*, *ep.c.*) is being separated from the axial cœlom. For diagrammatic purposes the preoral lobe is represented as standing out much straighter than it should be at this stage. It should now be bent so far to the left as to be almost entirely concealed by the disc.
- Fig. 56. Diagram from aboral side of specimen well advanced in metamorphosis. The epigastric cœlom is completely separated from the axial cœlom. As in fig. 55, the remains of the preoral lobe are straightened out for diagrammatic purposes.

J.F.G.

DEVELOPMENT OF SOLASTER ENDECA.