

VII. *The Development and Certain Points in the Adult Structure of the Starfish
Asterias rubens, L.*

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I. POSITION, STRUCTURE, GONADS.

The Asteriadæ rank among the Cryptozonia of SLADEN (87, xxiii *et seq.*, xxxiv), since they possess reduced marginal plates, while their papulæ or gills are not confined to that part of the abactinal surface which is bounded by the supero-marginal plates. Further, they carry stalked pedicellariæ both of the crossed and the straight varieties; they have never spinelets grouped in a paxilliform manner, and, except in early stages, their tube feet are arranged in quadriserial order.

At the present time the development of four starfish has been followed out. These are *Asterina gibbosa* (LUDWIG, 52; MACBRIDE, 55); *Asterias vulgaris* (AGASSIZ, 1; GOTO, 33); *Cribrella oculata* (MASTERMAN, 60); *Solaster endeca* (GEMMILL, 29). Much work has also been done on other but often unidentified larval forms. There need only be mentioned at this stage the classical papers of J. MÜLLER (74), the ‘Echinodermenlarven’ of MORTENSEN (71), and the studies of METSCHNIKOFF (63), BURY (8, 9) and FIELD (23).

As regards *Asterias rubens* L., the Common Starfish or Crossfish of British and European seas, although the general outline of its life-history is known, particularly from the work of MÜLLER (74), SARS (82), HENSEN (42), MORTENSEN (71), BURY (8, 9), and SEMON (86), still the available descriptions do not provide a set of connected data, important blanks remaining to be filled up as regards external features, and much more with reference to structure.

In the following paper I have tried to give an account of the development of this starfish, having succeeded in rearing it, in 1912 and also in 1913, from artificial fertilisations made at the Millport Marine Station, right through metamorphosis in the Embryological Laboratory at Glasgow University (p. 224). This work was undertaken, in continuation of a previous study of the development of *Solaster endeca* (29), mainly in order to contribute data for examining the view held by various zoologists, and shared by myself (p. 279), that the feeding, free swimming, brachiolarian Asterid larva probably represents the least modified larval type which has yet been studied either in the starfishes or in other groups of Echinoderms.

Asterias rubens agrees very closely with *A. vulgaris** (STIMPSON, MS.), Packard, the North American species studied by AGASSIZ (1), FIELD (23), and GOTO (33, 34), in the form and general history of the larva, and in many points of structural detail. This circumstance renders it probable that the discrepancies between GOTO'S account of internal development and mine are due to errors of interpretation, on whichever side committed. At the same time *A. rubens* and *A. vulgaris* are perfectly distinct species, and are recognised as such by VERRILL† (91, p. 347), JEFFREY BELL (4, p. 496), and SLADEN (87, pp. 816, 828).

Asterias forbesi,‡ Verrill (Desor), another American species, on the normal and experimental embryology of which much work has been done by AGASSIZ (1), WILSON and MATHEWS (93), and others, is also specifically distinct from *A. rubens*, as may be seen from VERRILL'S description (91, pp. 345-6).

The main facts of its development bring *A. rubens* into much closer relationship with the phanerozonte *Asterina* than with *Cribrella* and *Solaster* which like *Asterias* are cryptozonte forms. This is notwithstanding the fact that in having large yolky eggs and in the absence of pedicellariæ, *Asterina* agrees rather with *Cribrella* and *Solaster* than with *Asterias rubens*.

It may be added that *Porania pulvillus*, which is a phanerozonte form belonging to the Gymnasteriadae (87, xxxiii) a family not far removed from the Asterinidae, agrees with the cryptozonte *A. rubens*, in the principal details of its larval history.

We are not yet in a position to throw much light from embryology on many of the difficult questions of Asterid classification. New characters or groups of characters may have to be employed if a system based on, or agreeing with, developmental data is to be elaborated. At the present time this seems to be impossible; nevertheless, for convenience in making comparisons it may be well to preface this paper with a short account of the main external and internal characters of our species.

The abactinal skeleton is well developed, forming a moderately fine sub-regular reticulum made up of numerous small plates which are more or less elongated in the horizontal and flattened in the oral-aboral plane, but which in general have a shape suitable to their position in the meshwork, those which are placed at the nodes being angular or polygonal. The edges of the plates overlap each other, especially along the strands of the reticulum. Some of the larger plates carry one, or it may be two, rather short and thick spines. Although exhibiting a certain degree of order, for example forming a somewhat irregular row aborally in the middle line of each ray, these spines are not so systematically arranged as to produce definiteness of pattern. Small inconspicuous marginal plates are present as well as parambulacral and actinal intermediate plates (SLADEN, 87, p. xli). The primary plates of the young starfish, though never altogether lost, become relatively reduced during later growth and take an entirely inconspicuous place in the adult reticulum (p. 267).

The papulae or gills are numerous, emerging in groups through the interspaces of the reticulum all over the surface, not confined to the area bounded by the supero-marginal plates, but occurring also between and below the marginals. Straight (forcipiform) and crossed (forcipiform) pedicellariæ are present, both kinds being provided with a small basal piece or stalk. The crossed pedicellariæ† are

* Called by AGASSIZ *Asteracanthion pallidus*, Ag.

† Reference to the original description of *A. vulgaris* by VERRILL (91, p. 348) shows, among other points of difference between it and our species, that in the former the dorsal spines bear close wreaths of minute pedicellariæ which also form dense clusters at the outward sides of the lateral and ventral spines. The major pedicellariæ are . . . very numerous over the whole surface between the spines.

‡ Called by AGASSIZ *Asteracanthion berylinus*, Ag.

chiefly grouped around the bases of the spines, but they do not form dense tufts there. The mouth armature is of the ambulacral type, the oral ambulacral plates being relatively prominent at the actinostomial margin (87, p. xlii). The tube feet are quadriserially arranged.

The arms are five in number and have vertical lateral walls (SLADEN, 87, p. 562). The adambulacral ossicles are irregularly or alternately diplacanthid and monacanthid, that is, provided with a single spine or with two spines each. The madreporite is destitute of spines and the anal opening is slightly excentric in the direction of inter-radius V/I.

Structure and Function.—As regards internal anatomy *A. rubens* conforms to the usual Asterid type. We note, however, that Polian vesicles are absent, and there is a single Tiedemann's body in the madreporic inter-radius on the dextral* side of the stone canal, and two in each of the other inter-radii. The following points relating to adult structure and function on which additional light is thrown in this paper also fall to be mentioned here, fuller details being given on the pages indicated.

As regards the food-canal, the main gastric cavity is made up of pharyngeal, stomachal, and pyloric sac regions, while pyloric caeca, intestine, rectal sac, rectal caeca, and rectum are also to be distinguished (pp. 273, 274). A spiral curvature, much obscured, may be recognised in the course of the food canal, comparable with the curvatures found in echinoderms having a tubular gut (p. 274); the axial sinus communicates with the pore-canal system and with the stone canal under the madreporite (p. 267); a diverticulum from the pore-canal system rests against the aboral wall of the dorsal sac or madreporic vesicle (p. 268); the internal surface of the stone canal is increased by a longitudinal inwardly projecting ridge dividing into two scroll-like lamellæ (p. 257); there is a downward current within the stone canal, but in the pore-canal system taken by itself, as well as in the axial sinus, the currents have an upward or aboral tendency (p. 270). The aboral perihæmal sinus is interrupted in the madreporic inter-radius (p. 261): a large inter-radial branch of the external oral circular sinus occurs (p. 260); each gonad has a single duct opening by several apertures (p. 217); the hæmal system of channels has a definite arrangement which follows the usual asterid type (p. 271); the head process of the axial organ and certain other parts show rhythmic contractility (p. 272); a probable course of circulation is indicated (p. 273); the perihæmal cavities are ciliated (p. 246); the ciliation of the general perivisceral coelom and of the alimentary canal follows a definite plan (p. 246).

The Gonads.—The two gonads in each inter-radius are not confined to the disc but extend outwards, almost reaching the tips of the arms as the period of ripeness is approached. Each gonad is a single, simply branched, much lobulated sac lying free within the body cavity, except at its root, where a single efferent duct passes outwards to the body wall. This duct, after piercing the greater part of the body wall, becomes somewhat expanded, and is then interrupted by an uncalcified membrane having a number of perforations (4 to 7 in specimens examined) which lead directly to the surface and open a short distance outwards from the mid-interradial line, slightly to the aboral side.

* Throughout this paper, *dextral* and *sinistral* indicate respectively the sides towards which, or away from which, the hands of a watch would seem to move on the starfish disc as viewed aborally.

Gonad Walls.—Covering the whole gonad is a layer of low pavement epithelium, and during life the action of the cilia is such that currents of coelomic fluid pass outwards over the surface of the gonad from its root, as well as along each of the branches and lobules from their proximal to their distal extremities.

Under the ciliated covering, outer and inner layers of the gonad wall may be distinguished. These layers are separated from one another, in considerable part, by a network of irregular sinus spaces which, as in *Solaster endeca* (28, p. 5), possess an epithelial lining near the root of the gonad and for some distance outwards, but more distally a lining epithelium is absent or occurs only in patches. The outer layer of the gonad wall is much the stronger. It contains both connective tissue and muscular fibres and may itself be subdivided into a superficial and a deeper sheet; in the former both kinds of fibres have mainly a circular, and in the latter a longitudinal, arrangement. The inner layer of the gonad wall is very thin, being chiefly, if not entirely, fibrous in character. It is incorporated with the deeper sheets of the outer layer wherever the sinus spaces above referred to do not exist.

As in *Solaster endeca* (29, p. 4), the hæmal strand enclosed within each genital branch of the aboral circular sinus is continued on to the root of the corresponding gonad, and terminates by dividing up into small branches ramifying on the inner layer of the gonad wall within the sinus spaces there. In a specimen with arm-tips forming a circle 3 inches in diameter I was unable to identify remains of the germ cells of the genital rachis, either within the aboral circular sinus or within the genital branches of this sinus. The sinus spaces in question do not accompany the genital efferent duct in its passage through the body wall. This duct has a well marked connective tissue wall containing also fine muscular fibres, and it is lined by long ciliated columnar epithelium. As also in *Solaster* there is no definite septum walling off the contents of the gonad from the lumen of the efferent duct (29, p. 8).

Ova.—The peripherally placed germ cells rest directly against the inner layer of the gonad wall; but, except in very small ovaries, the majority of the ova have to be described as lying within the lumen of the gonad, being out of contact with its walls. The yolk granules are practically uniformly distributed and have a pale yellowish colour whether in transmitted or reflected light. The germinal vesicle, which is slightly excentric and is provided with a single large nucleolus, contributes all along about three-tenths to the entire diameter of the ovum. At full size the ovum measures 0·16 to 0·19 mm. in diameter. The egg membrane is at first thin, but in the middle and later periods of growth it reaches a thickness of 0·0075 mm. and shows radial striations, being perforated “by fine threads in which glittering granules may be seen” (HERTWIG, 43, 1878, p. 157). Later, this membrane is usually described as becoming thinner so that the radial canals disappear, but the egg remains closely surrounded by a fine apparently homogeneous covering. In eggs naturally spawned this is enveloped in a delicate mucous layer showing radial striæ.

Follicle Cells.—During active growth, all the ova have a covering of follicle cells except, as was indicated above, on surfaces which abut against the gonad walls. At first the follicle cells are cubical or polygonal in shape and may occur in more than a single layer round an ovum, or may be aggregated in heaps wherever space has to be filled up. Later, each ovum is found to have only a single layer of follicle cells, which in the end become flattened and finally disappear, apparently through undergoing mucoid degeneration after the ova have reached full size.

II. SPAWNING, MATURATION, FERTILISATION.

Spawning.—The sexes are indistinguishable externally, and occur in approximately equal numbers in the Firth of Clyde. The characteristic (though not invariable) spawning position for either sex shows the body bunched up, the arms brought together and adhering to the tank wall by their outer portions, or even only by their tips. I have counted as many as five distinct streams of ova or sperm emerging from the genital pores of a single gonad. A particular starfish measuring $5\frac{1}{2}$ inches across disc and arms was estimated to have extruded over 2,500,000 eggs at a single period. In this case the spawning, which lasted for about two hours, occurred when the specimen was under observation in a nature-study class at the station and the estimate of numbers was made by Mr. G. HUTCHEON, one of the students.

Period of Ripeness.—In the Firth of Clyde many specimens of *Asterias rubens* are facultatively ripe as early as the beginning of April, in the sense that a large proportion of their ova if shredded into sea-water will ripen and cultures may be obtained from them. Indeed, the broods which proceeded to metamorphosis under my care in 1912 were reared from cultures made on April 20. However, I have no records of young Bipinnariæ from tow-nettings till after the beginning of June. In 1911, the earliest natural spawning observed at the Millport Station occurred on June 3, and in 1912 on July 4. In 1913 spawning was noticed on April 23, and again on May 24 and 25. Even within such a small area as the Firth of Clyde there seems to be considerable difference from year to year in the duration of ripeness. Thus, at Millport, in 1911, all the available starfish somewhat suddenly became spent towards the middle of June, and in spite of many trials I failed to obtain later fertilisations, while in the summer of 1912 a similarly spent condition was not reached till the end of the first week in July.

Stimulus to Spawning.—As happens in the case of other starfish, *e.g.*, *Solaster* (29, p. 10), the shedding of ova or sperms may be induced during the ripe season by the presence of sperms or ova in the tanks. Thus, on May 24 of this year I brought some starfish which had been kept for a considerable time in the station into water containing shredded pieces of ovary and testis. This was followed within 24 hours by an epidemic of spawning among the starfish in question. There is some evidence

that mutual cross-stimulation can take effect between the two common species of starfish, *A. rubens* and *A. glacialis*.

In nature it is probable that very large numbers of ova complete their growth together in the ovaries, and then remain dormant till some physiological stimulus incites them to rapid maturation, and leads also at once to their extrusion. Probably this occurs at least twice in the same starfish in a single season.

Such records as are available from elsewhere show that in *A. rubens* the period of ripeness is probably a wide one and certainly differs in different localities. The brachiolaria of Helsingör (74, 1848) described by JOH. MÜLLER (some, if not all, of which belonged without doubt to *A. rubens*) occurred in autumn, and if we allow five or six weeks for the earlier stages, this means that spawning occurred about the middle of June. SARS (82) found brachiolaria which we can now say belonged to *A. rubens* at Molde as early as the month of June. HENSEN (42, p. 363), at Kiel, was able to make artificial fertilisations of *A. rubens* eggs in April and May. In the plankton the first young larvæ occurred on May 8, and advanced brachiolaria were observed as late as the end of July (42, p. 242 *et seq.*). E. v. BENEDEN (6) secured artificial fertilisations of *A. rubens* in April at Ostend, and SEMON (86, p. 18) at Heligoland in the end of the same month. On the other hand GREEF (37, 1876, p. 37) stated that the period of reproduction in *A. rubens* is during the spring months in the North and Baltic Seas and "it is an error to say that this species spawns at any other time than between about the end of March and the middle of May." MORTENSEN (71, p. 42) rightly corrects this latter statement, pointing out that the reproductive period seems to vary in different localities; that in the Limfjord the period in question is May till beginning of July, while in the Baltic Sea and the Cattegat the larvæ still occur in August and September. Later, in 'Nordisches Plankton' (72, 1 (ix), p. 12) the same author gives May to September as the period of occurrence of *A. rubens* larvæ in the North Sea. These dates are confirmed by an examination of the recent plankton records of the North Sea Fisheries Investigation.

We may add that Sir J. G. DALYELL believed the ova of *A. rubens* to be discharged during May and June (13, 1, p. 93), while MCINTOSH (62, pp. 332-5) has recorded the occurrence of brachiolaria in the plankton of St. Andrew's Bay towards the end of July.

Retained Ova.—It sometimes happens that numbers of full-sized ova remain within the ovary long after the spawning season is ended. I have come across examples of the kind in the end of December. Some of these ova had lost their large germinal vesicles, but in others this vesicle was still present. I obtained irregular segmentations as a result of artificial fertilisations. The appearance of most of the ova suggested that they had lost vitality and would soon become absorbed, as is well known to occur in the case of other retained ova. Instances like the above, if well marked, might readily give rise to the impression (MCINTOSH, 61, p. 216) that December or a succeeding month was the spawning period for our species.

Maturation.—It is stated by LUDWIG (54, p. 628) that in *A. glacialis* the eggs leave the ovary in a typically unripe condition. However, a natural spawning on the part of *A. rubens*, observed by me at the Millport Station in July, 1912, provided eggs in which the germinal vesicle and nucleolus were already reduced at the time of shedding, the maturation changes being completed in some and actively progressing in the majority. Spawnings observed in April and May, 1913, gave

exactly similar data. The varying position of the polar bodies with reference to the membrane of fertilisation (p. 223) may thus receive a natural explanation. In the case of *A. glacialis*, ova taken up as they emerged from the genital pores and fixed by the laboratory attendant at the station, showed the same features as those of *A. rubens*. In *Solaster endeca* I described the formation of the first polar body as being in progress at the time of extrusion (29, p. 9). A piece of ovary, excised from a spawning *A. rubens* and shredded out, showed practically all the full-sized ova it contained to be in the early stages of maturation.

WILSON and MATHEWS (93, p. 332) refer to the difficulty of obtaining starfish ovaries in course of maturation. E. v. BENEDEN (6, p. 66) noted that when an ovary was shredded out, it was only very exceptionally that an ovum occurred from which the large germinal vesicle had disappeared. Practically all other writers from HENSEN, AGASSIZ, GREEF onwards, speak of all the ova as being unripe when first teased out, and undergoing the ripening changes after admixture with the sea-water. The maturation processes in *Asterias* have been studied only from material obtained in this manner.

The Maturation Changes.—It is to O. HERTWIG that we owe the first full description of these changes in *Asterias* (43, 1878). A useful purpose may be served if the sequence of such of those stages as can be observed without the application of special methods be here given, since it is often of much importance that one should know as soon as possible whether a particular batch of eggs is healthy or ripe enough to promise a satisfactory culture

- 20 minutes after shredding, nucleolus shows signs of vacuolation and protoplasm begins to invade germinal vesicle ;
- 30 minutes after shredding the double star for the first karyokinetic spindle is first recognisable ;
- 45 minutes after shredding there is marked shrinkage of the germinal vesicle with loss of distinctness of the nucleolus ;
- 2–2½ hours after shredding, the first polar body is well pushed out or already completely separated ;
- 2¾–3 hours after shredding, as above for the second polar body.

The data are HERTWIG'S, whose work was done (*A. glacialis*) at Messina. To make them fit with my observations (*A. rubens*), made under presumably colder conditions at the Millport Station, in the Firth of Clyde, something like 20 per cent. has to be added to the various intervals.

Fate of Nucleolus.—The fate of the nucleolus in maturation and the origin of the chromosomes have proved a cytological problem of much interest. Including references to *Asterias* only we find that GREEF (37, p. 34) noticed when eggs of *A. rubens* were teased out into sea-water from an ovary during the breeding season that their nuclei underwent shrinkage and other changes, these changes taking place whether fertilisation supervened or not. He believed that the nucleolus gave rise to the ripe egg nucleus. E. VAN BENEDEN (quoted from 24, p. 358) thought that the contents of the germinal vesicle were extruded from the egg, while the female pronucleus took origin from fragments of the nucleolus. FOL (24) denied this, and gave a description agreeing more or less closely with HERTWIG'S results for *Toxopneustes*. HERTWIG'S (*A. glacialis*) important contribution is referred to above. He held that the nucleolus disappeared, and that the nuclei of the polar bodies and of the ripe ovum were derived from the germinal vesicle. Later, WILSON and MATHEWS (*A. forbesi*, 93, p. 353) described the chromatin masses of the first maturation spindle as coming from part of the chromatin of the unripe nucleus, adding that there is no persistence of chromosomes and that the greater portion of the chromatin of the unripe nucleus becomes converted into cytoplasm. Similar points are brought out or taken as understood by TENNENT and HOGUE (*A. forbesi*, 89). HARTMANN, however (40, p. 810, *A. glacialis*), gives an

account of maturation which bears out that the maturation-chromatin masses are evolved entirely out of the nucleoli.

Finally, JORDAN (45, p. 112, *A. forbesi*) states that the chromosomes in question "originate from the nuclear reticulum at the beginning of the growth period of the primary oöcyte and persist as a mass of minute bilobed bodies, sometimes in close proximity or even attached superficially to the nucleolus. The nucleolus fragments and contributes chromatin to the chromosomes in virtue of which they grow slightly in size. The residue of the nucleolar fragments is resorbed by the protoplasm." It may be added that amoeboid movements on the part of the contents of the germinal vesicle or of the nucleolus during maturation have been described by various authors, in particular by GREEF (37, 1876, pp. 35, 86; 1879, p. 47) and v. BENEDEN (5) and SCHNEIDER (83).

Chromosomes.—WILSON and MATHEWS (93, p. 334) state that in *A. forbesi* the number of chromosomes passing to each pole of the second polar spindle is approximately 17. This number was afterwards definitely estimated to be 18 by TENNENT and HOGUE (89). The former authors add that the chromosomes which remain within the egg proceed to form a group of four or five small vesicles which later unite to form the egg nucleus. The latter is slightly excentric in position, being nearer the side from which the polar bodies were extruded. The egg centrosome and its surrounding archoplasm disappear completely.

Shaking and Maturation.—MORGAN (70, pp. 149, 150) noted that maturation might be induced by shaking after echinoderm eggs are shredded into sea-water. WILSON and MATHEWS (93, p. 333) confirm this result for *A. forbesi*, noting an instance in which only 12 per cent. of the eggs matured when unshaken, whereas over 50 per cent. were induced to undergo the changes by a little agitation, and, "had the agitation been more violent or more prolonged, similar experiments on other eggs proved that the proportion would have been increased." In my Millport experiments, the ova when taken from healthy specimens near the period of ripeness matured spontaneously without further shaking than that involved in the method employed (p. 224). Other facts show, however, that shaking does increase the kinetic activity of the starfish egg; for instance MATHEWS was able by its means to increase the number of ova which underwent spontaneous or parthenogenetic development (LOEB, 50, p. 144).

Fertilisation.—Normally, only a single spermatozoon enters the egg, and it may do so at any point on the circumference. It proceeds towards the centre of the egg, and then towards the egg nucleus, with which it becomes united. An amphiaster appears in connection with the sperm nucleus shortly after the latter has entered the egg, and one pole of the amphiaster precedes, while the other follows the nucleus in question during its further course through the egg (93, p. 336). The membrane of fertilisation appears immediately after the entrance of the head of the sperm cell. Its formation begins at the place of entrance of the sperm cell, the surface of the egg often showing slight changes of shape here, as if amoeboid movement were going on. After complete separation, the membrane stands off from the egg at a distance which varies from a narrow slit to a half or more of the diameter of the egg itself.

Rapid osmosis of fluid through the egg membrane must be taking place at this time. RIES'S (77, p. 184) observations seem to indicate that this occurs by the throwing out from the egg at the place of entrance of the sperm of a clear mass which has the property of rapidly absorbing water so that it swells up greatly and extends quickly round the whole egg. Probably such a substance is thrown from the egg, beginning at the place of entrance of the sperm, but many circumstances indicate that the extrusion of this substance cannot be localised at the point in question, but takes place all round the surface of the egg. Among these circumstances are the facts (1) that the sperm may enter at any point on the surface

of the egg, (2) that the formation of the membrane of fertilisation may be artificially induced by numerous agents which bear on the egg equally all round, (3) that a membrane of fertilisation is formed and stands out widely from the egg even in such large ova (1 mm. in diameter) as those of *Solaster endeca* (29, p. 11). It is exceedingly improbable that the very large space thus formed could be filled by the swelling up of a tiny mass extruded from a minute portion of the surface of the egg.

The sperm cell can enter the egg and induce the formation of a membrane of fertilisation any time after the maturation changes have properly begun, that is (*a*) prior to the actual extrusion of the first polar body, or (*b*) prior to that of the second polar body, or (*c*) after both of these bodies have been separated off. In (*a*) both polar bodies will be inside the membrane of fertilisation, in (*b*) only the second polar body will be inside this membrane, and in (*c*) both polar bodies will lie outside. In a natural fertilisation at the Millport Station the (*a*) condition occurred in approximately 45 per cent., the (*b*) condition in 35 per cent., and the (*c*) condition in 10 per cent. of the ova examined. The segmentation stages figured by AGASSIZ (1) and HERTWIG (43) show the polar bodies inside the membrane. This is what one finds in ordinary cultures made shortly after the eggs are shredded out. If we wait long enough the (*c*) condition appears. A delay of one and a-half to two hours is advisable in order to secure healthy cultures, though even then most of the eggs will show the (*a*) or (*b*) condition.

Movements of Sperm.—The starfish sperms which crowd round an ovum are extremely active. If many are present they impart a rhythmic rocking motion, or even a rotation, to the ova as a result of their activity. The rocking period in particular instances averaged three seconds. Even unripe eggs are affected, and the rocking continues till well after the formation of the membrane of fertilisation. These movements are produced not at all or only in the faintest degree in *Echinus* eggs by the addition of *Echinus* or *Asterias* sperm, and they are not produced in *Asterias* eggs by *Echinus* sperm. As far back as 1878 AGASSIZ mentioned the rotary movements communicated to the eggs of *Asterias forbesi* (1, p. 6) by “the beating of the spermatic particles,” while v. BENEDEK had also noticed these still earlier in *A. rubens* (6, pp. 6–7).

Duration of Vitality.—The spermatozoa remain quiescent within the testes, but are immediately stimulated to activity by sea-water, the activity being more intense the greater the admixture of water. If so little water is used that the mixture looks white or milky, the spermatozoa will survive and be able to fertilise ova for two days or longer. But if the dilution is very great the fertilising power becomes lost in a few hours. Ova shredded out into sea-water have the best chance of developing normally if fertilised within the first four hours. This chance is slightly diminished at six hours and much more so at eight and ten. Thereafter only very irregular segmentations or cytolytic changes are induced by the addition of sperm. I am indebted to one of my students, Mr. J. K. RENNIE, for these facts, which may be compared with the corresponding data worked out by me for *Echinus esculentus* (26).

Cross-fertilisation.—The following data from a set of cross-fertilisation experiments carried out by me at the Millport Station in the spring of 1902 have reference to *Asterias rubens*:—

<i>A. rubens</i> , female	}	A very large proportion of the ova segmented and went on to blastula and gastrula formation. The converse crossing gave a similar result.
<i>A. glacialis</i> , male		
<i>Cribrella oculata</i> , male	}	About 15 per cent. of the eggs were fertilised. The converse crossing provided only about 1 per cent. of fertilisations.
<i>A. rubens</i> , female		
<i>Solaster papposus</i> , female	}	Irregular segmentation followed in about a third of the eggs.
<i>A. rubens</i> , male		

The sperms of *A. rubens* crowded more or less closely round the ova of *Luidia ciliaris*, *Echinus esculentus*, *Echinocardium cordatum*, and *Synapta digitata* without causing fertilisation. The same sperms were unaffected by the ova of *Astropecten aurantiacus* or *Brissopsis lyrifera*.

The ova of *Asterias* soon became closely surrounded by the spermatozoa of *Echinus esculentus*, and to a less degree by those of *Brissopsis lyrifera*, without further result, but had not an attracting influence on the sperm of *Astropecten aurantiacus*, *Echinocardium cordatum*, and *Solaster endeca*.

In these experiments no special methods of sensitising the ova were employed, such as have recently been found effective in inducing cross-fertilisations that would not otherwise occur, *e.g.*, between certain American species of starfish and other Echinoderms (50, pp. 138, 197).

III. REARING THE LARVÆ.

In preparing the cultures all apparatus used was carefully sterilised, and only water that had been passed through a Chamberland filter was employed. Portions of gonad from a number of starfish were examined microscopically, and a good male and two good females selected. These were washed repeatedly, and then opened in a fresh inter-radius. A gonad from each starfish was taken out entire, and after several washings was brought into a small dish with about an equal bulk of water, and then teased or shredded out. The male gonads needed no further treatment. After half an hour the dishes containing the ovaries were gently shaken up, and abundance of ova, now separate and discrete, were decanted into other dishes also with a small quantity of sea-water, leaving behind the more solid portions of the ovary. A double repetition of the process provided practically clean ova which were then brought into a larger dish with more water. It is an advantage that the first shredding out of the gonads should be done in a very small quantity of water, since thereby sudden and complete differences in the chemical and physical surroundings are avoided, and also by following this routine one gets the individual ova clean and free from mucus, follicle cells, or other *débris*. About two hours after the shredding out of the ova, the maturation changes being now well advanced, a little sperm was added. The sequence in time of the maturation and segmentation changes is given on p. 227.

The cultures were taken up the same day to the Embryological Laboratory at Glasgow University, and kept for the next two days under gentle aëration by means of an apparatus devised and employed in connection with work on the development of *Solaster endeca* (27). The character of the swarming larvæ now made it possible to form an opinion as to which of the cultures was the most promising, and this

having been done several convection-current hatching vessels* were stocked with plentiful supplies of the larvæ and left undisturbed for three days. These cultures were then examined, and, the best having been selected, a sufficient number of larvæ were transplanted into fresh hatching vessels, where they were fed with *Nitschia* culture and partly shaded from the light. The next transplantation was done 12 days afterwards, that is about 18 days after the fertilisation had been made, and the next not till the middle of the fifth week. No further changing was done, metamorphosis being attained in the hatching vessels as then left.

This account applies particularly to the practice adopted in 1912. The 1913 routine was much the same, except that the successful cultures received even fewer changes of water. Various experiments on feeding the larvæ were also carried out, and it was found that *Nitschia* plus a chance bacterial and flagellate infection provided even better results than *Nitschia* alone.

CHRONOLOGY.

- 1st day Segmentation completed.
 2nd day Blastulæ swarming; commencement of gastrulation.
 3rd day Gastrulation completed.
 4th day Mesenchyme given off; commencing formation of enterocœlic sacs.
 5th-6th day . . . Enterocœlic sacs separated; hydroporic canal formed; stomodæal pit appears; ciliated bands becoming definite; regions of alimentary canal distinct.
 7th-8th day . . . The posterior enterocœlic bud definite.
 10th day Distinct forward and backward extension of enterocœlic sacs.
 10th-12th day . . Separation of preoral and postoral bands.
 15th day Apposition of dorsal part of peristomal band to transverse portion of preoral ciliated band.
 21st day Union of right and left anterior cœloms in the preoral lobe; distinct lappets where the various ciliated processes will afterwards grow out.
 23rd day Commencement of formation of ventral horn of *l.p.c.*
 25th day Dorsal sac a minute vesicle.
 28th day *l.p.c.* and *r.p.c.* cut off from *l.m.c.* and *r.m.c.* respectively.
 to
 29th day Fusion of ventral horn of *l.p.c.* with *l.m.c.*
 31st day The hydrocœle pouches distinct.
 35th day First pulsation of floor of dorsal sac observed. Brachia now showing, and rudiment of sucker beginning to be seen.
 36th day Aboral arm rudiments evident, and already showing rudiments of the primary plates.
 38th day Papillæ for spines beginning to be seen.
 During 6th week. Ciliated processes reach full size. Ends of brachia become papillated, and two papillæ appear on each side of the sucker. Temporary attachment by means of brachia now possible.

* These hatching vessels are described in detail elsewhere (30). A U tube of glass, through which cold tap water is kept running, dips down from above into the middle of each. This produces a downward convection current in the middle of the vessel, while a compensating upward current takes place close to the wall of the vessel all round, due to conduction of heat from the air of the laboratory.

7th or 8th week. Definite fixation for metamorphosis by means of sucker; about seven days afterwards the young starfish ruptures its stalk and crawls away; two or three days thereafter the mouth appears, and the anus in about another week.

The above sequence has reference to successful cultures which were made towards the end of April, but its various steps are subject to wide variation as regards time. During the first week, temperature is the chief disturbing factor, and the rate of change may be hastened by more than a third under the influence of warmth, without apparent injury to health. Another factor of smaller but still appreciable importance depends on season. The nearer the eggs under observation are to the time when they would be shed naturally, the faster is the rate of their development during the first week, apart from the influence of temperature. In later growth, nutrition appears to be the all-important factor. The stage given above as characteristic of the 21st day has been reached as early as the 15th and as late as the 24th day without prejudice to subsequent development. It is an excellent sign of the future well-being of the larvæ if, during the fourth and succeeding weeks, their stomachs remain or have become moderately large and globular, thus giving the ventral horn of the *l.p.c.* some distance to travel over before it can unite with the cœlom of the right side.

MEASUREMENTS.

Blastula measures	(about) 0·2 mm. in diameter.
Late gastrula measures	„ 0·25 „ in length.
Bipinnaria of 5 days measures	„ 0·3 „ „
„ „ 8 „ „	„ 0·4 „ „
„ „ 15 „ „	„ 0·7 „ „
„ „ 21 „ „	„ 1 „ „
„ „ 31 „ „	„ 1·5-2 „ „

Towards the end of full growth it will be well to distinguish the length of the body from that of the ciliated processes. At this time my largest brachiolariae measured about 2·7 mm. in length of body, the postero-lateral ciliated processes streaming behind them for a distance of 1·2 mm., while the median dorsal-process was about 0·21 mm. in length. The total length of these larvæ as they moved about in the water was therefore a little over 4 mm. This is distinctly larger than the average measurements recorded. Thus JOH. MÜLLER gives the length of his brachiolariae of Helsingör (*A. rubens*) as about 1·5 mm. (74, p. 94, 1848); MORTENSEN (71, p. 42, *A. rubens*) up to 2 mm.; HENSEN (42, p. 242, *A. rubens*) up to 2·2 mm.; SARS (80, p. 126, *A. rubens*) up to 2 mm., and DELAGE (17, *A. glacialis*) up to 3 mm. Most of these measurements were, no doubt, done from preserved specimens which must have been more or less shrunken. Yet my own specimens, even after preservation, were larger than the brachiolariae from plankton material which I obtained for comparison. Probably the richness of the *Nitschia*-feeding and the warmth of the laboratory in which the larvæ were reared account for the increase in size.

As regards growth after metamorphosis, I have, as yet, no data of importance to give. AGASSIZ (1) states that a starfish (*A. forbesi*) is probably ready for spawning in its sixth or seventh year and reaches full size at about 14 years. In a single case observed by him, a small starfish of 1½ inches diameter across disc and arms grew in five months to a diameter of 3 inches.

M. and C. DELAP (19) give interesting notes regarding the growth of *Luidia sarsi*. The young starfish became separated from their bipinnarial appendages in November. One of them reached a measurement of 15 mm. across disc and arms at the end of May, 25 mm. at the end of July, 50 mm. in September, 70 mm. in October, and 95 mm. in December. It is certain, however, that the early growth of *A. rubens* proceeds at a much slower rate.

IV. SEGMENTATION, GASTRULATION, MESENCHYME FORMATION.

The first cleavage is vertical,* beginning at or near the place of formation of the polar bodies and dividing the eggs into two equal parts. The divisions producing the four-celled stage, which are also vertical and equal, occur in a plane at right angles to the first. The next cleavages are horizontal, leading to an eight-celled stage, with four usually rather smaller upper cells and four lower cells, the two sets as a rule lying, at any rate to begin with, in parallel horizontal planes. The succeeding divisions are sub-regular and the cells near the upper pole tend to remain a little smaller than those on the opposite side.

Formation of a blastocœle cavity begins as early as the sixteen- or even the eight-celled stage. The "membrane of fertilisation" remains intact until the blastula exhibits signs of ciliary activity. Losing the "membrane of fertilisation," the blastula swarms about freely, being spherical in shape and having only a single layer of cells forming its wall. These are slightly longer at the lower pole than elsewhere. No mesenchyme cells occur within the blastocœle cavities of the best blastulæ.

In ordinary cultures, when the addition of sperm is delayed till two or three hours after shredding out the ova, the membrane of fertilisation makes its appearance within the first few minutes after mixing. The two-celled stage is reached in $4\frac{1}{2}$ to 5 hours after shredding and about five hours thereafter all stages up to the sixteen-celled one can be obtained. A little before the end of the first day (22 hours) faint attempts at swarming occur. By the middle of the second day the blastulæ swarm actively all through the vessel, and preparation for gastrulation as evidenced by flattening at the lower pole may be recognised.

The flattened portion is now a little thicker and darker than the general blastula wall, partly because the latter has been increasing its surface area. The whole larva is elongating in the axis which has been termed vertical up till this stage, but may now be called antero-posterior. The anterior end is also becoming dome-shaped and distinctly wider than the posterior flattened one where gastrulation is about to take place. For movements see p. 237.

Archenteron and Mesenchyme.—The archenteron grows inwards as a narrow tube, the blind end of which projects into the blastocœle for about half the length of the larva. So far, no mesenchyme cells have been set free into the blastocœle. But now the blind end of the archenteron expands slightly, its cells proliferate, become clearer

* In *A. rubens* yolk-polarity is not so marked that the ova exhibit a compelling tendency to rest with that side uppermost from which the polar bodies were extruded, and to which the ripe nucleus lies nearest. However, one can detect some little preference for this position of equilibrium both before and after segmentation has begun. In any case, comparison with other ova, in particular with those of *Solaster endeca* (29, p. 10), which have plentiful yolk and in which the yolk pole is much the heavier, justifies the employment here of the convenient terms vertical, horizontal, upper, lower, etc.

and less regular, and many of them proceed to wander as stellate corpuscles in all directions, forwards, backwards, dorsally, ventrally, and to the sides. This is the principal period and place of origin of the mesenchyme, and produces the connective-tissue elements in general as well as the muscular elements for the body wall and for the œsophagus. The strands which pass downwards to join the epiblast of the stomodæal pit are referred to on p. 231. The upward and backward proliferation of cells provides the extensor (dorsal flexor) muscles of the back (p. 241), and probably also the cell or cells from which the dorsal sac arises at a much later period (p. 246). It seemed to me that a few mesenchyme cells also took origin at the present stage from the archenteron farther back, especially just internal to the blastoporic lip, and thus contributed to the tissue surrounding the posterior part of the stomach, the intestine, and the adjacent portions of the body wall.

Stellate mesenchymal cells are given off from time to time at later stages by the walls of the enterocoelic sacs. Occasionally indeed, especially at the anterior ends of the sacs, several cells become constricted off together, so as to enclose for a time a small isolated portion of the sac-cavity, before they separate completely from one another.

A small body, not absolutely constant in its occurrence, but having important homologies, arises later from the entoderm of the stomach and is referred to on pp. 233-234.

As regards the origin of the earliest mesenchyme in Asterids, the above description agrees with that of METSCHNIKOFF for *Astropecten* (65) in not recognising any special pole cells as being the parent cells of the tissue in question. The lateness of origin of the mesenchyme in *A. rubens* is also in harmony with the chief data available for other starfish. As early as 1863 HENSEN (42, pp. 243, 364) stated that the blastula of *A. rubens* contains no connective-tissue elements in its cavity, and that these only begin to be formed from the bottom of the archenteric sac after gastrulation. AGASSIZ (1) did not particularise regarding the origin of the tissue in question (*A. forbesi*), but his figures do not show its presence in the late blastula or early gastrula. In *Astropecten* METSCHNIKOFF (64, 65) describes the origin of the mesenchyme as being delayed till after gastrulation. MACBRIDE (55, p. 345) states that there is no mesenchyme in *Asterina* immediately after gastrulation has taken place, but that the formation of this tissue from the endoderm commences vigorously thereafter. In *Cribrella*, MASTERMAN (60, 381) finds that there are practically no cells between epiblast and hypoblast at the end of gastrulation. In *Solaster endeca* (29, p. 13) I noted that while a few stellate mesenchymal cells are present during gastrulation, the great bulk of the mesenchyme originates later, chiefly from the anterior portion of the archenteron.

There is thus a very considerable body of evidence that in Asterids generally the production of mesenchyme is delayed. Its early appearance in Echinoids and Ophiuroids, is recognised as probably related to the early formation of the calcareous larval skeleton.

GREEF (37, 1876, p. 35), FIELD (23, p. 108), and RUSSO (79) give a different account from the foregoing, the two former stating that mesenchyme production begins before gastrulation in *A. rubens* and in *A. vulgaris* respectively, while RUSSO (*A. glacialis*) describes the formation prior to gastrulation of an abundant temporary mesenchyme which afterwards breaks down and disappears, supplying gelatinous material for the blastocœle and thereby serving to nourish the larva. I have often seen such "mesenchyme" in *A. rubens* but always as I believe in abnormal or unhealthy larvæ. It certainly is no

longer evident in the more advanced stages, for the reason that such stages are never reached by the specimens which had it in quantity as young larvæ. We may add that *RUSO* (*loc. cit.*) describes segmentation as occurring in such a way that the set of larger cells gives rise to the dome of the blastula, while the part invaginated in gastrulation is derived from the smaller cells.

V. CHANGE TO THE BIPINNARIA.

Change of Shape.—The archenteron bends slightly towards the future ventral side, and the posterior end of the larva becomes bevelled in such a way that an acuter angle is formed at its postero-dorsal than at its postero-ventral edge. The blastopore also migrates from its original postero-median position towards the ventral side.

Stomodæum.—Meantime a pit (the stomodæal pit, see also p. 231), lined by columnar cells and having a prominent anterior lip, appears a little in front of the middle of the ventral surface. Behind and to the sides of this pit, the body wall becomes slightly depressed or dimpled inwards, while a compensating hump appears dorsally and in front. The depressed portion indicates the future circumoral field, outside of which in a very short time afterwards the track of the ciliated band can be made out (p. 232).

The Enterocœles.—As was stated on p. 227, the blind extremity of the archenteron becomes expanded at the end of gastrulation and buds off mesenchyme. The expanded part* then grows backwards on each side as a small hollow sac, and soon the two sacs become constricted at their necks and separated off. They are thus rightly to be described as arising in the form of a pair of cavities. However, it must not be forgotten that both take origin from a common modified portion of the archenteron, the walls of which have also produced the greater part of the mesenchyme. Having separated off, the sacs appear to travel backwards. This is partly through migration and partly owing to greater growth in length of the anterior half of the larva. Not infrequently at first, the left sac is slightly the larger. The sacs usually become separated very shortly before the mouth opens into the gut. According to *AGASSIZ* in *A. forbesi* (1, Plate 2, figs. 7, 10), and *GOETTE* in *A. glacialis* (32), the converse condition obtains. In *Porania pulvillus* it seemed to me that the two processes occurred at practically the same time. *FIELD* (23, p. 109) has called attention to considerable variation, as regards priority, in the larva of *A. vulgaris*.

* That mesenchyme formation and enterocœle formation are not essentially different is rendered probable by the above and also by the following analogous data relating to Echinoderms or their near allies. (1) In *A. rubens* (p. 246), the dorsal sac takes origin from mesenchymal cells, while in *Asterina*, *Cribrella*, and *Solaster* it has a direct enterocœlic origin (see p. 247); (2) *DAVIDOFF* (14) in his regeneration experiments found that the pericardial sac in the Enteropneust *Ptychodera minuta*, Kow., usually arose from the proboscis cœlom, but sometimes from mesenchyme; (3) Instances are noted in this paper (p. 228) where small cavities become constricted off from the enterocœle and provide mesenchyme; (4) In *A. rubens* and *Porania* a rudimentary posterior enterocœlic outgrowth gives rise to mesenchyme, while in *A. glacialis* the same outgrowth forms a small cœlomic vesicle (p. 233).

The Hydropore.—The left enterocœle grows at first more rapidly as a rule than the right one, and it sends out a hollow process tipped by two or three cells dorsally to unite with the skin to the left of the middle line almost opposite the junction of stomach and œsophagus. At the place of contact the epiblastic cells become thickened, but one cannot speak of an invagination of epiblast at this point such as occurs in *Asterina* (55, p. 347) and *Solaster* (29, pp. 14, 26). The difference is probably due to the very much smaller size of the *Asterias* larva at the present stage. However, since the pore-canal lumen afterwards appears in the epiblastic thickening as well as in the cap of cells before mentioned, the final result is the same in so far that the pore-canal at its outer end is lined by epiblast.

Variations.—The following variations of the above processes are of no little interest: (1) Origin of the two sacs by a single outgrowth; (2) formation of a right as well as a left hydropore; (3) persistence of a stalk connecting one or both enterocœles with the œsophagus.

(1) *Single Enterocœlic Outgrowth.*—This is a rare occurrence in *A. rubens*. The single pouch is elongated transversely or else horseshoe-shaped with the concavity directed backwards, and it comes off approximately in the middle line. It soon divides up into right and left sacs, the left being usually the larger and alone acquiring a hydropore. As a unique occurrence, I have noted a hydropore formed exactly in the mid-dorsal line and opening into the middle of a single crescentic enterocœle. GOETTE has put on record the occurrence of several similar variations in *A. glacialis* (32), and indeed irregularities of the kind appear to be more common in the latter species than in *A. rubens*. In the case of *Porania pulvillus* which I reared from an artificial fertilisation to the brachiolaria stage, the two sacs still communicate with one another, in over 50 per cent. of the larvæ, after their separation from the archenteron, and are accordingly to be described as arising by a single evagination.

Double Hydropore.—A tendency to the formation of two hydropores exists in *A. rubens*, as in other starfish and in Echinoderms generally. The strength of the tendency varies within wide limits in different broods of eggs. It is manifested most commonly in the following modified form. The right as well as the left enterocœle sends up a pocket towards the ectoderm, and this pocket shows at its tip a little clump of cells smaller than on the left side, and either actually coming, or almost coming, into contact with the ectoderm. The corresponding ectodermal thickening may not appear at all, or may be extremely slight. I have come across a culture (*A. rubens*) in which 10 per cent. or more of the larvæ showed this condition, and in one out of every three or four of such larvæ a right hydropore and hydroporic canal were ultimately formed. Occasionally the right side was absolutely symmetrical with the left as regards hydropore and hydroporic canal. An excellent example 15 days old is shown in Plate 18, fig. 4. Looking at this figure, one can hardly escape the conclusion that the cœlomic region on the right side into which the right pore canal is opening must be homologous with the correspondingly placed left cœlomic region connected with the left pore-canal. This point has an important bearing on the homologies of the hydrocœle (p. 275). However, I have not yet succeeded in keeping a double-hydropore larva under observation up till the time when the hydrocœle is marked off.

All the double-hydrocœle larvæ (p. 275) which were obtained had only left pore-canals, although in other respects their right and left sides were entirely symmetrical. As illustrating the variable incidence of double hydropore, it may be added that, all through, cultures of *A. rubens* during 1911 provided greater numbers of double-hydropore larvæ than those of 1912. In 1913 the proportion of double hydropores which appeared among larvæ from eggs spawned and fertilised naturally in the tanks was approximately 5 per cent.

Double Hydropore in A. glacialis, Porania, etc.—It was mentioned above that *A. glacialis* shows irregularities in the mode of separation of the enterocœles. This species also shows a very high

proportion of double hydropores. Alike in 1911 and in 1912 I have come across cultures exhibiting the condition in the complete or the modified form (see above), in at least 70 per cent. of the early larvæ, while later (14th day) one out of every three larvæ had symmetrical right and left openings. We may say therefore that double hydropore is normal for a large proportion of the early larvæ. The right hydropore and pore-canal gradually atrophy, as was described by FIELD (23, p. 111) in *A. vulgaris*. Almost as large a proportion of double-hydropores appeared in my cultures of *Porania pulvillus*, the subsequent history being the same. Out of very large numbers of early larvæ of *A. rubens*, *A. glacialis*, and *Porania* examined by me, I have only noted a single instance, and that in *Porania*, where the right hydropore alone occurred.

Neither GOETTE (32), RUSSO (79), nor DELAGE (17), who have all worked with *A. glacialis*, mention the occurrence of double hydropore. MORTENSEN (73, pp. 5, 6) noted the very frequent presence of the condition in his early larvæ of this species but believed it to be abnormal. In *A. vulgaris*, according to FIELD (23, p. 111), the condition is normal for early stages. MACBRIDE (55, p. 369) has described a larva of *Asterina* with a pair of hydropores and a left hydrocoele as well as two right hydrocoele rudiments. In *Cribrella* (60) and *Solaster* (29) doubling of the hydropore has not yet been put on record. However in these species the hydroporic canal although opening to the left side internally has its external aperture on the right side from the first, this aperture having apparently undergone early shifting towards its final aboral position. Complete bilateral hydroporic symmetry whether original or homœotic (imitative) in character is thus rendered impossible. A double-hydrocoele *Ophiothrix* larva described by MACBRIDE (56, p. 578, Plate 36, fig. 53) had two pore-canals, but in a similarly malformed pluteus of *Echinus* there appears to have been only a single hydropore (58, Plate 24, fig. 1). MACBRIDE has shown that two hydropores are often if not always present in the larva of *Echinocardium* (59).

Mouth and Œsophagus.—The stomodæal pit has already been referred to. The deepening of this pit and its fusion with the gut take place somewhat suddenly and are preceded by the formation of a connecting bridge of mesenchymal cells which, by their contractility, may have something to do with the rapid indrawing of the floor of the pit. The line of junction of epiblast and hypoblast is close in front of the place of separation of the enterocœlic sacs. For a time there is a slight narrowing at this line, enabling one to say that the junction lies well in from the mouth opening, so that the first fifth or possibly a larger portion of the œsophagus is stomodæal in origin. Not very infrequently, even in relatively late larvæ, the enterocœlic sac on one or both sides is found anchored to the œsophagus by a strand of cells, at the attachment of which there is an outward pouching of the œsophageal wall. The usual site of this pouching is slightly nearer the stomach than the junction of the lowest and middle thirds of the œsophagus. The connection, if it be considered as the remains of the original outgrowth from the archenteron, would entitle us to say that more than a half of the larval œsophagus is stomodæal. On the other hand, it is more likely that the pouching, etc., may represent a middle enterocœlic rudiment appearing as a rare abnormality (*cf.* p. 233).

Stomach, etc.—The constrictions between œsophagus and stomach, on the one hand, and between stomach and intestine, on the other, next appear. Feeding begins, and the stomach expands and becomes globular. Immediately behind it a very short, constricted part, which may be called the intestine, can be made out. This is followed by the longer rectum, the commencement of the latter being indicated

by a slight but constant dilatation on the side which is folded towards the stomach (Plate 18, fig. 2).

Formation of the Ciliated Bands.—The blastula and gastrula are richly covered with long cilia which appear as minute, very faint dots when viewed directly from above. Contrary to the statements of authors (LANG, 49, vol. 2, p. 507 ; LUDWIG, 54, p. 634 ; SEMON, 86, p. 19 ; FIELD, 23, p. 112 ; DELAGE, 16, vol. 3, p. 28), this ciliation is not now lost at any part, though it becomes reduced over certain areas and increased on the intervening tracts. The difference begins to be evident at the time of formation of the mouth and is associated with a massing together of epiderm along the tract lines, which has to do with changing the shape of the larva, and helps to produce the oral depression as well as to thicken the tracts and accumulate cilia on them, while leaving the intervening areas more sparsely ciliated and provided with a thinner epiblastic wall. As they first appear, the tracts in question are—(1) a loop in front of the mouth almost coronally disposed, enclosing the preoral field and losing itself posteriorly on a quadrate area with persisting rich ciliation and rather numerous gland cells ; and (2) an oblique loop also merging posteriorly into the area in question and passing therefrom downwards and backwards in front of the vent. The best marked portions of these loops are where they pass transversely across the ventral surface. Next, on each side, the dorsal ends of the loops unite, the quadrate area meantime becoming dumb-bell-shaped, but still for a brief period reproducing the typical auricularian form by intervening between the tracts of opposite sides which are here a little broader, but less definite than elsewhere. Next occurs union of the tracts in question behind the preoral field and this is slowly followed by division of the united portion into anterior and posterior parts, thereby isolating the preoral from the postoral ring. This last stage is reached, as a rule, about the 10th or 12th day. We may note again that over the intervening areas (preoral, postoral, and circumoral fields) the cilia, though fewer in number, are not reduced in length, adding that throughout the circumoral field they serve an important food-gathering function (p. 240). The ciliation of the general surface of the young starfish at metamorphosis is directly derived from that of the larva.

Apical Plate.—At first, as the blastula changes shape, the lateral walls expand more quickly than the dome, and accordingly the middle of the latter for a very brief period appears to be relatively thickened and well ciliated (*cf.* AGASSIZ, 1, Plate 1, figs. 26, 28). This appearance is entirely transitory (*cf.* AGASSIZ, 1, later figures), and does not, I think, entitle us to speak of a sensory apical plate in the gastrula of *A. rubens* larva as FIELD does in the case of *A. vulgaris* (23, p. 113). Later, there is no plate-like area enclosed within the circuit of the preoral ciliated ring, the only structure that could deserve the name being the quadrate antero-dorsal area above referred to from which the ciliated bands diverge. No doubt, this area corresponds with the region in which the apical sense-organ of the *Tornaria* is placed, although in the young *Asterias* larva this area is not apical

but antero-dorsal. Thus the question may be raised whether the sense-organ in *Tornaria* is not primarily supra-œsophageal rather than apical in position. While the latter position could be interpreted as indicating immediate trochophore affinities in the larva of the common ancestor of Balanoglossus and Echinoderms, the former would agree with certain other lines of evidence which make it probable that this and many of the larval characters common to Balanoglossus and Echinoderms are referable back to characters present in the adult bilateral ancestor of both.

In *Solaster endeca* the epidermal thickening which I described as probably nervous is placed antero-dorsally (29, p. 47). Here, the ciliated bands being absent, we have not their guidance as to its exact position, but later by referring to the brachia (the first of which in *A. rubens* marks the anterior limit of the preoral ciliated band, p. 235) we can see that the thickening in question must lie behind the preoral field.

Rudiment of Posterior Enterocœlic Outgrowths.—Towards the 6th day, that is about a day after the mouth opening is completed, in very many of the larvæ, there may be recognised a minute solid cell-mass dorsally on the left side opposite the middle of the stomach. This mass arises by proliferation on the part of hypoblast cells in the stomach wall. It becomes separated off (7th or 8th day) and lies in the blastocœle between stomach and epiderm. In most cases it breaks up into mesenchymal cells (9th and 10th days) which soon cease to be recognisable. Occasionally, in part at least, it joins the wall of the left enterocœle which is now beginning to extend backwards. In one instance I saw the mass still retaining its connection with the stomach wall, after it had linked on to the left enterocœle. Rarely a body of similar origin and nature appears on the right side, and still more rarely a single median dorsal mass replaces both.

The same structure can be recognised in the development of *A. glacialis*.* Indeed, I first observed it in this species three years ago. In *Porania pulvillus* the mass is more definite and constant than in *A. rubens* and *A. glacialis*, and occurs in the majority of instances on the right as well as on the left side, or is even larger on the right side than on the left. These are all the starfish with indirect development I have yet had the opportunity of studying.*

We have here, I think, rudiments of a paired posterior enterocœlic outgrowth, which in the common ancestor of Balanoglossus and Echinoderms gave rise to the cœlom of the body or trunk. At present, in the starfishes named above, this rudiment takes no part, or only a small part, in the formation of the wall of the posterior cœloms, but it still retains the function of producing mesenchyme.

* In a culture of *A. glacialis* made this year (1914) the posterior outgrowth was found to be constant on the left side, and it expanded (10th to 13th days) to form a perfectly distinct vesicle, which became applied to the posterior aspect of the left main enterocœle, and finally (15th day) fused with the latter cavity. On the other hand, the larvæ of *Luidia*, a culture of which was kindly sent to me by Dr. E. J. ALLEN, from Plymouth, do not appear to exhibit traces of the posterior outgrowth.

MORGAN (68, p. 413) describes the cœlom of the trunk in his New England *Tornaria* as arising posteriorly by cell-proliferation from the entoderm of the gut at a relatively late stage after the different regions of the larval gut have become differentiated. On the other hand DAVIS (15) states that in *Dolichoglossus pusillus* the formation of the trunk cœlom occurs through backward extension of the anterior cœlomic sacs. It is perfectly possible that both accounts are correct and if that is so, the former (MORGAN'S) account will exemplify an ancestral tendency, making for independent, *i.e.*, metameric, middle and posterior cœlomic formation. The tendency may be recognised as effective on both sides of the body in MORGAN'S *Tornaria*, in BATESON'S *Balanoglossus* (2), probably also in *Cephalodiscus* (HARMER, 39A) and, as regards the posterior cœloms, in *Antedon*. Among starfishes, *Solaster* (29) and *Cribrella* (60) are instances in which, as I here suggest, the tendency has been effective *on the left side* and as regards the greater part, if not the whole, of the (larval) posterior cœlomic cavity (future hypogastric cœlom), though MASTERMAN'S views would receive support were it shown to be operative on the right side as well. Conversely DAVIS'S description (15) may well illustrate an opposing tendency towards backward extension on the part of the anterior cœlomic vesicles, an extension which has become established as the recognised source of the posterior cœloms in *Dolichoglossus*, in the great majority of starfishes, in Echinids, in *Synapta* (85, pp. 183, 195) and in *Ophiothrix* (56, p. 582). In *Ophiura brevispina*, if GRAVE'S account (36) be substantiated (his material as he says himself was deficient in amount), we have an instance in which all the right cœlomic elements arise from an anterior vesicle, while on the left side not only does the *l.p.c.* take origin posteriorly, but by means of a forward extension it provides the hydrocœle as well.

MACBRIDE in 1896 (55, p. 397) proposed the term Protocœlomata for the ancestral stock of Echinodermata, Enteropneusta, and Chordata, the essential feature being that the cœlom was divided into three parts on each side, of which the most anterior were usually fused. Somewhat later, MASTERMAN suggested the term Archicœlomata for a similar group, and he also added to their characters (see 60, p. 404) the possession of a "central cœlom," the pericardium. We must adopt the first term both on grounds of priority and because archicœle is already in use with another meaning. It will be seen that the views I have expressed above, *i.e.*, the postulation of a potentially separate or metameric origin for the three cœloms, constitute a very natural extension of the essential characteristic of the Protocœlomata* to the ontogenetic history of the descendants of the group.

Here the Chordata are not specially under consideration, but it will readily be understood that certain important features in the development of their cœlomic cavities, *e.g.*, the independent origin of the head-cavity in *Amphioxus*, may receive a comparatively simple explanation along the lines indicated above (*cf.* Masterman in 'Proc. Roy. Soc. Edin.,' vol. 22, pp. 270-310).

VI. THE BIPINNARIA AND BRACHIOLARIA.

(a) *External Features* (Plates 18-20, figs. 1-11).

M. SARS, to whom we owe the term bipinnaria, at first conjectured that the young starfish was parasitic on the *Bipinnaria asterigera* which he described (80, p. 37). Then, in 1844 (81, p. 176), he stated that these bipinnariæ would probably prove to be larval starfish provided for the time being with a large swimming organ. KOREN (46, p. 348) had expressed the same view in 1842, and in 1847 he and DANIELSSEN (46) gave a lively description of the bipinnariæ, stating that the young starfishes became separated from them and then crawled away on their own account. This last point has recently been confirmed by M. and C. DELAP (19, pp. 153-4). JOH. MÜLLER gave an account of other bipinnariæ (74), and also first named and described the brachiolaria and recognised it as a starfish larva (74, 1848). We can be certain that some of his specimens belonged to *A. rubens*, as probably also did the *brachina* of which P. J. v. BENEDEEN provided an account a little later (5). SARS (82) next described as new a brachiolaria

* The term Protocœlomata is used here strictly in the sense indicated, and not with the wider meaning afterwards applied to it by MACBRIDE, in his account of the development of *Ophiothrix* (56, p. 594).

which seems, without doubt, to have been that of *A. rubens*. It was believed that all bipinnariæ and brachiolariæ resembled *Bip. asterigera* in throwing off the larval swimming organ, etc., at metamorphosis; and WYVILLE THOMSON, reviewing the subject in 1863 (90), gave it as the accepted view that this organ was simply an embryonic appendage not destined to be included in the body of the adult. HENSEN (42) showed that the bipinnariæ of Kiel Harbour (almost certainly belonging to *A. rubens*) became brachiolariæ, and later attached themselves before becoming starfish, but he did not state in so many words that no parts were thrown off. GREEF (37, 1876, pp. 34–37) managed to rear bipinnariæ and brachiolariæ of *A. rubens* from artificial fertilisations, but did not succeed in obtaining the stages of metamorphosis. AGASSIZ (1), from cultures and plankton material, described larval and post-larval stages of *A. vulgaris* and *A. forbesi*, adding a full and beautiful series of illustrations. He believed that nothing was lost at metamorphosis, and that the whole larva was utilised one way or another. METSCHNIKOFF came to the same conclusion in the case of the bipinnaria of Spezia (63, p. 46), a larva which apparently undergoes metamorphosis without fixation (see also p. 255).

MORTENSEN (71, p. 5) standardised the nomenclature for bipinnariæ in general, and figured and described the bipinnaria and brachiolaria of our species. The notices of larvæ by METSCHNIKOFF (63, 64), BURY (8, 9), GOETTE (31), SEMON (86), and FIELD (23) are chiefly of importance from the point of view of internal structure, but certain features of external form, particularly in regard to the development of the ciliated tracts, are emphasised by the two authors cited last. The papers of DELAGE (17, 18) on rearing parthenogenetic larvæ of *A. glacialis* should also be referred to here. Although not primarily dealing with form and structure, they provide some useful data regarding the appearance and habits of the larvæ at different stages, and mention the shrinkage and absorption of the preoral lobe, and the fact of fixation at metamorphosis.

Processes.—The growth of the bipinnaria, and its change to the brachiolaria, as well as the gradual development and final proportions of the ciliated processes, brachia and sucker will be followed from the illustrations on Plates 18–20, particularly from figs. 5–11. Using MORTENSEN'S (71, pp. 6–7) terminology, we distinguish at such a stage as is shown in fig. 10, (1) *belonging to the preoral band*, the preoral process (paired), and the three brachia; (2) *belonging to the postoral band*, the postoral process (paired), the posterior lateral process (paired), the posterior dorsal process (paired), the anterior dorsal process (paired), and the median dorsal process (single). It will be convenient also to apply the term “circumoral field” (pp. 229 and 240) to the area which lies between the preoral and postoral bands.

The paired processes above named are represented in the holothurian auricularia by blunt lobes or lappets. In addition, the auricularia has a middle dorsal lappet (paired) opposite the region of the mouth. It is of interest to note that this lappet is represented by a distinct fold without a process in the late bipinnaria and brachiolaria of *A. rubens*. In the larva of *Porania* the fold in question is relatively better marked and more sharply defined, though still unprovided with an outgrowing process. It can be seen in MORTENSEN'S figures (73, figs. 3, 4) of the four weeks old bipinnaria of *A. glacialis*.

The longest of the processes are the paired postero-laterals, and these also exhibit the greatest power of movement. The unpaired median dorsal is the shortest, and, indeed, is not infrequently little more than a stump (see p. 236).

The brachia are hollow, containing prolongations from the preoral cœlom. The anterior brachium, as it grows out (25th day), pushes in front of it the extreme apex of the preoral ciliated band, which thus comes to travel up one side of the brachium

in question and down the other. The same thing happens in the case of the other two brachia a short distance further back. In passing from these brachia to the anterior one, the band runs on either side of the developing sucker. Two papillæ occur on each side just internal to this part of the band, one slightly in front of and the other slightly behind the centre of the sucker. Occasionally a third, and even a fourth, papilla are present on one or on both sides, in front of the others. The band is weaker on the brachia and between the median and paired brachia than elsewhere. There is no transverse connection between the bands immediately behind the brachia. The brachia have flat truncated extremities, carrying six to ten papillæ, of which 1-3 are central and 5-7 marginal in position. In the late larva ciliation is lost over the sucker and the tips of the papillæ.

The relationship of the brachia to the ciliated band was left uncertain by JOH. MÜLLER who, in his brachiolaria of Helsingör (74, 1848, p. 96), described the band as crossing from side to side behind the brachia, leaving the latter outside of it. Yet, in his figures (*loc. cit.*, Taf. III, figs. 3, 4) as well as in the text (*loc. cit.*, p. 96), he gives an indication of the true arrangement. HENSEN'S (42) all too brief description is correct so far as it goes. AGASSIZ does not mention the point, although some of his figures, *e.g.*, Plate VIII, fig. 15, show faint lines on the brachia which, no doubt, indicate the band in question. GOTO'S (33) illustrations leave out the band entirely on the brachia. MORTENSEN, in his earlier work (71, p. 45) stated that the *Bipinnaria papillata* (74, 1855, p. 35) alone has the preoral band produced on to the brachia, this condition not being found in *A. rubens*, but, later (72, p. 9), was still the first to give the true description. DELAGE (17) and BURY (8, 9) do not refer particularly to the matter, while text-books generally present the older view. The brachiolaria of *Porania pulvillus* agrees with that of *A. rubens* in the feature under discussion.

Gland Cells.—All round its circuit the peristomal (p. 239) band tends to show cells with small clear vesicles, whether mucoid or chordoid I cannot say. Regarding the distribution of gland cells we have to note that the wall of the late blastula exhibits scattered swollen cells which are probably unicellular mucous glands. In the bipinnaria they occur along the ciliated bands especially at the edges abutting on the preoral and postoral fields. They are present also throughout these areas, but occur very sparingly or not at all on the circumoral field. In the early larva they are numerous on the antero-dorsal area where the ciliated bands meet, and they subsequently form small groups on the apices of the bands when these separate from one another. In late larvæ which are becoming unhealthy the gland cells all over appear to increase in number and size.

COMPARISON WITH OTHER BRACHIOLARLÆ.—An interesting variation was observed in about half of the larvæ from one of the hatching vessels. The variation consisted in absence of the median dorsal process, the body ending bluntly in front. The larvæ were undoubtedly those of *A. rubens*, and Dr. TH. MORTENSEN, to whom I showed them, agreed with me that they allow us to put down as belonging also to this species the brachiolaria of Helsingör, figured and described by JOH. MÜLLER (74, 1848) most, if not all, of which showed the same peculiarity. Accordingly, the *Bipinnaria levis* of MORTENSEN (71, p. 43), founded on MÜLLER'S description, does not need to be retained as a separate species. It may be added that those of my *A. rubens* larvæ which were destitute of a median dorsal process, tended to show an unusually large number of papillæ on each side of the sucker. Exactly the

same condition is indicated in MÜLLER'S illustrations (74, 1848, Taf. III, fig. 2). We may note also that the presence of numerous papillæ on the brachia is correlated with reduction of the dorsal median process in *Porania* (see below), but not in *Bip. papillata*, Mortensen (see MÜLLER, 74, 1854, Taf. IX, figs. 7-12).

A. glacialis.—DELAGÉ'S (17, pp. 36-7) paper, if his specimens may be counted as normal, supplies a differential character for the brachiolaria of *A. glacialis*, namely that the sucker is surrounded by a circle of small papillæ, 14 of which are shown in the illustration appended. Other distinguishing features in this species are the globular swelling with about fifteen separate papillæ at the end of each brachium and the massive character of the preoral lobe, particularly in its dorso-ventral diameter.

A. vulgaris.—As regards the only other fully described brachiolaria of which the species is known, namely that of *A. vulgaris*, there appears to be hardly any character by which one might differentiate it from *A. rubens*. MORTENSEN states (71, p. 42) that there is none. It is barely possible that in reality there is absence or complete reduction of the preoral ciliated band on and between the brachia in *A. vulgaris* (see p. 236). AGASSIZ (1, p. 25) says that the larva of *A. vulgaris* can be distinguished from the brachina of v. BENEDEN (probably belonging to *A. rubens*) by the shortness of the ciliated processes on the latter and the less elongated shape of the whole larva. The first difference is not valid since, as it happens, the brachina in question was not at a late stage, and accordingly did not have its ciliated processes as yet fully developed. The second character is probably present, but not in a sufficient degree to make it of practical use in dealing with preserved material. However, *the position of the papillæ at the sides of the sucker* may afford a feature of differential value for the late brachiolaria. In *A. rubens* the posterior papilla on either side is a very little behind the centre of the sucker, while the next one is in front of this point, and the third, when present, is yet a little farther forward. In *A. vulgaris*, on the other hand, according to AGASSIZ'S description and figures, and according to such of GOTO'S figures as bear on the point, papillæ are present in the same number, but they lie in front of the centre of the sucker.

Porania pulvillus.—The brachiolaria of *Porania* has relatively short ciliated processes, and the brachia are convex, not truncated, at their extremities. Papillæ occur on the sides as well as on the extremities of the brachia, and there is a row of about fifteen papillæ on each side of the sucker extending between the median and the lateral brachia. In late examples the median dorsal process becomes very small or practically absent.

(b) *Locomotion*.

Normal blastulæ rotate round an axis which passes through the middle of the area invaginated at gastrulation. The rotation, in the great majority of instances, is in the dextral or watch-hand direction as seen from the opposite pole, and continues without reversal. Occasionally reversals occur, and in rare cases the changes are rhythmic. Very soon progression is added to rotation, so that the larvæ (36 hours after fertilisation) rise from the bottom and distribute themselves more or less uniformly throughout the hatching vessel. AGASSIZ (1, p. 8) and FIELD (23, p. 109) state that in *A. pallidus* and *A. vulgaris* it is the blastoporic end which leads the way in progression. I have paid particular attention to the point and find that exactly the opposite is the invariable rule in *A. rubens*, *A. glacialis*, *Porania pulvillus*, and *Luidia*.

During the third and fourth days in undisturbed uniformly lighted aquaria, the larvæ frequently show a tendency to arrange themselves in columns within which they move upwards or downwards, and which are probably vortex formations due to the ciliary action of groups of larvæ. At this stage the larvæ are phototropic,

a characteristic which is lost after several days. Until the sixth day or thereby my larvæ kept well up from the bottom of the dish, but thereafter till about the 18th day, they tended to sink. Rotation is still dextral,* and in progression the anterior end still leads the way, describing, as it rotates, a wider circle than the posterior end. The path is thus spiral, and the anterior end often shows, in addition, a characteristic backward swerve which may be so extreme that the larva is continually turning itself right over in its course. The cause is as follows: Everywhere along the ciliated bands the cilia lash backwards. Owing to the shape of the early larva a greater length of ciliated tract lies on the ventral than on the dorsal side of the larval mid-frontal plane. This produces an epicyclic movement which, taken along with spiral progression, gives rise to the swerve above referred to. An abrupt change in the direction of progression also occurs in consequence of the dorsal flexion movements described on p. 241. As the processes of the ciliated band grow out, one begins to find that their cilia are lashing in such a manner as to cause currents of water to flow from the attached to the free extremity of each. This is of importance in locomotion since the posterior end of the larva is now increasing in weight owing to the development of the calcareous plates of the aboral disc. In the perfectly undisturbed condition all the processes tend to droop, and in particular the long postero-lateral pair hang downwards, are stretched out to their full length, and exhibit extremely active ciliation. In this position the cilia combine to keep the larvæ rising slowly upwards in the water, and, if the processes are evenly extended, very little rotation takes place. Such larvæ are exceedingly beautiful and graceful objects. It is usually the very largest specimens which have the longest and most symmetrical arms, and the movements may readily be followed by the unaided eye or with the help of a lens. If the larvæ be touched or shaken they will often bend their ciliated processes, and particularly the postero-lateral ones, rapidly in an upward direction. The cilia on all the processes now combine to push the larvæ downwards (Plate 20, fig. 11), making them sink for short distances with surprising speed. Such fallings occur from time to time without apparent cause, or they may take place should the larva come up to the surface of the water. Simple balancing with little or no rotation or progression may also occur; the ciliated processes being moved gently and gracefully in all directions (Plate 19, fig. 10). A larva may also be observed to employ its processes for oblique, horizontal, or even downward movement. It will thus be seen that the ciliated processes serve alike for progression and for influencing the direction of progression. How far they are individually under the control of the larva one cannot say, but the largest and best specimens spent the greater part of the fortnight prior to metamorphosis in an upright or approximately upright position. However, in many of the larvæ there are differences in the length of the individual processes on either

* MORTENSEN (73, p. 6) makes a statement, difficult to understand, that the larvæ of *A. glacialis*, and of all the other species he reared, rotate round their longitudinal axis always turning to the left.

side, and particularly the right postero-lateral process is frequently much smaller than the left one. Such larvæ move irregularly, and sooner or later find their way to the bottom of the aquarium, where they tend to remain. In the end they seldom proceed to full metamorphosis.

We may note that in his *Brachina*, P. J. VAN BENEDEEN (5, p. 510) described the direction of progression as being always a backward one. The statement is difficult to explain if *Brachina* really belongs to *A. rubens*.

(c) *Mode of Feeding.*

Cilia Employed (see Plate 22, fig. 22).—From its first appearance the stomodæal opening is surrounded by a ciliated border which we may call the peristomal ring (Plate 18, figs. 1–3). Later this border becomes inflected inwards so that it looks towards the buccal cavity. The dorsal part of the ring is broad and well marked from the first and (about the 12th day) becomes apposed to the transverse portion of the preoral ciliated tract, without, however, losing its identity. The ventral portion of the band is well marked in the early larva and forms a shallow loop on the true lower lip. This part appears to have a special function (p. 241), and may be distinguished as the inferior labial loop. The peristomal circuit above described marks the boundary of the original stomodæal pit. Superficial to this a vestibule is added partly through the inflection above referred to and partly through the formation of a deep hollow between the mouth and the transverse portion of the postoral band.

While the whole lining of the buccal cavity and œsophagus is ciliated, we have to distinguish in the latter two special ridges (one on each side) which are continuous at the sides of the mouth with the peristomal ring, and pass backwards therefrom, converging in the floor of the first or stomodæal portion of the œsophagus. They appear to be developed as backward extensions from the peristomal ring. During the first half of larval life, as may be made out by careful examination of serial sections, the ridges in question do not meet ventrally but are separated by a groove. Later the groove is lost and the ridges become continuous, forming the special adoral loop described by SEMON (86, p. 16) as being characteristic of the larvæ of Asterids and of Echinoderms generally. We may call it here the œsophageal ciliated loop to distinguish it from the inferior labial loop above referred to. Relatively the latter is more prominent in the early larva, and the former in the late larva. Indeed just prior to metamorphosis the labial loop is entirely inconspicuous. However, its apex still marks the point at which the peristaltic contractions of swallowing begin. The relations of the various ciliated tracts connected with the mouth are shown in Plate 22, fig. 22. The circumoral area (p. 235) retains its ciliation. The transverse portion of the preoral band is at first well in front of the stomodæal pit, but later its mesial part forms a prominent "upper lip" hanging back over the mouth. The transverse portion of the postoral band is also prominent, giving rise to a well marked shelf between mouth and anus.

It seems advisable for the sake of clearness and on developmental grounds to break up SEMON'S adoral band into a peristomal ring and an œsophageal loop, as has been done in the above description. In any case SEMON'S (86, p. 16 *et seq.*) account of the larval ciliation, which has been generally accepted although FIELD'S (23, p. 114) description is the more correct, requires in my view to be amended in the following points: (1) The general ciliation of the surface of the larva is not lost; (2) the general ciliation of the buccal cavity and œsophagus is not lost; (3) the ciliation of the peristomal ring over the lower lip is not lost; (4) the œsophageal loop (adoral loop of SEMON) is deficient at its apex (that is across the mid-ventral line) during approximately the first half of larval life.

Collecting Food.—The circumoral field or depression (pp. 229, 235) is the great food-gathering area. In advanced larvæ, it forms a complex groove or gutter between the preoral and the postoral ciliated bands on either side of as well as across the middle of the larva. Its cilia, which are long and powerful though not closely set, act from behind, from in front, and from the sides in such a manner as to bring all sorts of particles to the corners of the mouth and direct them inwards under the overhanging "upper lip." Here the transverse portion of the preoral band, being somewhat in-turned, strikes the particles into the buccal cavity, aided in this work by the dorsal and dorso-lateral portions of the peristomal band, the cilia of which lash inwards. Within the œsophagus the entire ciliation including that of the œsophageal loop is towards the stomach, but on the inferior labial loop (p. 239) the cilia act sometimes, if not always, in the reverse direction. Since only the smallest quantity of water is actually swallowed there is naturally a considerable outward central eddy up the middle of the œsophageal funnel. The eddy emerges from the mouth aperture ventrally, flowing over the lower lip.

Feeding.—When the particles brought into the mouth are suitable and the larva is accepting them, the entrance to the œsophagus is kept freely open, the cilia on the œsophageal loop are in full activity, and the particles, often after whirling up and down through coming under the influence of inward and outward currents, pass down the œsophagus and gather quietly in its lower portion where the ciliation is at its faintest. The direct striking action of the long cilia on the œsophageal loop is important here, since by this means particles, which would otherwise be carried away by the central outward eddy, are forced back towards the bottom of the œsophagus. From time to time a bolus of these particles is shot into the stomach by strong œsophageal peristalsis, the orifice between stomach and œsophagus opening quickly and closing afterwards with equal speed. Inside the stomach, the food is churned round through ciliary action. In the case of early larvæ (up till 21st day or thereby) the movement is chiefly in the larval transverse plane, and dextrally (see note on p. 217) as viewed from in front. In older larvæ this becomes obscured since now most of the gastric cilia, except in the pyloric region, lash towards the œsophageal opening causing peripheral currents in this direction while centrally a great compensating backward eddy down the middle of the stomach cavity can be made out. In the pyloric region the ciliation is chiefly towards the pyloric opening. Excreta gather gradually in the intestine and rectum, and from time to time slow evacuation takes place, partly as it

seemed through the action of the cilia lining these tracts, and partly through feeble contractions of the walls, the anus meantime becoming dilated.

Rejection of Particles.—When the particles are not suitable, or the larva is not accepting them, the entrance to the œsophagus is kept narrow, the cilia on the œsophageal loop are inactive, and an outward action on the part of the inferior labial loop reinforces that of the central upward eddy in removing most of the particles brought into the buccal cavity. Accordingly very little finds its way down the œsophagus. The transverse portion of the postoral band also acts at all times as a final sweeper-away of particles emerging from the buccal cavity by the central outward eddy.

Movements causing active emptying of buccal cavity and first part of œsophagus also occur from time to time in normal larvæ, and can readily be induced by irritating the larvæ or mixing unusual ingredients in the water, while in unhealthy larvæ they are often persistent. The action depends on quick and powerful dorsal flexion (extension) of the preoral lobe on the rest of the body, accompanied by contraction of the transverse muscular fibres of the back. The result is to compress the œsophagus and buccal cavity, while the mouth is thrown widely open and the overhanging anterior lip lifted up. Part at least of the contents is forced out and if, as frequently happens, all this is repeated several times, the buccal cavity and the first part of the œsophagus may be completely emptied. Meanwhile the larva looks as if it were making violent efforts at emesis, but reflux from the stomach never occurs. AGASSIZ (1, p. 26) mentioned the movement of extreme dorsal flexion as a “strange habit” in the larva of *A. vulgaris*, but without hinting at its function. The longitudinal muscular fibres of the back were noted by METSCHNIKOFF (63, p. 35), SEMON (86, p. 24) and others. From GARSTANG’S (25, pp. 455–6) description it is evident that in *Bip. asterigera* (or an allied form) the same set of muscle fibres continued further forward effect progression through rhythmically repeated flexion of the median dorsal lobe over the back of the larva.

It remains to be added that feeding continues right up to the commencement of metamorphosis, but is then completely interrupted for a time until the permanent mouth is formed.

(d) *The Enterocœlic Vesicles.*

The two vesicles (p. 229) grow forwards on either side of the œsophagus into the preoral lobe, and backwards towards the posterior end of the body on either side of the stomach. The forward extension is tubular or sausage-shaped, while the backward one is flattened, being compressed between body wall and stomach. In *A. rubens* normally the forward growth takes place at an equal rate on both sides (see Plate 18, figs. 1–6), so that in the end the two cavities meet and unite symmetrically in the middle line within the preoral lobe in front of the mouth. The posterior extension is sometimes quite symmetrical, but usually shows rather greater rapidity on the

left than on the right side. Just behind the hydropore there now appears a notch (fig. 5) marking the formation of a septum which gradually passes through from the dorsal to the ventral side and separates the left posterior from the left middle cœlomic region. Exactly the same feature appears on the right side at the same period or a little later, and cuts off the right posterior from the right middle cœlomic region. Meantime the right and left posterior cavities, especially the latter, after reaching the posterior end of the stomach, begin to curve ventrally following the course of the intestine.

For the sake of brevity we may now designate the right and left posterior cœloms as the *r.p.c.* and the *l.p.c.* respectively. The corresponding middle cœlomic regions are the *r.m.c.* and the *l.m.c.* These two are equivalent morphologically, and while normally the *l.m.c.* alone gives rise to a hydrocœle, in double-hydrocœle larvæ the *r.m.c.* does the same. We must be careful to note that the terms anterior and middle cœloms or cœlomic regions are used here for descriptive convenience and not as indicating separate morphological units (see p. 254).

Ventral Horn of l.p.c.—There next appears the first certain indication that the *l.p.c.* is about to overtop the *r.p.c.* in growth. The former cavity sends (23rd day) a ventral horn across the middle line to the right between the stomach and the rectum (fig. 6). The growing end of this horn expands, and is applied to the wall of the right middle cœlomic region (28th day). A little later the intervening tissue breaks down, and we find the cavity of the ventral horn communicating with the *r.m.c.* (fig. 8). After this has taken place it is no longer possible to tell exactly where the one cavity begins and the other ends, but in any case there is no doubt about the invasion of the right side by the ventral horn of the *l.p.c.*, and later one of the terminal ossicles—that of ray I—appears over this portion of the left body cavity. Meanwhile the dorsal constrictions between the middle and the posterior cœlomic regions on both sides, which have been gradually deepening, are completed (29th day). The *r.p.c.* is the so-called epigastric cœlom, and it remains isolated during the rest of larval life as well as throughout metamorphosis and on into the stages of early growth.

This account of the mode of origin of the right and left posterior cœloms agrees with MACBRIDE'S results for *Asterina* (55, pp. 348-9), BURY'S for brachiolaria (8, p. 72, Plate 7, fig. 27; 9, p. 71) and for *Bip. asterigera* (8, p. 66, *et seq.*), and also with METSCHNIKOFF'S (63, pp. 32-40) and BURY'S (8, p. 414) description of the left cœlomic cavities in their small Mediterranean bipinnaria. Apparently, however, in this last instance on the right side no separation ever occurred (BURY, 8, p. 415), the right anterior and middle cœlomic regions being virtually unrepresented. In any case it is certain that no union of the right and left anterior cœloms in the preoral lobe occurred in these small bipinnariæ, which seem to have belonged to *Astropecten* (66, p. 69), or in the similar bipinnaria described by MÜLLER (74, 1850, Taf. III-V). As regards the *l.p.c.*, GOTO in *Asterina* and *Ast. vulgaris* (33, p. 254) lays much stress on the addition to this cavity of a portion of the *r.p.c.* He describes the transference as taking place by the breaking down of septa and their re-formation along new lines and calls the resulting composite cavity the *secondary left posterior cœlom*. The question is of much interest in view of MASTERMAN'S (60, pp. 396, 414) interpretation of the development of the cœlomic cavities in *Cribrella*. In *A. rubens* I cannot find

evidence of such shiftings of mesentery as GOTO described, and MACBRIDE has stated that they do not occur in *Asterina* (55, p. 348). GOTO himself speaks (33, p. 257) of "the somewhat accentuated tendency to form septa" in the region he is describing. He thought that his secondary left posterior coelom gave rise to the hypogastric cavity, which thus included a right coelomic element. But in *A. rubens*—and this agrees with MACBRIDE's results for *Asterina*—the hypogastric coelom as we find it at the end of metamorphosis is entirely a derivative of the *l.p.c.* (pp. 254, 259). The communication we have been discussing between the right and left coelomic cavities appears to me to be established (like that next described between the *l.p.c.* and the *l.m.c.*) in order to meet a physiological rather than a structural purpose.

We may here note other observed instances in Asterid larvæ of a secondary communication between the ventral horn of the *l.p.c.* and the right middle or, what comes to the same thing, the right anterior coelomic region. Some of AGASSIZ'S (1) figures (Plate 3, figs. 6, 10; 4, fig. 1) indicate the presence of such a canal in the larva of *A. vulgaris*, and on p. 26 he speaks of a *cul-de-sac* of one branch of the water tube passing between stomach and intestine. However, AGASSIZ thought that all the posterior coelomic chambers opened into one another, the septa between them being apparent and not real. A ventral fusion of the right and left coeloms was described by METSCHNIKOFF in the bipinnaria from Spezia (63, p. 36). BURY (9, p. 66) noted the communication in *Bip. asterigera* as well as in Brachiolaria and described its mode of development in the latter (9, pp. 72, 73). GOTO (33, p. 256) found it also in the case of *A. vulgaris*. DELAGE (17, p. 35) in *A. glacialis* speaks of the separation between the right and left splanchnocoeloms, ventral to the stomach, becoming lost in later stages. MACBRIDE (55, p. 350) found the ventral horn of the *l.p.c.* opening secondarily into the anterior coelom in *A. gibbosa*. In *Solaster* (29, pp. 35, 36) the presence of the canal in question was not demonstrated to be constant but its occasional occurrence was noted.

Hydrocoele before Metamorphosis.—The hydrocoele pouches next appear (32nd to 34th day) as thickened out-pouchings of the crescentic margin of the left middle coelomic region. Pouch I* lies dorsally a little in front and to the left of the hydropore, while pouch II is slightly behind this opening. Pouches III and IV project backwards from the posterior convexity of the crescent, while V continues the series ventrally and forwards to the ventral tip of the crescent. III and IV are, by a little, the earliest to appear; next come II and V, while I is very slightly later than these. For stone canal, see p. 256.

Although the left posterior coelom is cut off behind the hydrocoele, since the crescent of the latter follows the curvature of the alimentary canal from œsophagus to anus, it is reasonable to look on the hydrocoele pouches, in spite of their slightly different times of formation, as forming a series in which pouch I is morphologically the most anterior and pouch V the most posterior. METSCHNIKOFF (63, p. 34) long ago called attention to the fact that the true posterior end of the larva is at the anal opening, since the latter is the ventrally shifted blastopore. BURY (8, p. 431) has also expressed the view that the most anterior of the hydrocoele pouches are those between which the hydropore and the stone canal come to lie.

Dorsal Horn of l.p.c.—Meantime the *l.p.c.* has been extending in other directions, and in particular it has grown out dorsally and to the right in the form of a process well known in Asterid development as the dorsal horn of the *l.p.c.* (Plates 18, 19, figs. 8, 10). This horn never acquires a communication with the right middle or right posterior coeloms. However, during the later larval stages it comes to open

* For numbering of hydrocoele pouches and arm rudiments, see p. 276 and text-fig. 1.

secondarily into the left middle cœlom by a passage (fig. 10) situated in the interval between I and II of the hydrocœle pouches.

The presence of this opening may be inferred from AGASSIZ'S (1) description and figures. GOTO (33, p. 252) shows it also, but apparently he believed it to be primary, *i.e.*, a remainder from the original continuity of the cœloms in question. BURY (8, p. 415; 9, p. 65), in *Bip. asterigera*, mentions an opening connecting the dorsal horn of the *l.p.c.* with the anterior cœlom or with the hydrocœle. No doubt this is the same canal, the early tucking off of the hydrocœle being responsible for the descriptive difference. In brachiolaria it is likely that BURY refers to the communication in question when he states (9, p. 103) that the dorsal horn of the left cavity fuses with the axial sinus.* MACBRIDE in *Asterina* (55, p. 350), and MASTERMAN in *Cribrella* (60, p. 392), described the dorsal horn of the *l.p.c.* as forming openings secondarily into the anterior cœlom. In *Solaster* I have mentioned the occasional, or perhaps normal, occurrence of such an opening (29, pp. 35–36). DELAGE'S (17, fig. 2, p. 33) description and illustration speak clearly for its presence in *A. glacialis*. They also indicate (17, fig. 2, p. 33) that there is a dorsal communication between the right and left posterior cœloms. Should this be right, *A. glacialis* is altogether exceptional in exhibiting this latter feature.

We have now to describe the manner in which the rectum and the distal portion of the intestine come to be enclosed within a cœlomic sheath belonging to the *l.p.c.* The process is illustrated in Plates 18–20, figs. 7, 9–11. Hollow folds grow round on the right and left sides of the rectum from the ventral horn of the *l.p.c.*, and these meet and fuse, absorption of the intervening walls subsequently taking place as in the case of amniotic folds, except that there is no amnion cavity, the rectum filling its place. To begin with, the section of rectum enclosed is comparatively short, but in the late larva nearly half of the intestinal tube is surrounded by the *l.p.c.*, the remaining moiety, *i.e.*, that next to the stomach, lying in the mesentery between *l.p.c.* and *r.p.c.* For pharyngeal cœlom, see p. 259.

Variations in above Processes.

1. More rapid growth anteriorly on the part of the left than of the right cœlomic vesicle.
2. Fusion of ventral horn of *l.p.c.* with right cœlom prior to complete separation of *r.p.c.* from *r.m.c.*
3. Failure of ventral horn of *l.p.c.* to unite with *r.m.c.*, a failure frequently followed by double-hydrocœle formation.
4. Septa in right middle cœlom.

1. Parallels to this variation appear in the development of other Asterids. In *A. glacialis*, GOETTE (32) describes the left pouch as being often a good deal larger than the right one at the time of its separation from the archenteron. RUSSO (79, Tav. II, figs. 22–24) illustrates a similar condition in slightly older larvæ of the same species, but without mentioning the point in his letterpress; while DELAGE, in his work on the parthenogenetic development of *A. glacialis* (17, p. 34), describes the left cœlom as growing forward so much more rapidly than the right one that the whole of the cœlomic space within the median

* Apparently, however, in the small bipinnaria described by METSCHNIKOFF (63, pp. 32–40) and examined also by BURY at Naples (8, p. 415), no communication existed between the hydrocœle and the *l.p.c.*

portion of the preoral lobe is a derivative of the former. METSCHNIKOFF, in the description of his small bipinnaria from Spezia (63, p. 34, Taf. XI, figs. 4, 6; see also MÜLLER, 74, 1849, and BURY, 8, p. 414), provides us with an example in which left-sided cœlomic preponderance is still more striking. In this instance the right middle cœlomic region is extremely small or possibly absent (BURY, 8, p. 415), and never joins up with the corresponding left cœlomic region in the preoral lobe, while the *r.p.c.* has the form of a flattened disc, which is no doubt the epigastric cœlom. A bipinnaria figured by GOETTE (31, Plate XXVII, fig. 46) shows the same features. However, according to AGASSIZ'S (1) and FIELD'S (23) illustrations and descriptions, *A. vulgaris* and *A. forbesi* agree with *A. rubens* in the symmetrical forward extension of the two anterior cœloms. To these I am able to add the pin-cushion starfish *P. pulvillus* (O.F.M.).

2. Occasionally specimens are found in which all the cœlomic regions communicate with one another, the *l.p.c.* opening by a narrow passage ventrally into the *l.m.c.*, the latter being continued forward into the *l.a.c.*, which in turn communicates freely in the preoral lobe with the *r.a.c.*, and thus also with the *r.m.c.* and the *r.p.c.* According to BURY (9, p. 65) the condition just described is found at a certain stage in *Bip. asterigera*.

3. The stage at which the *l.p.c.* should unite with the *r.m.c.* is a somewhat critical one in the development of the bipinnariæ. Many larvæ, though otherwise apparently healthy, fail to effect the union. Of these, the majority cease to differentiate further and finally die off. However, in some cases, the *l.p.c.* unites instead with the *r.p.c.* between rectum and stomach, and the *r.m.c.*, now left with the same relations as the *l.m.c.*, differentiates like the latter cavity, giving rise to the double-hydrocœle condition (p. 275).

4. Sometimes a separate cavity is cut out from the right cœlom at the junction of its middle and anterior regions, or a single transverse septum crosses the cavity at this part. In 1911 the only *A. rubens* larva which I succeeded in rearing to the full brachiolaria stage exhibited the first-mentioned condition. Experience shows that both conditions, like other abnormalities, appear with widely different frequencies in different broods of larvæ. The subsidiary divisions in question have nothing to do with the formation of the dorsal sac. Probably they have their origin in the circumstance that the region in which they occur, while having potential equivalence to a (right) hydrocœle, normally undergoes reduction.

Cœlomic Circulation.—The archenteron is ciliated from the first, as also is the stomodæal pit. As regards the lining of the enteric sacs in *A. rubens*, I have seen evidence of ciliary action on the sixth day. AGASSIZ (1) speaks of particles being swept into and out of the sacs during their formation. When the stage shown in Plate 19, figs. 9, 10, is reached, particles are usually carried in the following circuit—forwards through left middle and anterior cœloms to preoral lobe, then across to right side and backwards along right anterior and right middle cavities, then to the left across the mid-ventral line into the *l.p.c.*, and from there into the left middle cœlom again. Minor streams enter each brachium passing up one side and down the other. Not all the cilia in the cavities named lash in the direction required for this circuit. There are eddies at various points but the general result is as indicated above. Regarding the hydroporic canal I have not been able to make out the direction of movement, but in the adult, although there is strong downward ciliation within the stone canal, the pore-canal cilia by themselves cause weak outward currents (p. 270).

LUDWIG has stated that there is an inward current in the pore-canal of auricularia (53, p. 379), but on the other hand BURY (8, p. 421) seems to have found the opposite in brachiolaria and other larvæ (see p. 271).

MÜLLER in his brachiolaria of Helsingör observed streaming of particles in the brachia (74, 1848, p. 97) up one side and down the other. P. J. VAN BENEDEN noted that particles were swept about in various directions in the cavities of his brachina (5, p. 512). In the late larva of *A. glacialis*, DELAGE (17, p. 35) describes a circuit of particles like mine but apparently in the converse direction and passing from left to right through a dorsal communication between the left and right cœlomic cavities (see p. 244).

No doubt a physiological purpose is served by these currents. In the perivisceral cavities of the adult there is definiteness of ciliary action over particular areas. A fuller account of the adult perivisceral ciliation is reserved for a separate paper, but, meantime, we may note as characteristic of *A. rubens*: (1) outward or centrifugal action of the cilia on parietal lining of disc aborally, and on roof of arms at and near the middle line; (2) centripetal action along ventro-lateral angles of the rays and bases of the interbrachial septa; (3) aboral-ward action within the axial sinus (p. 270); (4) aboral-ward action on outer aspect of stomach and pyloric sac. The subsidiary details are all towards ensuring constant circulation and mixing of the cœlomic fluid.

The same general principle applies to the ciliation of the different portions of the alimentary tract if one adds a definite sweeping of particles into and along the intestine and rectum.

The lining of the perihæmal cavities (external oral, radial, aboral circular, and genital), as well as that of the internal oral circular sinus, is feebly ciliated. The ciliary action is strongest on those parts of the lining which clothe hæmal tissue.

VII. DORSAL SAC OR MADREPORIC VESICLE.

Origin.—In serial sections of larvæ about 25 days old, the dorsal sac appears as a small horizontally flattened vesicle (Plate 23, fig. 24) on the dorsal aspect of the larva above the junction of œsophagus and stomach, immediately to the right of the pore-canal and often connected with the wall of the latter by a cellular strand, but unconnected with the right cœlomic cavity. The vesicle, while usually mesial in position, is not unfrequently to the left of the middle line. These points can also be made out, but not so definitely, in whole specimens examined either alive or after fixation and staining. At a slightly earlier stage the vesicle is represented by a clump of two or three cells (Plate 23, fig. 23), and still earlier often by a single cell close under the epiderm in a corresponding position, but rarely linked up with the wall of the pore-canal. What is the origin of these cells? Having cut and examined a great many series of sections and paid close attention to the living larvæ, I can give no other answer than that the cells in question are probably budded off from the archenteron as early as the period at which the general mesenchyme is formed. At this period cells arise singly or several together, dorsally between the stalks of the enterocœles, and although it is impossible at

the time to identify any particular cells as those which will give rise to the dorsal sac, yet sections of larvæ at all later stages till the vesicle is unmistakable, show one or two mesenchyme cells already near the requisite position, and fail to demonstrate a derivation of these cells from adjacent pre-existing structures. I therefore believe that in *A. rubens* the dorsal sac has its origin in the form of one or more cells indistinguishable from mesenchyme arising dorsally at the same time as the general mesenchyme, and from that expanded and modified region of archenteron which produces the mesenchyme and the enterocœlic sacs. Thereafter the cell or cells in question remain without further development, close to the dorsal ectoderm or to the pore canal, until about a third of the entire larval life has passed.

The sac increases in size, and as the adjacent cœlomic cavities have also been expanding, it comes into contact with the *r.m.c.*, the dorsal angles of the *l.p.c.* and of the *r.p.c.*, and lastly with the *l.m.c.* From all these cavities, however, it remains distinct alike during larval life, throughout metamorphosis, and in the adult condition, when it is known as the madreporic vesicle. In the late brachiolaria the sac measures 0.2 mm. in length, and 0.1 mm. in breadth, and thus bears no inconsiderable proportion to the total size of the larva. Meantime, the basal skeletal plates have appeared (see p. 266), and of these the earliest formed and largest overlies the dorsal sac. At metamorphosis this plate will be recognisable as inter-radial I/II. In sections, the floor of the sac is seen to be slightly thicker than the roof, probably owing to the presence of muscular fibres. The tissue immediately under the sac is spongy in character.

Data regarding the origin of the dorsal sac in Asterid larvæ are provided by BURY (8, p. 74), MACBRIDE (55, p. 349), FIELD (23, p. 117), GOTO (33, p. 255), MASTERMAN (60, p. 385) and GEMMILL (29, p. 26, 29).

BURY (*A. rubens*) and FIELD (*A. vulgaris*) agree that the sac is of mesenchymatous or schizocœlic origin. The former states that "the pulsating vesicle arises at a fairly early period from a group of cells situated in the middle line over the œsophagus to the right and rather in front of the hydropore. It is certainly distinct from the cœlom in its origin and to the best of my belief during larval and adult life." GOTO (*A. vulgaris*) concluded that the sac arises by an extension of the left anterior enterocœle on the dorsal side of the stomach, but that this extension in the adult is incorporated in the axial sinus while the definitive madreporic vesicle is constricted off from the axial sinus at a later stage. GOTO'S account is, however, unsatisfactory on other grounds and it seems to me that in Plate XXI, figs. 19 and 20, he has mistaken for epigastric cœlom what is really the dorsal sac. MACBRIDE (*Asterina gibbosa*) (55, p. 349), MASTERMAN (*Cribrella*) (60, p. 385), and GEMMILL (*Solaster*) (29, p. 29), make the sac in question arise from the anterior cœlom, in the middle line according to MASTERMAN and a little to the right of the middle line according to the two others. If I am right in tracing back the origin of the mesenchymal cells for the sac in *A. rubens* to the period when the enterocœles are given off, we have a means of substantially reconciling* the accounts of all the authors named except GOTO. *Asterina* and *Solaster*

* Somewhat similar differences appear in the case of the homologous structure in *Tornaria*, viz., the pericardium. Although BOURNE (7, figs. 6-10) and SPENGLER (88, p. 418) have stated that this cavity arises from epiblast, it seems more likely on comparative grounds that BATESON (3, p. 525) and MORGAN (68, p. 411) are right in assigning to it a mesenchymatous origin. But DAVIDOFF'S (14) experiments

and *Cribrella* agree in having yolky eggs and an abbreviated development. In all three the sac is described as having only the briefest connection with the parent cœlom. The right-sided origin of the sac in the first and third will be due to "hastening" on the part of the sac to assume its adult position on the aboral side of the disc, and will be comparable with the fact that, at any rate, in the last two of them the hydroporic opening is from the first to the right of the middle line.

Even in the case of larvæ with indirect development, the appearances which have been interpreted as indicating very early juxtaposition or even direct connection between dorsal sac and pore canal or left cœlom (p. 246 above; FIELD, 23, fig. 27; GOTO, 33, p. 255; METSCHNIKOFF, 64, p. 63) are no doubt to be explained in terms of similar developmental hastening.

MACBRIDE (55, 56, 57) identified the dorsal sac with a right hydrocœlic rudiment in *Asterina* and other echinoderms, assigning a right cœlomic origin to the sac. This view, which has been fruitful in stimulating exact comparisons between the structures of right and left larval origin, was put forward on comparative grounds and seemed to be established by the circumstance that no dorsal sac could be detected in his double-hydrocœle larvæ of *Asterina*. However, I had the opportunity of showing Prof. MACBRIDE the evidence from double-hydropore, double-hydrocœle, and normal development provided by *A. rubens*, and in particular the series of sections of double-hydrocœle larvæ possessing a dorsal sac, and he desires me to express his agreement with the conclusion that this evidence renders a homology between the dorsal sac and a right hydrocœlic rudiment no longer sustainable.

I hold that the sac in question is homologous (see p. 278) with the pericardium of *Balanoglossus*, a view referred to as probable by MORGAN (68, p. 442), put forward definitely by BURY (9, pp. 129-130), and more recently supported by MASTERMAN (60). *Cephalodiscus*, the affinities of which with *Balanoglossus* are generally recognised, appears to possess a similar dorsal vesicle.

Pulsations.—The point of greatest interest noted in observations from day to day on the living larvæ, was that the wall of the sac, and particularly its floor, contracts in a rhythmic or sub-rhythmic manner. So far as one can judge, in the resting intervals the floor of the sac swells irregularly upwards and is invaginated into the sac, being filled with fluid from the underlying tissue spaces. In each contraction the floor of the sac descends, losing whatever degree of invagination it had undergone. The contained fluid is displaced, and the sac now bulges downwards, all the more that in late larvæ it is prevented from expanding towards the surface owing to the presence above it of the large basal skeletal plate belonging to inter-radius I/II (see p. 266).

The contractions when first recognisable (35th day) occurred once in every six or seven seconds. Later the rate became slower, being approximately once in twelve seconds during the fifth week, and once in nineteen seconds just before metamorphosis. In order to observe the contractions one needs to be watching healthy larvæ as nearly as possible at rest. I used to bring a single larva into a watch-glass, leave it undisturbed on the stage of the microscope for a time, then pipetting out some of the water try to get the larva just stranded with its dorsal side uppermost. A binocular microscope with a sub-stage condenser of suitable focus is of use. I never failed to observe the pulsation under the conditions above mentioned, and have not the slightest doubt that it is a normal function of the sac and has a physiological show that in regeneration, when presumably there is accelerated tissue formation, the pericardial sac usually arises directly from the proboscis cœlom.

meaning. At metamorphosis the pulsations can be made out until the growing opacity of the body wall renders further observation impossible.

The pulsations of the sac and the character of the spongy tissue under it strongly suggest that we have already in this tissue something of the nature of a hæmal node or centre for the distribution or circulation of a nutritive fluid. The circulation will no doubt be highly imperfect, but probably the general result is that an afferent stream* comes from the stomach where absorption is taking place and efferent streams pass to the tissues generally, some of the latter being far removed from any other supply of nutritive fluid than that provided by the cœlomic fluid. At metamorphosis the invagination of the dorsal sac by the underlying spongy tissue becomes permanent, giving rise to the upper portion or aboral process of the axial organ. Here at this stage sections often show what seem to be definite cavities. No doubt these are parts of the spongy tissue dilated with fluid and serving as vessels but without proper walls. When at metamorphosis some of the mesenchymal cells have broken down to form fatty and other granules, the latter occur abundantly in the cavities referred to. Side by side with the upper portion of the axial organ, and like it invaginating the wall of the sac, we may find a hollow outgrowth from the axial sinus, due to very early formation of the so-called "ampulla of the stone canal" (p. 268). The question of pulsation and circulation in the adult hæmal system, and the homologies of the system, are discussed on pp. 271 and 278.

The only two authors who refer from first-hand knowledge to the presence of a contractile organ in *Asterias larvæ* are HENSEN and BURY. The former, as far back as 1863, mentioned (42, p. 246) in his description of the brachiolaria of Kiel Harbour that there is a pulsating heart tube on the dorsal side over the junction of œsophagus and stomach, which contracts about five or six times a minute. This observation seems to have been lost sight of, the next reference being an independent one of BURY's, who says (9, p. 74), "in very old brachiolaria just before metamorphosis I have in a few cases observed a faint pulsation in this region—apparently in the floor of this cavity, but the opacity and activity of the larvæ make it very hard to study, and it is, moreover, much slower and less regular than in echinid plutei." Then with reference to the pluteus of *Echinus microtuberculatus*, he tells us (9, p. 76) that the floor of the vesicle projects far up into its cavity, and that the pulsation "is certainly continued in the earliest post-larval stages, though whether it occurs in the adult I am unable to say." METSCHNIKOFF had already (64, p. 63) referred to the presence of a pulsating heart-like tube close to the pore-canal in late echinid plutei. Rhythmic pulsation on the part of the pericardium of *Tornaria* has been mentioned by various authors, and first apparently by FRITZ MÜLLER (SPENGEL, 88, p. 3).

* The dorsal sac is large and definite in the brachiolaria of *Porania*. I had the opportunity of watching its contractions in a late double-hydrocele larva of this species. Here, no doubt owing to restriction of space, the sac was narrow from side to side though elongated from before backwards. The very significant fact emerged that, on the whole, the contractions of the floor of the sac began posteriorly and progressed in a forward direction. The posteriorly placed spongy spaces underneath the sac, *i.e.*, those nearest to the stomach, were therefore the first, and the anteriorly placed spaces were the last to be emptied of their contents. It will be remembered that in *Balanoglossus* the dorsal vessel of the trunk which collects blood from the gut walls is afferent to the "heart sinus" underneath the pericardium.

VIII. FIXATION.

The brachia are moved about very freely during the period immediately preceding fixation (beginning of seventh week or thereby). They can be extended, drawn in, spread out, or brought together, and as a rule the first and third and the second and fourth of these movements are associated together respectively. The distension of the brachia varies with the general internal coelomic pressure, and is greatest at the initiation of metamorphosis. The brachia do not necessarily act together, for example, the anterior or median one may be indrawn while the others are extended, or, more rarely, one of the latter is out of harmony with its fellow. Towards the end of the free-swimming stage any one of the brachia may provide temporary attachment, though in the instances I observed, the anterior or unpaired brachium was oftenest in use. The hold was firm enough to maintain attachment even against moderate shaking of the aquarium and disturbance of the contained water, but could be voluntarily released.

I was able on two occasions to observe attachment by the brachia and sucker on the part of a larva in a watch-glass under the microscope at a stage which promised metamorphosis. The brachia were divaricated so that the sucker was widely exposed. The papillated ends of one or more of the brachia were pressed from time to time against the bottom of the glass. This gave sufficient fixation to allow the sucker to be brought into use, its actual application being effected by contractions of the body wall which increased the coelomic pressure so much that the sucker bulged outwards. Probably, on slackening of the contractions, the sucker takes a first hold through atmospheric pressure, being cup-like in normal shape and having a slightly thickened outer rim. An equally powerful subsequent contraction will readily enable this kind of hold to be relaxed. In the instances observed, loosening and renewal of sucker-attachment occurred several times, one or other of the brachia meanwhile maintaining a hold, and the new attachments being in slightly different positions from the former ones, so that the larva could be described as crawling by means of its brachia and sucker. After such releases of the sucker, and after the first releases of the brachia I failed to find any trace of adhesive substance. Later, in the case of the brachia, material from the tips adhered to the glass after each release. From this, as well as on grounds of shape and texture, it appeared that adhesion of the brachia was effected by means of a cement at first so small in amount and so transparent as to escape observation.

In the middle stages of metamorphosis fixation is still by the sucker, and is firm enough to resist strong suction with a pipette or dipping tube, although under the pull the little starfish disc is lifted up at once like a flap. Stronger force will tear the stalk right through, leaving the sucker still attached, but it is certain that long before this time cement fixation has taken the place of suction. Indeed, I believe that suction attachment accounts only for the very earliest moments of definite fixation, that is, for the short time required to allow the cells of the sucker

to shed their cement. In specimens which had only just begun to metamorphose, I have seen the sucker holding on firmly to masses of *débris*, or holding on equally firmly by half its area to a small frond of seaweed, the other half projecting freely beyond the edge of the frond. Sections of the sucker after fixation show the presence on its surface of a very distinct layer of homogeneous cement substance, which was previously absent (Plate 23, fig. 27).

It was during the seventh week in my good cultures that the best specimens became attached. There is little hope of normal metamorphosis, if attachment is delayed beyond the commencement of the ninth, or, at any rate, the tenth week.

JOH. MÜLLER, who first described the brachiolaria, was not in a position to recognise the uses of the brachia and the cup or disc between their bases. SARS, however (82, pp. 127–8), noted and described the attaching function of the arms and sucker. HENSEN (42) found that his brachiolariae became fixed at metamorphosis, but he did not define the attaching organs. Indeed he believed the discs and the tips of the brachia to be sensory or nervous in function. AGASSIZ (1, p. 28) noted fixation at metamorphosis, and surmised that it was effected by the brachia. Curiously enough GOTO (33, pp. 247–8), working with the same species, did not find that fixation occurred at all. MORTENSEN, in a verbal communication to me, stated that he had long ago observed living plankton-gathered larvæ of *A. rubens* to become attached at metamorphosis, and in his 'Echinodermlarven' (71, p. 41) applied the term *Saugnapf* to the sucker. BURY (9, p. 74) stated that the metamorphosis of *A. rubens* is ushered in by the fixation of the larva by the knobbed arms and the "ciliated pit" which they surround, and that this fixation, at first voluntary, soon becomes complete. DELAGE (17, p. 40, 18) put on record that his late brachiolariae of *A. glacialis* crawled along the bottom and attached themselves temporarily by means of the adhesive papillæ at the ends of the brachia. As regards the sucker, or "cupule dite ciliée," he did not ascribe to it an attaching function, though, like WILLEY later (92), he found that it did not show evidence of ciliary action.

Disc or sucker-like attaching organs have, of course, become familiar from the life-histories of various species of starfish having yolky eggs and an abbreviated development. Most text-books, however, still ascribe the attachment of the ordinary brachiolaria to the tips of the brachia (KORSCHOLT and HEIDER, 47, p. 421; DELAGE, 16, vol. 3, p. 80); although some (*e.g.* SEDGWICK, 84, vol. 3, p. 141) have recognised that definitive fixation is by the sucker. Quite recently WILLEY (92) has given a notice of fixation first by the brachia and afterwards by the sucker in a brachiolaria apparently identical with that of *A. vulgaris*.

IX. METAMORPHOSIS (EXTERNAL FEATURES) (*cf.* Plates 20–22, figs. 12–18).

Strong, more or less rhythmic, contractions of the body wall take place, chiefly in the longitudinal direction, and by this means the preoral lobe is bent sharply backwards (Plates 20, 21, figs. 12, 13), while the anterior and middle portions of the larva are gradually shortened and reduced, the anterior portion in particular being destined in part to form the attaching "stalk." The posterior or disc portion of the larva expands and bends leftwards, until its left side is parallel with and looks towards the surface which the sucker is adhering to, while the right side of the disc looks away from the surface in question. At the same time the disc undergoes torsion through about 75° in the (starfish) horizontal plane, counter-clockwise as viewed from the sucker. This movement brings the median brachium opposite or a little past pouch I of the hydrocœle (Plate 21, figs. 13, 14), while the larval mouth is carried a little past pouch IV. It will now be understood that the right side of

the disc portion of the larva is destined to give rise unaided to the aboral surface of the starfish, the oral surface being formed from the left side of the larval disc, with the addition of tissue incorporated from the anterior and middle portions of the larva during their reduction. This reduction is marked by gradual indrawing of the preoral lobe and brachia, and of the various ciliated processes. Although no breach of surface occurs, there is considerable absorption of epidermal tissue, *e.g.*, over the tips of the brachia where histolysis of the papillæ occurs, and over those portions of the retracted structures that are covered by flattened indifferent epithelium. The remaining epidermal cells, as they crowd together on the oral aspect of the young starfish, become much elongated. By contrast, the layer of aboral epiderm is attenuated as the disc expands. On the oral aspect, the final stages of retraction of the ciliated processes coincide with and partly account for a rapid increase now observable in the size of the hydrocœle lobes, which send out swellings for the first, and shortly afterwards for the second pairs of sucker feet (Plate 21, fig. 14).

On the aboral (right larval) side, at the commencement of metamorphosis, there is a wide interval which we may call the aboral brachiolarian notch between arm rudiments I and II (Plate 20, fig. 12). The latter are gradually brought together through sub-rhythmic contraction of transversely placed muscular fibres, and the notch becomes so far reduced that it forms inter-radius I/II, the inter-radius which contains the hydroporic canal, and the other structures included in the axial complex. It is worthy of special mention that not only the preoral lobe and the mouth, but all the larval ciliated processes, *as well as the larval anus* (Plate 21, fig. 13) *for the short period during which it can still be recognised*, are now on the oral side of starfish disc. The closure of the larval anus and of the larval mouth are referred to respectively on pp. 262 and 263.

In the early stages of metamorphosis the structures belonging to the middle and anterior parts of the larva bulk very largely on the oral aspect of the disc (Plates 20, 21, figs. 12–14). As reduction proceeds the larval mouth closes, and the stalk (a remnant of the preoral lobe) is attached not in the centre of the disc, but outwards from that point in the direction of the gap between hydrocœle pouches I and V, the first and the last respectively of the hydrocœle pouches (pp. 243, 276). As the stalk becomes smaller its attachment to the disc shifts outwards still further in the direction named (Plate 21, fig. 15). However, in the end the ring canal of the hydrocœle is completed in such a way that the remains of the cavity passing outwards from the axial sinus into the root of the stalk are encircled by the hydrocœle (Plate 24, fig. 30). This important fact in asterid ontogeny was first demonstrated by MACBRIDE in the case of *Asterina gibbosa* (55, p. 356), and afterwards noted by myself in *Solaster* (29, p. 27). But whereas in *A. rubens* (p. 254) a portion of the left cœlom intervenes between the stalk cavity and the region which will become adult axial sinus, in the other two starfish named there is from the first a common anterior cœlomic chamber, so that the question of a left cœlomic element

intervening between stalk cavity and axial sinus proper was naturally not raised at all. The point has a bearing on the relation of the crinoid to the asterid stalk (p. 255).

Towards the fourth day after fixation the two pairs of podial outgrowths on each of the hydrocele pouches come into active use as sucker feet. A third pair also appears, distal to those already formed. The stalk now becomes further reduced, and the first two pairs of sucker feet take on the principal attaching function, at the same time exhibiting movements of locomotion (Plate 21, fig. 15). The little starfish may now make short excursions in any direction, being allowed to do so, since the stalk can lengthen, growing thinner when stretched like a piece of indiarubber. One gets the impression that the starfish is tugging to free itself from its attachment. Freedom is soon obtained through rupture of the stalk. The rupture is difficult to observe, but seemed to me to take place normally close to the disc, where a narrow line, marked by constriction and transparency, appears on the stalk (Plate 21, fig. 16). In two of the observed instances rupture took place some distance away from the disc, but probably this was because the process occurred prematurely by reason of the manipulation needed to keep the stalk in a favourable position under the microscope. In one of the specimens just referred to, which was allowed to develop further, the portion of stalk left distal to the line underwent necrosis. Probably the line marks the normal limit of absorption of the stalk.

At the end of metamorphosis accordingly the sucker and what remains of the stalk are left behind. The sucker now measures about .25 mm. transversely, and serial sections show that it still retains its cellular structure. For comparative data and discussion see pp. 255 and 280.

The early changes in metamorphosis occur with such rapidity that in less than 24 hours after fixation the stage shown in Plate 21, fig. 14, may have been reached. The profound alteration of shape and the redistribution of tissue involved are facilitated by the following circumstance:—Throughout the anterior portion of the larval body and especially within the ciliated processes the purely mesenchymatous tissue breaks down in great part, forming a thick lymph which contains numerous cells, as well as granules of fat and other substances. This lymph so far “circulates” under the influence of the muscular contractions that much of it is transferred directly from the regions that are being reduced (anterior and middle portions of the larva) into the growing disc. The transference takes place chiefly at the inter-radial notches in the rudiments of the interbrachial septa. Round the periphery of the disc between the skin and the outer wall of the *l.p.c.* there is a temporary circular channel which receives the lymph and distributes it to the disc (Plate 23, fig. 27). Just at this period the contents of the “channel” are found to be in movement whenever a strong muscular contraction occurs. Not a little of the lymph reaches the space between the gut hypoblast and the coelomic wall, travelling by way of the mesenteric attachments. No doubt it provides much of the material which swells up the gut walls so rapidly at this time (p. 262).

X. METAMORPHOSIS (CAVITIES AND ORGANS).

(a) *Anterior and Middle Cœlomic Regions.*

Early in metamorphosis, the cœlomic fluid, under pressure from the muscular contractions, dilates the median anterior cœlomic cavity behind the sucker, while the paired portions of the anterior cœlom through shortening are directly taken into the median cavity just named. The anterior cœlom as a whole has now the form of a fairly large common chamber (Plate 23, fig. 27), dorsal to the œsophagus, opening (*a*) on the one side into the left middle* cœlomic region (axial sinus and hydrocœle), and through that into the dorsal horn of the *l.p.c.*; (*b*) on the other side, into the right middle cœlomic region (homologue of hydrocœle, etc.), and through that into the ventral horn of the *l.p.c.* By means of these communications, during the muscular contractions, cœlomic fluid passes under pressure into the left middle and posterior cœloms, serving the useful purpose of dilating the hydrocœle and the *l.p.c.* in correspondence with the rapid increase which is now taking place in the size of the disc. Wherever active retraction is taking place, the cœlomic lining becomes altered, its cells being crowded together and increased in height to form a relatively thick but irregular layer. Many of these cells are shed, and, as metamorphosis proceeds, find their way into the hydrocœle, or into the *l.p.c.*, where, after degenerating, they are absorbed.

The openings from the ventral and dorsal horns of the *l.p.c.* into the right and left middle cœlomic regions next become closed. The *r.m.c.* grows smaller and disappears, now or a little later, without leaving any vestiges that can be recognised.

Meantime the larval œsophagus has divided (see p. 262) and its deeper portion is being retracted towards the stomach. This process further obliterates the distinction between right and left anterior cœloms, which are meantime being tilted completely over to the oral (left larval) side with the other preoral structures, the result being a large irregular cavity which lies under the stomach (Plate 23, fig. 28) and enters the stalk. This cavity may be called the provisional axial sinus, and it is made up of a right and left anterior as well as a left middle cœlomic constituent. The greater part of it afterwards disappears. Though boundaries are now difficult to recognise, we may say for certain that the adult axial sinus, the hydrocœle, and the whole or almost the whole of the internal oral circular sinus (including the segment in inter-radius I/II), belong to the left side, and in particular to the left middle cœlomic region, as defined on p. 242 and in the note on this page.

* It must be noted again (p. 242) that the terms anterior and middle cœloms or cœlomic regions are employed here for descriptive convenience and not because the cavities to which they refer can be strictly demarcated from one another, nor with the implication that they correspond respectively to the proboscis and the collar cœloms of *Balanoglossus*. Combined they do so, but not singly. Our left middle cœlomic region includes, for example, the hydropore and the portion of body cavity it opens into, although the homologues of these parts in *Balanoglossus* belong to the proboscis cœlom (see p. 278).

As the stalk lengthens, we find that its distal portion is solid, there being now no cavity close under the sucker. This takes place in part through obliteration, but chiefly by a rearrangement of tissue which keeps the cavity receding towards the disc as the stalk grows longer. At the stage shown in Plate 21, fig. 15, there is only a short funnel passing up into the root of the stalk from the remains of the provisional axial sinus (see also Plate 24, fig. 30).

A large portion of the provisional axial sinus becomes obliterated during the oral formation of the mouth. The ring left round mouth and pharynx is the internal circular sinus (Plates 23, 24, figs. 26, 28, 30, 31), and is at first very spacious towards ray V, where it includes the region which was provided by the united right and left anterior cœloms. Did any vestiges remain of the *r.m.c.* (right hydrocœle) they would have to be looked for here. It is from this region of the provisional axial sinus also that the cavity entering the stalk arises (Plate 24, fig. 30). After the stalk is lost, the adjacent portions of the internal oral sinus gradually become narrowed down to their proper size. Probably this last process, which is not completed till well after metamorphosis, obliterates the anterior cœlomic constituents, leaving the whole circular sinus a derivative of the *l.m.c.*, like the hydrocœle and axial sinus. The point, however, is hardly capable of exact demonstration.

The loss of the sucker and stalk as above described has not been mentioned in any previous account of the metamorphosis of a free swimming brachiolarian larva (AGASSIZ, 1; GOTO, 33; WILLEY, 92). Nor does a similar loss seem to occur in the case of the other attaching asterid larvæ, the development of which has been described (*Asterias mülleri*, SARS, 81; *Asterina*, LUDWIG, 52; MACBRIDE, 55; *Cribrella*, MASTERMAN, 60; *Solaster*, GEMMILL, 29). If these facts are compared with the data given on pp. 234, 235, the probable conclusion will emerge that alike among the brachiata and the abrachiate Asterid larvæ, there are some forms which lose nothing at metamorphosis, and others in which particular parts are separated off.

Comparison with Antedon.—A comparison with the *Antedon* larva suggests itself all the more, since, as was noted on p. 252 in *Asterias* the larval anus as well as the larval mouth is on the oral aspect of the disc at the time when the brachiolarian notch closes up. MACBRIDE pointed out that though the stalk projects in *Asterina* from the oral side of the completed hydrocœle ring, and in the crinoid from the middle of the aboral surface, nevertheless the two stalks are equivalent or homologous structures, both being derived from a primitive preoral lobe which became modified for attaching purposes (55, p. 392). We have just seen (pp. 252, 253) that in *A. rubens* there is a left cœlomic intermediary between stalk cavity and axial sinus proper. If it were shown that in the development of *Antedon*, there was a corresponding connection which included a right anterior cœlomic element, the homology between the asterid and the crinoid stalk could be made more definite and we might reasonably say that the ontogenetic processes above referred to, indicate the course of evolutionary change actually followed during the separation of the primitive asterid from the primitive crinoid stock, at the critical period when the common ancestor of both came to adopt a fixed instead of a creeping habit and thereby to acquire its radial symmetry (p. 280).

Axial Sinus.—The axial sinus is a derivative of the left middle cœlomic region (see note on p. 254), and acquires its characteristic tubular shape as well as its mesenteric relations, through the extension of the dorsal and ventral horns of the *l.p.c.* (see p. 259). The relations of its upper end to the pore-canal system, the

stone canal, and the dorsal sac are referred to under the next heading and on pp. 267–269. As in other starfish it opens orally into the internal oral circular sinus.

Hydrocoele.—During the progress of metamorphosis the hydrocoele crescent expands so as to enclose a relatively large area within its horns. The ring canal, which at the time of fixation forms a groove all round the margin of the crescent, begins to be nipped off during the following day, and first in the region connecting pouches I, II, and III (Plates 23, 24, figs. 26–32).

The formation of the provisional axial sinus (p. 255) and the retraction of the larval œsophagus (p. 262) (about third day after fixation) leave the two horns of the hydrocoele crescent free to approach each other in inter-radius I/V. However, since the approach occurs across a part where reduction of other structures has recently taken place, much extra cellular tissue is still in evidence here, and even after the horns of the crescent have met, the ring canal remains solid for a time in the inter-radius named.

In having the hydrocoele crescent widely open to the left anterior cœlom until metamorphosis has supervened, the *Asterias* larva differs from *Bip. asterigera* (BURY, 8, 9, p. 73), where the hydrocoele seems to become practically separated off from the anterior cœlom relatively early in the free-swimming stage.

In *Asterias* the larval gap on the left (*i.e.*, oral) side is between pouches I and V, and it is here that closure of the ring canal finally takes place, while closure of the aboral brachiolarian notch occurs between arm rudiments I and II. It was noted that the stalk is attached in inter-radius I/V, and that the deep opening of the stone canal, as well as the pore-canal and the dorsal sac, lie in inter-radius I/II. In all these respects there is agreement with *Asterias mülleri*; *Asterina* (MACBRIDE, 55); *Brachiolaria* (BURY, 8, 9); *A. vulgaris* (GOTO, 33); *Cribrella* (MASTERMAN, 60); and *Solaster* (GEMMILL, 29), allowing in the case of the last species for the increased number of rays. In *Bip. asterigera*, according to BURY, the closure of the hydrocoele ring takes place in our inter-radius I/II, while the deep opening of the stone canal and the various structures forming the axial complex are situated in the same inter-radius (9, p. 68). In this larva the (brachiolarian) hydrocoele gap being reduced, pouch I of the hydrocoele has moved round so far that its apex is directed anteriorly, or even antero-ventrally, instead of antero-dorsally (see BURY, 8, Plate XXXVIII, fig. 7). Little or no adjustment is accordingly required between pouch I and arm rudiment I during the formation of ray I of the starfish (BURY, 9, p. 68).

It is only after the preoral lobe has become much reduced (*cf.* Plate 21, figs. 13 and 14) that lateral swellings for the first and second pairs of sucker feet make their appearance. This corresponds with what occurs in the development of *Asterina*, *Cribrella*, and *Solaster* and *Asterias vulgaris*, but in some specimens of *Bip. asterigera* before metamorphosis examined by me, as many as 12 pairs of sucker feet are already present in each ray. The circumstance is probably related to the fact that in this species the larval swimming organ is cast off abruptly (KOREN and DANIELSEN, 46; DELAP, 19), and, since there is no sucker which can provide temporary fixation, the tube feet must be ready for early functional use.

Stone Canal.—The stone canal takes origin on the right posterior wall of the *l.m.c.*, five or six days before metamorphosis, as a groove lined by elongated strongly ciliated cells beginning near the inner opening of the pore-canal and ending at the bottom of

the hydrocoele crescent between pouches I and II.* (In *Solaster* the stone canal appears to burrow out in part from the hydrocoele groove through thickened tissue towards its outer opening (29, p. 31).) At metamorphosis the groove is roofed in to form a canal entering the circular canal of the hydrocoele in the position named. The outer end of the stone canal remains open to the axial sinus near the entrance of the pore-canal. The fate of this opening is discussed on p. 268, in connection with the madreporite. In a young starfish, $\frac{1}{2}$ inch in total diameter, the wall of the stone canal is folded inwards longitudinally along the external aspect of the canal, *i.e.*, the aspect facing inter-radius I/II. A longitudinal ridge is thus formed projecting into the lumen of the canal, and almost from the first this ridge is covered by cells that are smaller and less strongly ciliated than those which form the general lining of the canal. Still later, the ridge in question becomes bifid along its summit, dividing into two leaves which gradually fold over in scroll-like fashion to either side. In a specimen of 8 inches total diameter each scroll describes one and a half circles. All over the surfaces which are concave towards the lumen of the canal the lining is of elongated strongly ciliated cells, but on the surfaces which are convex towards the lumen the cells and the cilia are considerably smaller. In longitudinal sections of the stone canal at metamorphosis and during early growth the cilia are long in proportion to the diameter of the tube, and their tips often point oralwards. It is not unusual to find that cilia within relatively narrow canals slant in the direction of the currents which they produce (see pp. 269–271).

Axial Organ, etc.—The axial organ takes origin from the wall of the *l.m.c.* as a loosely cellular fold or thickening, parallel with and close to the stone canal, and on the (larval) anterior side of this canal. At the period of metamorphosis the axial organ is already prominent and well marked along its whole length. It lies over (*cf.* Plate 24, fig. 32) the first part of the pharyngeal cœlom (p. 259), and its upper or aboral end is continued into the spongy tissue beneath the dorsal sac. This tissue afterwards becomes invaginated into the sac and forms the so-called glandular process or head of the axial organ. The process in question is connected with the rest of the axial organ by a constricted part which may be called the neck. In the adult the axial organ projects inwards from the wall of the axial sinus on the dextral side of the latter as one looks at it from the aboral aspect. After metamorphosis the lower end of the axial organ is found to be continued directly into the ring of hæmal tissue which surrounds the mouth. So far as I can make out in *A. rubens*, this ring grows first in the direction of rays II and III, and from there extends round to

* In *A. rubens* at metamorphosis and also in the adult the stone canal opens into the ring canal rather closer to ray II than to ray I (*cf.* text-fig. 1, p. 276). This allows a Tiedemann's body to be present on the dextral side (see note on p. 217) of the stone canal. Young and adult *Solasters* show the same features, which are also found in many other starfish (54, p. 572). In *Solaster endeca* (29, p. 31) I described the deep opening of the stone canal groove at the time of its first appearance as being situated opposite pouch II of the hydrocoele.

IV and V. The homologies of the axial organ have been very differently interpreted by different authors. It will be seen later that, in my opinion, the axial organ corresponds with the left pharyngeal vessel of *Balanoglossus*, a spongy efferent blood channel projecting into the collar cavity in the edge of a fold which contains the pharyngeal cœlom, the latter cavity being a forward prolongation from the cœlom of the trunk (see further on p. 278).

(b) *Right Posterior Cœlom* (cf. Plates 18–20, 23, 24, figs. 5–9, 11, 26–32).

The mode of separation of the *r.p.c.* (epigastric cœlom) was described on pp. 242, 243. Prior to metamorphosis this cavity is limited everywhere except anteriorly by the mesentery between *r.p.c.* and *l.p.c.*, but anteriorly it is bounded by the septum which divides the *r.p.c.* from the *r.m.c.* At metamorphosis this septal portion becomes drawn together at its dorsal and ventral corners, and thus shortened out of existence during the process by which the aboral brachiolarian notch is narrowed, and finally obliterated. Except for the small portion abutting on the dorsal sac and axial sinus, the epigastric cœlom is now surrounded by what may be called the circular epigastric mesentery, which is thus derived from the original sagittal mesentery of the larva. Later, as the radial cœca grow outwards from the pyloric sac, the epigastric cœlom sends a pocket over each. The walls of these pockets remain intact, and serve as suspensory sheets, whereby the cœca are slung to the aboral body wall. Still later, in each inter-radius the circular epigastric mesentery is drawn towards the centre of the aboral surface, at the same time breaking up to form the numerous aboral ligaments belonging to the stomach, these processes being responsible in part, at least, for the characteristic adradial grouping of the ligaments. Just prior to metamorphosis the circular epigastric mesentery is anchored aborally to the posterior wall of the axial sinus. Later this connection breaks down in part, leaving the axial sinus enclosed within the inner edge of the madreporic interbrachial septum. Two strands are, however, left, as MACBRIDE indicated in *Asterina* (55, p. 376), passing from the dorsal aspect of the stomach to the wall of the axial sinus. These strands, though inconspicuous during early growth, become the great gastric hæmal tufts of the adult starfish (pp. 272, 277, 278).

At the end of metamorphosis the intestine, rectum, and rectal sac lie between the layers of the circular epigastric mesentery, though the rectal sac bulges chiefly into the *l.p.c.* The anus is at first some distance outwards from the centre of the aboral surface. As it progresses centrally, carrying rectum and intestine with it, it causes a specially deep bay or indentation in the outline of the circular epigastric mesentery in inter-radius I/V, the bay being occupied by the extension of the *l.p.c.* into which the rectal sac projects. Rectum and intestine may now be described as being slung to the aboral wall by a dextral (see note on p. 217) and a sinistral wing of mesentery. Of these, for some reason, the dextral wing early shows itself as the thicker, stronger, and more persistent, but in the end both break up to form suspensory

ligaments. The first lobules (rectal cæca) from the rectal sac grow out in inter-radius V/I, and are covered by the *l.p.c.* They are the only lobules present in a young starfish measuring 11 mm. across disc and arms. In a specimen measuring 2 mm. more, lobules for inter-radius V/IV were also present. The remaining ones appear to grow out later in dextral sequence.

The above account of the development of the circular epigastric mesentery agrees in its essentials with the details given by BURY (8, 9) regarding the formation of the same structure in *Bipinnaria asterigera* and in Brachiolaria. It corresponds with MACBRIDE'S description for *Asterina gibbosa* (55, p. 366), and also with mine for *Solaster endeca* (29, p. 33), if one assumes in the latter case, as I think may rightly be done, that the larval posterior cœlom is an *l.p.c.* alone (see pp. 234 and 280). The same thing would apply to MASTERMAN'S (60) description for *Cribrella* if the same assumption be made, but this author believes the larval posterior cœlom of *Cribrella* to represent both *r.p.c.* and *l.p.c.*, and the epigastric cœlom to be the homologue of the hydrocœle. The absorption and re-formation of septa described by GOTO in *A. vulgaris* make his account of the above mesentery differ from mine (see p. 243).

(c) *The Left Posterior Cœlom* (cf. Plates 18–20, 23, 24, figs. 4–11, 25–32).

The left posterior cœlom gives rise to the hypogastric and pharyngeal cœloms, the external oral, radial, and aboral perihæmal sinuses, and to the genital rachis.

At metamorphosis the dorsal and ventral horns of the *l.p.c.* curve round to meet each other, the ventral horn in particular travelling across the aboral brachiolarian notch within arm rudiment I. For a time the two horns are separated by the axial sinus, as well as by that portion of the larval dorsal mesentery which contains the dorsal sac. The horns next become lost in the general perivisceral cœlom through uniting with each other between the stomach on the one hand, and the dorsal sac and axial sinus on the other, the two latter structures being left enclosed within the inner portion of interbrachial septum I/II. It is at this stage that the rudiments of the gastric hæmal tufts are left behind (p. 258). Prior to this the dorsal horn has given rise to the commencement of the genital rachis and of the aboral perihæmal sinus.

Pharyngeal Cœlom and Circular Hypogastric Mesentery (Plates 23, 24, figs. 26–32).—The pharyngeal cœlom (oral cœlom of MACBRIDE, peri-œsophageal cœlom of GOTO, peri-pharyngeal cœlom of MASTERMAN) takes origin about the 36th day as a single hollow evagination from the dorsal horn of the left posterior cœlom, pushing out to the right and then downwards within the somewhat expanded visceral attachment of the mesentery which separates the left middle from the left posterior cœlom. Following the line of this mesentery, it curves ventrally and then forwards to near the tip of the ventral horn of the left posterior cœlom. Meantime its stalk of origin has become closed. At metamorphosis its dorsal and ventral extremities are approximated partly by their own further extension and partly through the narrowing and subsequent obliteration of the larval gaps between I and V of the hydrocœle pouches, and between I and II of the aboral arm rudiments. The two extremities of the pharyngeal cœlom next unite and the whole forms a ring-shaped cavity flattened against the left (oral) aspect of the stomach, and rapidly increasing in size. It encloses

the area of stomach wall in which the mouth will afterwards open. We may now speak of a mesenteric sheet separating the pharyngeal from the hypogastric cœlom, as well as of a sheet separating the pharyngeal cœlom from the *l.m.c.* The former sheet becomes the circular hypogastric mesentery (*cf.* in *Solaster*, 29, p. 33). Later, this mesentery breaks down in each inter-radial and still later in each mid-radial line. In the end it thus forms the ten chief sets of ligaments which attach the stomach wall on its oral side to the body wall over the adambulacral ossicles. The sheet which separated the pharyngeal cœlom from the *l.m.c.* forms the floor of the adult cœlom in the neighbourhood of the mouth. For mesentery of intestine and rectum see p. 258.

Oral Perihæmal Diverticula (Plates 23, 24, figs. 27–31).—The perihæmal diverticula make their appearance shortly after the commencement of metamorphosis in the inter-radii between the pouches of the hydrocœle. There is no difficulty in following the development of diverticula II/III, III/IV, IV/V, and V/I, which, as MACBRIDE first showed in *Asterina*, arise in the form of hollow outgrowths from the *l.p.c.* (fig. 27), become constricted off and then extend as U-shaped canals within the interradii, the apposed bases of the U's forming so many sections of the external oral perihæmal ring, while the limbs of adjacent U's form the double radial perihæmal canal in the floor of each ray. Diverticulum I/II is more difficult to follow, but according to my observations, it takes origin from the dorsal horn of the *l.p.c.* close to the communication between this horn and the axial sinus (p. 244). The subsequent closure of the perihæmal stalk, and of the communication just named, occurring almost simultaneously, make it appear as if the diverticulum originated from the axial sinus. In *Asterina*, MACBRIDE (55, p. 360) and GOTO (35, p. 235), in *Cribrella*, MASTERMAN (60, p. 392), found that perihæmal diverticulum I/II arises from the axial sinus (anterior cœlom). In *Solaster*, on the other hand, this diverticulum certainly arises from the *l.p.c.* (29, p. 35).

Perihæmal diverticulum I/V is at first separated by a considerable interval from pouch I of the hydrocœle. Afterwards, as the brachiolarian notch closes, this interval disappears. In *Solaster* the interval is larger and persists longer since the extra rays are added one by one in series from ray V onwards after the commencement of metamorphosis. In this species it seemed to me that a rudiment for perihæmal pouch I/V arose at a comparatively early stage from the anterior cœlom. Probably all the perihæmal pouches belong primitively to the *l.p.c.*,* and the exceptions to this rule have arisen in connection with the communications secondarily established between the anterior cœlom and the dorsal and ventral horns of the *l.p.c.*

We have to note that, at the end of metamorphosis, each perihæmal pocket is found to give rise to an inter-radial branch of considerable size. The branch, as in the case of *Solaster*, is readily recognisable in the adult starfish (28, p. 188).

* In *Asterias pallida*, GOTO (33, p. 274) has stated that all the perihæmal spaces take origin from mesenchyme!

Gonad Rudiment.—The rudiment of the gonad tissue appears at metamorphosis as a group of “primitive germ cells” in or closely beneath the wall of the dorsal horn of the *l.p.c.* The dorsal horn of the *l.p.c.* is here separated from the *r.p.c.* or epigastric coelom by the circular epigastric mesentery, and the primitive germ cells are on the oral or left (larval) side of this mesentery. (In serial sections of *Asterias mülleri* during early metamorphosis, I believed I could recognise primitive germ cells in a corresponding position on the right side of this mesentery, and therefore connected with the *r.p.c.* If this is correct it points to a primitively bilateral condition of the genital rudiment.) These cells are a little larger and rounder than those of adjacent tissues, while their nuclei show an intra-nuclear network. The cells in question next form a small compact mass lying at the bottom of a groove in the wall of the dorsal horn of the *l.p.c.* The mass then pushes outwards from the wall of the *l.p.c.* into the tissue between the dorsal sac and the axial organ, carrying with it the lumen of the groove, which becomes nipped off from the *l.p.c.* and forms the rudiment of the aboral perihæmal sinus, in the manner described by MACBRIDE* (55, p. 371) for *Asterina gibbosa*. Later, a “genital rachis” is found to have grown round in the (starfish) horizontal plane on the inner aspect of the aboral body wall, forming a circle which gives off two branches passing oralwards in each inter-radius, one on each side of the interbrachial septum. These branches become thickened at their extremities where the gonads appear. In further development the latter are cut off from the branches by the formation of the inner layer of the gonad wall. The growth of the rachis proceeds sinistrally (see note on p. 217) as viewed from the aboral side. Whether it proceeds dextrally as well I have not been able to determine with exactness in the case of *A. rubens*, but in *Asterina* it would appear (MACBRIDE, 55, Plate XXV, fig. 117) that extension is in both the directions named. MACBRIDE also notes the interesting point that the lateral branches of the rachis may begin to be formed in certain inter-radii before the circle of the rachis is elsewhere complete (*l.c.*, p. 377).

Cells continuous with, and of the same nature as, the hæmal tissue of the axial organ are early found to accompany the genital rachis, and they form the hæmal tissue which surrounds the rachis within the aboral sinus. Later, the rachis ceases to be evident and the hæmal tissue increases in amount. As in *Solaster* (28, p. 186) there is an interruption of the aboral sinus in the madreporic inter-radius. This interruption is probably complete normally in the adult. An extremely minute connecting canal still remained, however, in one of the specimens examined which had reached about three-quarter growth.

In *A. rubens*, the axial organ is formed (Plate 24, fig. 32) before the genital rudiment has separated off from its coelomic origin, and, so far as I can make out, the genital rudiment does not extend oralwards into the axial organ. The same thing is true in the case of *A. mülleri*. In *Solaster* I described the germ cells as extending downwards a short distance into the substance of the axial organ but leaving the middle

and lower portions uninvaded (29, p. 36). This seems to be quite natural if the genital rachis is for the purpose of providing germ cells for the various inter-radii and if it is to extend, sinistrally (see note on p. 217) as well as dextrally, to form a circle. The rachis must cross the madreporic inter-radius somewhere, and it appears to do so by extending horizontally through or in contact with the neck of the axial organ. The downward dip in the case of *Solaster* (29, p. 36) may be explained by the irregularity of shape of the dorsal sac. In the three species named I am unable to find an extension of the genital rudiment to the oral end of the axial organ, such as MACBRIDE has described for *Asterina* (55, p. 373). Accordingly on the evidence provided by these species (viz., *Solaster endeca*, *A. rubens*, *A. mülleri*), I do not see reason for believing the axial organ to be of the nature of a genital stolon. What seems a sound homology for this organ is referred to on pp. 278, 279. However, assuming the validity of MACBRIDE'S evidence it would, perhaps, be competent to add that the core of the axial organ may be a rudimentary representative of the gonad of the left middle or collar coelomic region of the ancestor.

(d) *Alimentary Canal* (cf. Plates 23, 24, figs. 26–31).

Œsophagus.—About 24 hours after fixation (p. 250) there occurs constriction and then complete division* of the larval œsophagus close to its junction with the buccal cavity. The vestibule, buccal cavity, and commencement of œsophagus are everted and contribute to the epiderm of the oral surface; the main portion of the œsophagus shortens, becomes thicker walled and is finally incorporated with the stomach. As Goro (33, p. 249) points out, one would naturally expect the division of the larval œsophagus to take place at the junction of its stomodæal and entodermic portions. This is probably the case, though it seemed to me that the line of separation was sometimes so far forward that a portion of the larval stomodæum could hardly fail to be retained.

With the onset of metamorphosis the stomach becomes gradually flattened from left to right—that is, in the starfish horizontal plane—this flattening being caused by the *l.p.c.*, which swells up strongly during each contraction of the body wall. At the same time the insertion of œsophagus into stomach is dragged towards the middle of the oral surface. The rudiments of the paired radial cæca now appear. It is of some importance to note that cæca I and II arise most anteriorly with reference to the original course of the food canal, cæcum I being a little to the right of the œsophageal opening and cæcum II a little to the left of this opening, while cæca III,

* Comparison of my different series of sections shows that retention of the larval mouth and œsophagus must have occurred in several instances in which, as far as external characters were concerned, metamorphosis appeared to be progressing along normal lines. On careful examination all such specimens were found to exhibit defects of various kinds—in particular smallness of the stomach and imperfect formation of the radial cæca. While it is altogether unlikely that the resulting starfish would have survived, the circumstance noted above emphasises the directness of the relationship between the mouth and œsophagus of the larva and those of the adult.

IV, and V continue the series along the convex aspect of the stomach, cæcum V being therefore morphologically the most posterior to all. These points have a bearing on the question of the proper numbering of the rays (p. 276).

The lining of the stomach increases greatly in area and thickness, and its cells losing their boundaries become syncytial and their nuclei undergo rapid proliferation. The cells also appear to swallow fatty granules and other *débris*, which are probably provided by breaking down of the lymph cells previously referred to. The lining of that part of the œsophagus which is retained undergoes a similar change, but more slowly and without becoming so markedly syncytial.

Meantime the larval œsophagus has practically reached the middle of the oral surface. Through gradual expansion of its cardiac orifice it comes to form a short cone-like projection from the floor of the stomach (fig. 28). Complete flattening of the cone may or may not ensue before the formation of the adult mouth (*cf.* figs. 29–31).

The retained portion of the œsophagus after its separation may be described as swinging relatively within the provisional axial sinus from a slanting position to one in which it points directly towards the middle of the surface enclosed by the hydrocœle ring, that is, the surface on which the mouth afterwards appears. In this process we see a means whereby a left hydrocœle may without much difficulty be brought to encompass an adult pharynx derived from the larval one. The condition is different in *Luidia*, where at an early stage the hydrocœle forms a rosette in the wall of the *l.m.c.* and the centre of the rosette is afterwards perforated by the adult mouth and pharynx, which arise independently of the corresponding larval structures.

The adult mouth begins to form about 10 days after the commencement of metamorphosis as a shallow pit externally, near the middle of the oral surface opposite to the larval œsophageal cone or to a downward pouching from that part of the stomach with which the cone was incorporated (*cf.* fig. 31). The intervening portion of the axial sinus is obliterated, and the opposed layers of skin and stomach wall become thinner and then break down. The meeting of oral membrane and mucous membrane at the margin of the adult mouth corresponds with the junction between oral surface epiderm with stomach wall in the formation of this mouth, which accordingly has no stomodæum of its own.

Less than 12 hours after the commencement of metamorphosis the larval intestine is constricted and broken off close to the anus, which then becomes everted and lost on the epiderm near the margin of the oral surface close to the interval between arm rudiments I and V. The intestine is now, as a rule, pressed so closely against that part of the stomach wall which is growing out to form radial cæca I as to lose its lumen. Meantime the stomach wall is changing shape and undergoing the histological changes described below. The intestinal wall shares in these changes, and accordingly its fate is difficult to follow, but comparison of different stages shows that: (1) a proximal portion of larval intestine enclosed between layers of the circular

epigastric mesentary (p. 258) gives rise to the intestine of the starfish ; (2) a terminal moiety surrounded by the *l.p.c.* (p. 244) disappears by absorption ; (3) the stump shortens and becomes solid for a time, but afterwards dilates to form the rectal sac, being covered chiefly by the *l.p.c.* (see further on pp. 258).

At a much later date the adult rectum grows out from near the blind end of the rectal sac through the aboral body wall in inter-radius I/V, meeting about half-way a corresponding ectodermal pit. The starfish rectum as defined here and on p. 274 is, therefore, a new formation, while the intestine and rectal sac are regions of the larval gut. All three are found in inter-radius I/V (p. 276).

(e) *Nervous System.*

While I cannot throw much light on the problem of the larval nervous system, the following data are of significance :—

(1) Applying the method of staining the larvæ *intra vitam* with methylene blue in my laboratory, Miss W. ABEL, D.Sc., found evidence that a sub-epidermal network of nerve fibres exists, certain cells connected with this network being picked out here and there after a fashion recalling that in which the stain selects nerve cells in the tissues of other animals. The cells and network were well marked in front of the hydroporic region dorsal to the œsophagus, and they appeared to be quite distinct from the muscular tissue found under the skin in this quarter. Scarcity of material prevented Miss ABEL from making the investigation complete, particularly as regards the ciliated tracts and the preoral region.

(2) As is well known, the walls of the enterocœlic sacs develop muscular fibres. At rest these fibres are for the most part invisible, showing up only during the contractions. In late larvæ there may sometimes be made out a "skeleton" set of fibres which resemble muscular fibres, but do not quite disappear when the contractions cease. This set of fibres was very definite in the late larvæ of my cultures of *Porania*, and could be seen to have a practically uniform arrangement in different individuals. The fibres were too few in number to have any appreciable power of effecting movement by themselves. Careful observation showed that they underwent some shortening when the neighbouring muscular tissue was in contraction. Their definiteness, the regularity of their arrangement, and the fact that one or more fibrils from them passed to all the ciliated processes and to the different regions of the ciliated tracts made it difficult to believe them abnormal or without meaning, and, indeed, left little doubt that they are specialised for some purpose, probably for conducting stimuli. In that case, whatever their origin, they may be called neuromuscular, and the fact of their existence in the larva may be comparable with, and related to, the occurrence in the adult of the so-called entoneural nervous system.

While in the case of many important adult organs (hydrocœle, axial sinus, axial organ, gonads, pharyngeal cœlom), a left ancestral structure has persisted, we need not say the same of the adult nerve ring. This ring may have arisen through gradual modification of the whole of a circumoral nerve

circuit including the dorsal and possibly also the ventral nerve centres. The point will be apparent if one remembers that the entire area in front of the postoral ciliated band (excepting only sucker and stalk), together with the band itself and the various larval ciliated processes, is brought at metamorphosis to the oral surface of the starfish within an area enclosed by the ring canal of the hydrocœle. If a circumoral nerve ring existed in the larva it could therefore be transferred to the adult as easily as the larval œsophagus. However, as far as I have yet made out, the formation of the adult nerve ring in *A. rubens* is independent of pre-existing specialised nerve centres or tracts. This independence must be absolute in *Bip. asterigera*. At the same time we see in the *Solaster* larva (29, p. 47) a case where the dorsal nerve centre, though imperfectly represented, is carried at metamorphosis into the area where the nerve ring is developing, while in the Echinid larva, as MACBRIDE has shown (57), there is a definite nerve centre dorsal to the mouth entrance, though it takes no part in the formation of the adult nervous system. Parallel facts are to be found in the case of other Echinoderms, and if we take *Balanoglossus* into account we shall probably be justified in concluding (1) that the bilateral ancestor had a circumoral nerve ring or commissure with dorsal and ventral nerve centres; (2) that the various types of echinoderm larvæ have developed only what they actually required in the way of a nervous system, and that the adult circumoral nerve ring is now in some cases entirely, and in others almost entirely, an independent formation; (3) the phylogenetic derivation of this ring from the circumoral nervous circuit of the ancestor is, in the absence of contrary evidence, a reasonable possibility. As regards the crinoids, if it be correct (p. 255) to say that the stalk represents phylogenetically a preoral lobe which has become twisted towards the right instead of towards the left side, we may perhaps find in the neuro-muscular fibres of the anterior part of the ancestral larva a starting point for the remarkable development of the apical entoneural nervous system which is characteristic of this class.

We must be careful to note that in *A. rubens*, at metamorphosis, the insertion of the larval stalk into the body is outside (*i.e.*, not surrounded by) the developing oral circular nerve tract. This is in direct contrast with the relation of hydrocœle ring to cavity of stalk at the corresponding stage.

(f) *Development of Skeleton* (*cf.* Plates 20–22, figs. 12, 18).

Skeleton.—In what follows, the terminal ossicles have the same numbers as the hydrocœle pouches with which they finally become associated to form the rays of the starfish (see p. 276 and text-fig. 1). About the 36th day a calcification appears in each of the arm rudiments even before these are separated by distinct notches. All five ossicles lie over the crescentic edge of the left posterior cœlom, ossicle I being a little to the right of the rectum, superficial to the expanded ventral horn of the left posterior cœlom (p. 242). The rest of the ossicles are at first almost exactly in the middle line. Each ossicle appears as a rod-like calcification approximately parallel with the future margin of the disc, and bifurcating at either extremity. A delicate reticulum with hexagonal meshes results through growth of the ends, followed by a second bifurcation, and that again by further growth and bifurcation with anastomosis of adjacent tips, the new meshes being all added at this period in a single plane. There is, naturally, a stage at which each ossicle is made up of two lateral portions connected by only one or only a few bars across the middle line. This is interesting, since, as I showed in *Solaster* (29, p. 42), two separate

terminals appear in each ray. I have also seen this condition as a rare variation in one or other of the arm rudiments of *A. rubens*. Terminal I covers the greatest area, while terminals II and III abut closely on one another. The five terminals are arranged in a crescent, the gap of the aboral brachiolarian notch intervening between I and II.

The next plates to appear are the five primary inter-radials, or basals, or genitals of various authors. These arise from tiny nodules which first become tri-radiate and then develop a reticulum similar to that of the terminals, but never suggesting division into two parts. The primary inter-radials form a crescent which is smaller than, and lies within, that of the terminals, and has also a gap between its horns corresponding with the brachiolarian notch. The inter-radial ossicle immediately to the right of the hydropore (fig. 12), *i.e.*, ossicle I/II, appears somewhat earlier than the other inter-radials and also reaches a greater size than these. It lies over the dorsal sac and probably provides support for the wall of the sac, so that the mechanical effect of the pulsations will be transmitted without loss to the underlying spongy tissue (p. 248).

LUDWIG (52, pp. 49–50) described the relatively early formation of the ossicle in *Asterina*, and BURY in a bipinnaria (8, p. 436). On the other hand, FEWKES (22, p. 30) did not find the feature to be a characteristic of *Ast. vulgaris*, but in my healthiest *A. rubens* larvæ it could usually be made out.

The last of the primary plates to appear is the dorso-central, which develops in the same manner as the inter-radials, and somewhat to the inter-radial II/III side of the centre of the disc. The dorso-central, like the primary inter-radials (excepting the madreporic one (*viz.*, inter-radial I/II) develops over the *r.p.c.* or epigastric coelom. The madreporic inter-radial, as BURY pointed out (8, p. 437), develops over the cavity of the dorsal sac (pp. 246–248).

Even before the formation of the dorso-central, calcifications for the spines have appeared in the layer superficial to that in which the primary plates are developed. They are tri-radiate in the horizontal plane, but have a small additional upstanding ray. They grow in essentially the same manner as the plates, except that their horizontal extension remains extremely limited, while, on the other hand, they increase in an upward direction, as LUDWIG has described for *Asterina* (52, p. 68). At first the spines show definiteness of arrangement. Thus at metamorphosis we find that a single large one overlies the dorso-central; while each terminal carries 12 spines, *viz.*, 6 along its external edge, 2 on each lateral edge, and 2 on the mid-radial line. The primary inter-radials have each a set of three spines over them, and each set forms a triangle, with the apex directed centrally. Only two of the three spines are, however, present at this stage over inter-radial I/II, namely, the apical and the sinistral-corner ones.

The first ambulacrals or oral ambulacrals can be recognised shortly after fixation as rod-shaped calcifications lying on either side of the radial pouches of the hydrocœle and lengthwise along their walls (FEWKES, 22). The circle of the hydrocœle being

small there is little space between the pouches. Later, as the disc expands and the pouches become separated more widely from one another, the ossicles in question take up their proper position, parallel with the circular hydrocœle canal. The oral ambulacrals are, of course, on the oral side of the first-formed sucker feet. As successive pairs of sucker feet develop, new ambulacrals appear, but always later by one or two steps than the correspondingly numbered sucker feet.

I must borrow the description of the subsequent development of the skeleton from FEWKES (22), to whose paper reference may be made for fuller details and for descriptive and historical notes. In general, this author points out that each plate arises from a single calcification, that coalescence of calcifications does not occur, and that a plate never divides to form two separate pieces. He shows that the reduction of the primarily formed plates is only relative, since they do not become absorbed, but are incorporated in the adult reticulum. A primary radial* appears in the mid-dorsal line of each ray after the formation of three pairs of ambulacrals. The first of the arm radials* are formed just beyond the primary radials, while succeeding ones appear in order beyond these last. The disc or body radials* are formed in similar sequence, but the series begins internal to the primary radials and progresses towards the dorso-central. The first circle of body radials appears about the stage when there are four arm radials in addition to the primary radial in each ray (22, Plate IV, figs. 3, 4). Three circles of body radials are present before the first of the secondary inter-radials appears on the disc. The first pair of adambulacrals develops about the same time as the primary radials, while the earliest marginals appear just prior to the first arm radials. Pedicellariæ may be seen in formation over the terminals at a stage when there are three arm radials in each ray. The first interbrachials (odontophores) are formed after three pairs of ambulacrals have appeared in each ray. The first adambulacrals (interambulacrals) arise later than the corresponding ambulacrals, and a little later than the first marginals. The dorso-laterals do not take origin in the same sequence as the arm radials, that is, the earliest dorso-laterals to appear need not be those which are nearest to the body. The inter-radial belonging to the madreporic inter-radius early shows on one side a notch which lodges the pore-canal. The inter-radial in question "grows round the madreporic body . . . and . . . the madreporic body or madreporite is a late formation (after the rudiments of the stone canal)".

XI. POINTS IN ADULT STRUCTURE AND FUNCTION.

(a) *Structure of Madreporite.*

A. rubens.—New pore-canals do not originate by outgrowth from the axial sinus as CUÉNOT (12, p. 536) supposed, but are formed in the manner described by PERRIER (quoted from CUÉNOT, 12, p. 536) and MACBRIDE (55, p. 373) through longitudinal constriction from previously existing canals (and therefore, to begin with, from the original hydroporic canal), the constriction not in all cases passing along the full length of the parent tubes, but sometimes stopping short and thus giving rise to stems branching towards the surface. In view of the calcareous nature of the madreporite, the production of new pore-canals will have to take place around its margin.

The arrangement of the pore-canals is adequately described in text-books generally, but the relations of axial sinus, stone canal, and pore-canals require attention. As is

* FEWKES thinks that the primary radials (or first median dorsals of other authors) should be counted as belonging to the arms. Here they are called simply the primary radials, while the radials immediately external and internal to them are named respectively the first arm radials and the first body radials.

well known, at metamorphosis the hydroporic canal enters the axial sinus close to the opening from axial sinus into stone canal. Subsequently the margin of the latter opening may be described as growing up aboralwards to form a funnel under the pore-canals, the funnel having on its dextral (see note on p. 217) side a gap—the original opening into the main cavity of the axial sinus. Most of the adult pore-canals must be described as opening into the stone-canal funnel, but it is obvious that developmentally the funnel is a portion of the axial sinus. In an account of the madreporite of *Solaster* (28, p. 179) I suggested for this funnel the term ampullary region of axial sinus.

Ampulla of Stone Canal.—The next important point to be noted during growth in *A. rubens* is the development, over the dorsal sac aborally, of a diverticulum from the stone-canal funnel. This is the ampulla of the stone canal as described by GREEF (37, 1872, p. 100) and LUDWIG (51, p. 108; 54, p. 563), and we see that in reality it is a special part of the ampullary region of the axial sinus. Its periphery becomes somewhat deeply indented by one or more notches which give it a lobed form. The neck of the ampulla opens by one or more apertures into the stone-canal funnel (Plate 24, fig. 34) on the dorso-central aspect of the latter, being also connected directly with the pore-canal system and indirectly with the axial sinus. The roof of the ampulla is very thin and is adherent to the roof of the intramadreporic cavity, which also lodges the dorsal sac. Its floor rests on the dorsal sac, and is made up of connective tissue with, as it seemed to me, an intermixture of muscular fibres. The muscular tissue is by no means prominent, but in different madreporites the floor of the ampulla was found to be thinner or thicker according as the cavity was more or less widely distended.

We may describe the axial sinus during the above changes as sending up a long dextral (see note on p. 217) and a short sinistral horn under the madreporite, the two horns being separated by the insertion of stone canal into the wall of the axial sinus and the under surface of the madreporite. The sinistral horn ends blindly; the dextral horn expands greatly at its tip to form stone-canal funnel and ampulla, then narrows to form the gap or opening between these and the rest of the axial sinus.

During growth to full adult size the following changes appear to occur: (1) Division of the gap last named into two or more channels; (2) amalgamation of the sinistral horn of the axial sinus with that part of the dextral horn which lies to the oral side of these channels, thus forming what is recognised in adult anatomy as the aboral end of the axial sinus; (3) outgrowth of numerous small branches or diverticula from the region just named into the sub-madreporic tissue; (4) formation (probably by rupture or absorption of septa) of an occasional small secondary opening between an axial sinus branch and some adjacent part of the funnel or of the pore-canal system.

The ridge with scrolled edges which comes to project into the stone canal (p. 257) may be described as dividing the canal into dextral and sinistral portions (*cf.* fig. 34).

In the madreporite of a large *Asterias* investigated by serial sections the axial sinus showed four aboral openings, one leading into neck of ampulla of stone canal (fig. 33), two into dextral corner of stone-canal funnel (fig. 34) and one into sinistral corner of stone-canal funnel (fig. 33). All of these I took to be primary in the sense that they were derived from the primary opening from axial sinus into stone canal, though the last was possibly secondary in the sense noted under (3) above.

It remains to be added that the powerfully ciliated lining of the stone-canal funnel extends upwards so as to be separated from the surface of the madreporite overlying it by only a short interval of pore-canal epithelium. This ensures the possibility of direct inward suction near the centre of the madreporite.

In a very large *Solaster endeca* the ampulla of the stone canal was represented by a narrow-necked diverticulum from the pore-canal system invaginated into the dorsal sac (28, p. 180, fig. 5), possessing thick, partly glandular, partly muscular walls. In this specimen the number of openings from the axial sinus into the pore-canal system (and thereby into the stone canal) was estimated at eight or nine, most or perhaps all of them having arisen through subdivision of the primary connection. Young examples of *Solaster papposus* (up to $1\frac{1}{4}$ inches in diameter across disc and arms) show the primary opening still single but wide in horizontal extent, while the ampulla, already thick walled, indents but is hardly invaginated into the dorsal sac. A half-grown *Asterias mülleri* showed similar features as regards the ampulla. In a young *Porania* measuring $\frac{3}{4}$ inch diameter across disc and arms the ampulla was represented by a part of the wall of the axial sinus at its extreme upper end, which was slightly thickened and rested directly against the wall of the dorsal sac. In this specimen there were two separate openings from axial sinus into pore-canal system and through that into the stone canal.

The relations of the ampulla of the stone canal in *Asterias* to the dorsal sac, etc., do not seem to have received adequate previous description. Those who first paid attention to the ampulla (GREEF, 37, 1872, p. 100; LUDWIG, 51, 54) did not recognise that there is associated with it an independent closed cavity, the dorsal sac, while later workers who recognised the closed nature of the dorsal sac have not apparently believed in or emphasised the independent existence of the ampulla. An indication of its presence is given in a figure by DURHAM (20, fig. 2), while HAMANN (38, p. 72) mentions that there was already in a young starfish of 1.2 mm. diameter an ampulla-like dilatation of the stone canal where it opened into the pore canals. GOTO (33) who held that the dorsal sac is the closed upper portion of the axial sinus showed the ampulla in quite a number of his figures (Plate 22, fig. 31; Plate 23, figs. 42-43, and Plate 24, figs. 45, 47), and mentioned that in *Cribrella sanguinolenta* there is an ampulla under the madreporite on the right side of the median plane and connected with the axial sinus, but he omits to describe the important relations (see p. 252) of this ampulla to his "closed portion of the axial sinus."

(b) *Function of Madreporite Stone Canal, &c.*

Asterids.—As regards *Asterias rubens*, *Asterias glacialis*, *Solaster papposus* and *Solaster endeca*, two of my students, Mr. J. C. KNOX and Mr. R. S. GIBSON, working at the Millport Station, obtained the following results which I had the opportunity of

confirming. In excised stone canals the current is always from the aboral to the oral end, and there are no contrary currents on the convex internal surfaces of the canal. It is different, however, with the ciliation of the pore-canals and their stems and with the ciliation on the general surface of the madreporite. These points were investigated in the first and third of the starfish named. The surface of the madreporite is grooved and strongly ciliated. The cilia sweep across it, and have the action of clearing away all *débris*. In so doing they produce slight but appreciable suction through the outer ends of the pore-canals, in small isolated pieces of madreporite. The pore-canals themselves, together with their collecting stems, exhibit feeble ciliary action in an outward direction and thus continue the aboralward ciliation of the lining of the axial sinus (p. 246). The combined action of the surface cilia and of the pore-canal cilia is not strong enough to compete with the inward suction of the stone canal and cannot accordingly prevent the entrance of water from outside into the stone canal, at any rate by way of the centrally placed pores, should other circumstances be favourable.

The following physiological results are thus rendered possible (1) passage of water from outside through madreporite into stone canal; (2) prevention of entrance of foreign particles into stone canal; (3) passage of coelomic fluid from axial sinus into stone canal; (4) escape of axial sinus fluid through those marginal pore canals with which this sinus is most directly connected.

Whether, or to what extent, any one of the above processes occurs at a particular time must depend on the conditions as to pressure obtaining within the stone canal and axial sinus. If much fluid passes from axial sinus into stone canal there will be approximation physiologically to the condition in those echinoderms which have an internal madreporite. In living preparations of *Porania pulvillus* I have found it easy to demonstrate the sweeping of carmine particles from the axial sinus into and down the stone canal.

The coelomic fluid contains proteid matter, and probably, under ordinary circumstances, its escape and dilution are as far as possible avoided. In any case, as was emphasised in particular by HARTOG (41), abundance of fluid can be absorbed by a starfish through its skin.* The oralward ciliation of the stone canal will always be able to maintain a useful *extra* pressure within the water-vascular spaces by drawing on the axial sinus fluid, or, the axial sinus being small, by introducing outside water through the madreporic pores.

We can be certain that the stone canal was not the duct of a nephridium related to the hydropore, but the evidence from adult ciliation in *Asterias*, if it be relevant, agrees with the view that the hydropore itself was originally a nephridial opening.

Echinus esculentus.—In the stone canal of *Echinus esculentus*, which I have investigated myself, the currents are always oralwards. Colouring matter will be carried down the entire length of an excised canal in rather less than 15 seconds. If

* Mr. J. C. KNOX found that a full-sized starfish could take in as much as 50 c.c. in less than three-quarters of an hour.

the aboral end be occluded, the ciliary action will empty the canal, causing it to collapse. If, next, the aboral end be opened and the oral end occluded, the canal will swell out again and become turgid. The canal is too small to carry much water, but, if the volume suffices, the pressure will go far to ensure distension of the water-vascular system.

As in *Asterias*, the cilia on the surface of the madreporite act tangentially, and tend to sweep away foreign particles. The pore-canal system, as a whole, has its cilia acting oralwards, but in each pore-canal there is a short superficial segment which shows the converse condition. Probably the transition is not an abrupt one, but takes place in spiral fashion. These points were made out in the course of examining preparations obtained by sacrificing the edge of a keen razor in cutting very thin tangential sections of fresh madreporites.

In *Echinocardium cordatum*, Mr. A. L. THOMSON, working at the Millport Station, found the currents within the madreporic canal system and the sub-apical ampullary space, and the short ciliated "stone canal" to be in a downward or oral direction. Parallel observations on my part agreed with these results. The question of outward ciliation at the extreme outer ends of the madreporic canals was not satisfactorily decided.

Those who have worked at the madreporic currents do not seem to have differentiated particularly in the adult between the function of the stone-canal ciliation and that of the pore-canal system and of the axial sinus. On the whole, there has been agreement that the currents are in an oral direction, though HARTOG (41) adduced various arguments to the contrary, and HAMANN (39, p. 731) thought that the cilia on those surfaces within the stone canal which are lined by low epithelium (see p. 246) might act aborally, while various authors have referred to the presence of corpuscles within channels belonging to the pore-canal system, apparently in course of being swept out therefrom. Among those who speak for oralward currents are LUDWIG (53, 54), PROUHO (76), CUÉNOT (12), and MACBRIDE (55). CUÉNOT notes that the stone canal is almost always free from corpuscles though these may be present abundantly in the rest of the hydrocœle (11, pp. 317-8), but he lays stress on the fact that, in the uninjured starfish, inward currents are exceedingly difficult to observe and probably only occur intermittently. He also calls attention to the cleaning action of the superficial madreporic cilia, the probable passage of fluid from axial sinus into the stone canal, and the influence of the stone-canal ciliation on pressure in the water vascular system. LUDWIG (53, pp. 378-9) holds that the pore-canals as well as the stone canal in echinoderms generally have an inward ciliation, bringing evidence as regards the pore-canals from observed currents in the internal madreporite of Holothurians, the openings on the oral surface of the discs of Crinoids, and the hydropores of Auricularia larvæ. He does not seem, however, to have investigated the pore-canal system by itself in Asterids and Echinids. BURY (8, p. 421) has stated that he saw evidence of outward ciliary action in the hydroporic canals of Echinid plutei, Bipinnaria, Auricularia, and Tornaria. MACBRIDE (55, p. 381) found that suspended particles passed into the pore canal of *Amphiura squamata* and were in some cases apparently ingested by the cells lining it. He lays stress also on the pressure-maintaining function of the stone-canal ciliation.

(c) *Hæmal System; Probable Circulation.*

The hæmal system has in general the arrangement elucidated by LUDWIG (51, 54), the disposition of its more centrally placed parts resembling also that of *Solaster*

(28, p. 186). I can confirm LUDWIG's view that the so-called gastric hæmal strands are really hæmal in character, and HAMANN's (38, pp. 69, 70) statement that the spongy channels in these strands take origin in the connective tissue spaces of the wall of the alimentary canal.

In the larva, as was noted on p. 248, the floor of the dorsal sac is muscular and pulsates rhythmically. At metamorphosis this floor is invaginated by the spongy tissue underneath, and finally the tissue in question projects into the cavity of the sac, as the so-called head process or glandular process of the axial organ. It is a point of much interest whether rhythmic contractions of this process occur, and, if so, what is their rhythm. There is also the question whether similar contractions occur in the rest of the axial organ and in the gastric hæmal tufts. Working with fresh specimens at the Millport Marine Station, I observed rhythmic contraction in the head process of the axial organ in the following species: *A. rubens*, *Solaster papposus*, *Porania pulvillus*, *Echinocardium cordatum*, and *Echinus esculentus*. The contractions are slight but definite, the average period of rhythm in *A. rubens* being 30 seconds. As regards the axial organ, I have noticed faint rhythmic contractions of its upper part in *Echinus esculentus*, while in *A. rubens* the results of observation were at times positive, and at times negative, the period of rhythm in the former instances being again approximately 30 seconds. The gastric hæmal tufts in *Asterias* were found to exhibit rhythmic contractions in the case of specimens which were allowed to feed freely after they had been starved for several days.* Slow contractions of the hæmal tissue within the aboral sinus also occur.

Contractions of the head process of the axial organ have been put on record in *Dorocidaris papillata* by PROUHO (76, p. 331). The axial organ itself has been described as showing contractions by TIEDEMANN (quoted from LUDWIG, 51, p. 119) in *Astropecten aurantiacus*, by HOFFMANN (44, p. 22) and DURHAM (21, p. 106) in *A. rubens*, and by KOWALEVSKY (48, p. 74) in Echinids. HOFFMANN described rhythmic changes of volume in the gastric hæmal tufts of *A. rubens* (44, p. 21).

Taking the reasonable view that the contractions of the head process of the axial organ are normal and of functional significance, we note that in starfish the dorsal sac is completely, or almost completely, embedded in the calcareous madreporite. The rigidity of this structure would put an obstacle in the way of any change of volume in the head process were it not for the ampulla of the stone canal (p. 268), which, being open to the axial sinus and to the pore-canal system, can readily increase or diminish passively in size. The ampulla seems to be provided specially for some such purpose, and while I have not observed contractions of its floor, such contrac-

* The experiment was instituted, as it occurred to me that, since respiration is cared for otherwise, the activity of transference of the hæmal fluid might depend in great part on whether a supply of absorbed nutritive material was available or required. It is not improbable that in the severance of the respiratory and nutritive functions we have a key not only to the reduced condition of the vascular system throughout Echinoderms, but also to many of the structural and physiological peculiarities of the system in this phylum.

tions, by creating negative pressure within the dorsal sac, could draw hæmal fluid into the spaces within the head process of the axial organ. Indeed, it is just possible that there may be rhythmic contractions of the ampulla alternating with those of the head process. This looks feasible in *Solaster*, where the equivalent of the ampulla is a thick-walled diverticulum invaginated into the dorsal sac (p. 249). Even in *Asterias* there is no reason why the ampulla should not have the function in question at least in some slight degree. In any case, whether the ampulla is active or passive, its relation to the dorsal sac receives a natural explanation on the lines indicated above.

I cannot but conclude that there is a circulation in the hæmal system of *Asterias*, and that the following are probably among its chief features: (1) A transference of fluid, nutritive but not respiratory in function, takes place along the gastric hæmal strands from the stomach absorbents to a node at the junction of head process with the axial organ; (2) the head process of the axial organ acts as a pulsating ampulla, or "heart," connected with this node and also with the tissue spaces of the aboral body wall; (3) the axial organ contains efferent channels which supply the oral hæmal ring, and through that the various radial hæmal strands; (4) other main efferent vessels pass along the aboral perihæmal sinus, and send off branches to the gonads in each inter-radius.

According to this view "hæmal" channels efferent from the heart are distributed in the near neighbourhood of all the structures (not belonging to the digestive system) which have the greater physiological activity, viz., the nervous system, the gonads, the muscles of the tube feet and of the ambulacral ossicles.

This account of the probable circulation in the Asterid hæmal system is supported by the fact that there is a corresponding circulation in what I believe to be the homologous hæmal structures of *Balanoglossus* (see p. 278). It will also be remembered (p. 248) that contraction of the floor of the dorsal sac in a double-hydrocœle larva progressed from behind forwards. Whether there is a full circle in the starfish circulation, and what may be the probable course of circulation within the hæmal system of other echinoderms, are too wide questions to be discussed here, but it may be noted that while in Holothurians a dorsal sac and an axial organ are apparently absent, contractions of the longitudinal vessels of the intestine occur (49, vol. 2, p. 450). We may correlate the absence of a central pulsating complex with the elongated shape of the animal and the contractility of the body wall (*cf.* various Annelida).

(d) *Food Canal.*

Stomach.—In all starfish having an anus, according to MÜLLER and TROSCHER (quoted from LUDWIG, 54, p. 581), an aboral portion of the digestive cavity, the so-called pyloric sac, can be distinguished from the lower or stomachal portion.

In *A. rubens* a separation of this kind appears with great distinctness just after metamorphosis and during early growth, but later (*e.g.*, in specimens measuring 3 inches total diameter) becomes obscured through widening out of the pyloric sac. The paired radial cæca arise from this sac, each pair by a duct which is at first relatively long and slender but is afterwards almost shortened out of existence, during the widening process referred to above. The roof of the pyloric sac will now be found to exhibit downward radial folds, of which there are five main ones, passing outwards from a central point. There is also a distinct groove or channel continuing the stalk of each pair of radial cæca towards the centre of the pyloric roof, but not forming a long duct, in the manner which is characteristic of *Solaster*. A slit-like aperture, with the long axis radially directed, leads from the pyloric sac region into the intestine (*cf.* p. 82). This aperture is not situated in the middle of the roof of the pyloric sac, but is excentric in the direction of inter-radius V/I. At the end of metamorphosis and in early growth (the specimen sectioned measured 1 inch in total diameter), it lies between the stalks of cæca I and V, if anything rather nearer to the latter than the former. Later (the specimen sectioned measured 3 inches in total diameter), and in adult anatomy the aperture is still excentric as judged by the point of convergence of the radial folds above referred to, the displacement being again towards inter-radius V/I.

Intestine, etc.—The intestine is short and ends in a large rectal sac, the aperture looking towards inter-radius V/I. Just before its termination, in the 3-inch specimen sectioned, it gave off towards the centre of the disc a small diverticulum ending blindly in the connective and muscular tissue around the intestine. The rectal sac is much expanded and lobulated in inter-radius V/I and it also sends round clockwise as viewed aborally, lobules for inter-radii V/IV, IV/III, and III/II. These lobules decrease in size in the order given, and the last one, or even the last two, may be absent. The rectal sac gives rise to a short canal—the rectum proper—which opens on the inter-radius V/I side of the middle of the aboral surface.

In the Holothurians, the regular and irregular Echinoids, and the Crinoids, the alimentary canal is tubular, and, being longer than the mouth-anal axis, naturally falls into coils. These vary greatly in form but have in common that the final result is a curvature in the watch hand direction from mouth to anus as seen from the oral side. Diagrams of the course of the food canal illustrating this point appear in various text-books, *e.g.*, that of A. LANG (49, p. 475). The Asterid food canal has not so far been included in this series, but from what has been said above, it will be seen that in spite of the globular condition of the main part of the digestive cavity the same primary curvature can here also be made out, as is shown by (*a*) the position of the anus in inter-radius V/I, and (*b*) by the place of opening of the intestine into the roof of the pyloric sac. The relation to the larval condition is illustrated in Plate 22, fig. 21), and, for comparison, a diagram of the curvature of the crinoid food canal is also given (fig. 20). MACBRIDE (57, p. 312, text-fig. 6) demonstrated similar features in the case of *Echinus*.

The characteristic curvature of the alimentary tract in any Echinoderm will of course receive a natural explanation if one assumes that the primitive larval type resembled the Asterid one in having a functional food canal, the posterior end of which curved ventrally and then forwards. The permanent mouth and anus, even as new formations, would naturally become connected with the food canal at points

as near as might be to the larval oesophagus and rectum. Viewed therefore from the aboral (larval right) side, the main curvature of the adult food canal must run in the sinistral (see note on p. 217) direction. In *A. rubens* this curvature, though almost obscured out of recognition, should be counted as practically accomplishing a full circle, since at metamorphosis the stalk (a remnant of the larval preoral lobe) is last found in inter-radius V/I, *i.e.*, the anal inter-radius.

XII. GENERAL AND SUMMARY.

(a) *Double Hydrocoele.*

A surprisingly large number of the larvæ developed double hydrocoele. Adequate description of the condition will entail a separate paper, but the following facts should be noted here, since they have a bearing on the homologies of certain important structures, particularly the hydrocoele, the dorsal sac, the epigastric and the hypogastric cœlom. In perfect double-hydrocoele larvæ the right enterocœle behaved exactly like the left one in the following respects: (1) The right posterior cœlom became cut off completely from the right middle cœlom (*cf.* p. 242). (2) The antero-ventral corner of the right posterior cœlom extended downwards and to the left, further than in the normal condition, forming a ventral "horn." This horn met and united near the middle line with the corresponding horn of the *l.p.c.*, and from the common cavity there grew up folds which finally encircled the rectum (*cf.* p. 244). (3) Five hydrocoele lobes developed in the wall of the *r.m.c.* (*cf.* p. 243). (4) A secondary communication became established between the dorsal horn of the *r.p.c.* and *r.m.c.* (*cf.* p. 243). (5) In very late larvæ a stone-canal groove and the rudiment of an axial organ appeared on the right as well as on the left side (*cf.* pp. 256, 257). (6) A pharyngeal cœlomic outgrowth developed from the dorsal horn of the *r.p.c.* (*cf.* p. 259).

A dorsal sac or madreporic vesicle was present in the middle line, and pulsed during larval life with the same rhythm as in normal larvæ (see also p. 249.) Series of sections showed that the sac was an entirely separate structure from either the left or the right hydrocoele.

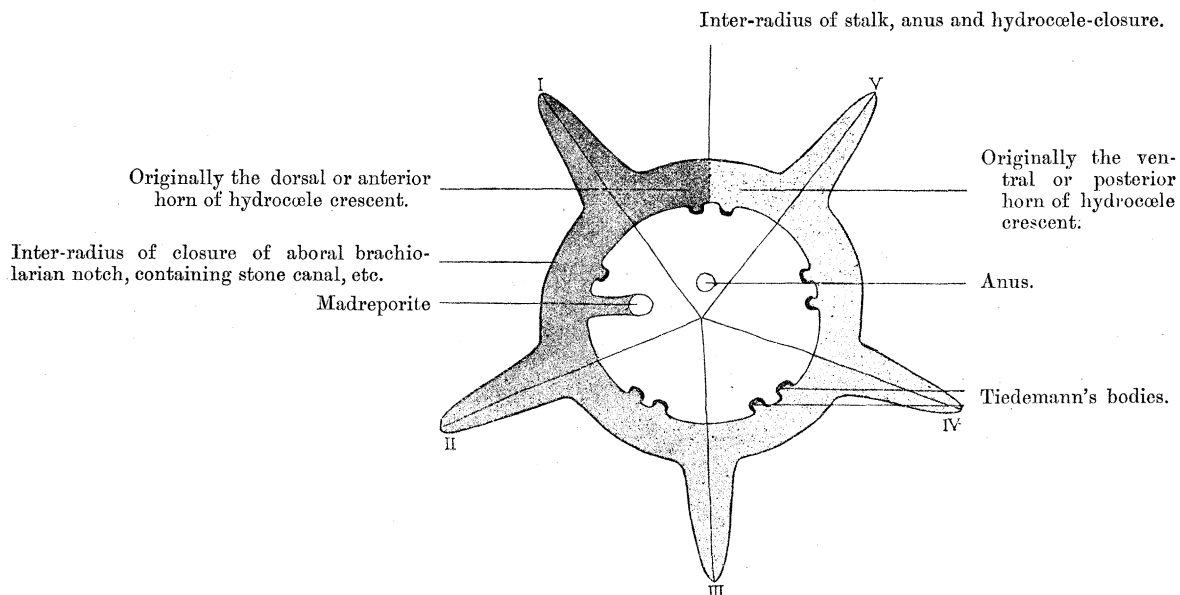
More than one of the double-hydrocoele specimens proceeded to metamorphose. The anterior and middle regions of the larva became retracted as in normal metamorphosis but joined the ventral surface. The larval mouth closed and the preoral lobe gave rise to a stalk joining the body in the middle line of the ventral surface. This stalk gradually became more slender and finally ruptured near the disc, leaving sucker and stalk behind, as in ordinary metamorphosis.

Two points are obvious from the above:—(a) The right posterior (epigastric) and the left posterior cœloms correspond with one another. The evidence from other Echinoderm life-histories *against* MASTERMAN'S (60) view that the hydrocoele corresponds with the epigastric cœlom is thereby completely confirmed. (On p. 234 I have suggested an explanation of the exceptional features in the development of the enterocœles in *Solaster* and *Cribrella*.) (b) The dorsal sac or madreporic vesicle is a median structure and cannot represent a right hydrocoele, as it does according to the

view which was put forward by MACBRIDE (see p. 248). Even apart from the evidence provided by double hydrocœle, the view just referred to could not readily be reconciled with the data from *A. rubens* regarding the mode of development, activity, and adult relations of the sac. It will be remembered also that the right hydropore when present opens into the right enterocœle exactly in the region afterwards recognisable as the *r.m.c.* (see Plate 18, fig. 4) and that the dorsal sac in its origin is entirely independent of this cavity.

(b) *Numbering of Rays.*

Three important sets of adult radial structures appear sufficiently early for us to try to place their constituents in series with reference to the antero-posterior axis of the larva. These are the hydrocœle pouches, the radial cœca, and the aboral arm rudiments. It was noted earlier that hydrocœle pouch I should be considered the most anterior of the hydrocœle rudiments (p. 243), and that radial cœca I belong



TEXT-FIG. 1.—Diagram to illustrate the Numbering of the Rays adopted on the developmental grounds explained below. The view is from the aboral side. For purposes of illustration, the original anterior horn of the hydrocœle crescent has been darkened and made to shade gradually into the middle and posterior portions. The point referred to in note on p. 257 is brought out in slightly exaggerated form, namely, that the stone canal opens into the ring canal rather nearer ray II than ray I. The diagram also indicates that stalk, anus, and closure of hydrocœle ring are to be looked for in inter-radius I/V, while the position of the madreporite, and the closure of the aboral brachiolarian notch (p. 252) are in inter-radius I/II.

The numbering is the same as that used by MACBRIDE (55), and exactly the converse of that adopted by LUDWIG (52, 54), GOTO (33), and MASTERMAN (60). SEDGWICK'S (84, p. 120) and DELAGE'S (16, p. 36) numbering makes the anal and the madreporic inter-radii I/II and II/III respectively.

to an anterior region of the stomach wall (p. 262). The position of the adult anus in inter-radius I/V separates the ray I structures from the ray V structures, associating the former with those of ray II, a ray which certainly belongs to the anterior portion of the series.

These facts strengthen the evidence provided by the nine-rayed sun-star *Solaster endeca* (29, pp. 28, 29). Here the four extra rays are developed one by one in order from ray V onwards, so that we cannot but enumerate the series as beginning with pouch I. This view is still further confirmed by evidence from the double-hydrocœle larvæ of *Asterias* (p. 275), one of which underwent metamorphosis, producing a bilateral "starfish" with a right and left set of hydrocœle pouches, the two pouches I being on opposite sides at the anterior end of the animal.

It follows from the above that inter-radius I/V is morphologically both the most anterior and the most posterior of the inter-radii. The first and last of the rays, viz., rays I and V, have become approximated like the outside radii of an almost fully opened circular fan, ray V undergoing the principal part of the movement. This inter-radius contains the adult anus, and although the adult mouth is central, still the attachment of the stalk at metamorphosis indicates that the mouth has travelled to its final position by way of the inter-radius named.

Arm rudiment I does not fit into the above scheme, being developed at the ventral end of the series of arm rudiments, but in view of the other data given above we must look on this arm rudiment as having somehow become displaced from its primitive position. This has entailed the consequence, as seen in the development of the epigastric mesentery (p. 258), that the anterior and posterior ends of the larval sagittal mesentery are brought together at metamorphosis in inter-radius I/II. Possibly of the two gastric hæmal tufts the sinistral one belongs to the anterior, and the dextral one to the posterior extremity of the larva (p. 258). It is from the attachment of the epigastric mesentery to the body wall that the tufts emerge side by side in inter-radius I/II.

(c) *Nearest Allies of Echinoderms.*

Primitive Larval Characters: the Ancestor.—The data provided by this paper support the view put forward by METSCHNIKOFF (64) and adopted by many recent workers, that there is a direct relationship between *Balanoglossus* and Echinoderms. Indeed, it would seem that the Enteropneusts and the Pterobranchia (*Cephalodiscus*, *Rhabdopleura*) are the only groups with which the Echinoderms are closely connected. We may omit the Pterobranchia from the following comparison, since their larval history is not yet fully known, while their resemblances to *Balanoglossus* in adult structure are too obvious to need tabulation :—

Comparison with Balanoglossus.—We owe to METSCHNIKOFF (64) the groundwork of the comparison between the Asterids and *Balanoglossus*. MORGAN (68, p. 442), followed by BURY (9, p. 128), and afterwards by MASTERMAN (60), extended it in the important matter of the pulsating vesicle or dorsal

sac. The points in which the comparison is continued still further in this paper have reference chiefly to the body and head of the axial organ, the principal hæmal trunks, the pharyngeal cœlom, and the regions of the axial sinus.

The Larva.—In addition to the well known similarities between Tornaria and Bipinnaria we may note as regards the cœloms that the alternative between an independent and a common anterior origin for the cavities has evidently presented itself in the history of the Echinoderm as well as of the Enteropneust phylum, and has received something like the same answer in both (see p. 233). It may be added that the antero-dorsal position of the junction between preoral and postoral bands in the early bipinnaria of *A. rubens* permits us to hold the view that the so-called apical sense-organ of Tornaria represents a supra-cæsophageal ancestral structure.

The Adult.—The following table gives the homologies which, I think, are to be drawn between Asterids and Enteropneusts. The major comparisons seem to be reasonable, and if that is so the minor ones should also be counted as valid, so long as they rest on the same grounds as those by which the others are decided, and do not conflict with ascertained facts :—

ENTEROPNEUSTS.	ASTERIDS.
Proboscis pore	Pore-canals.
Proboscis cœlom	Aboral part of axial sinus including ampullary portion (p. 268).
Left collar cœlom	Deeper part of axial sinus. Hydrocœle. Internal oral circular sinus.
Right collar cœlom	Not represented except in double-hydrocœle specimens.
Right trunk cœlom	Epigastric cœlom.
Left „ „	Hypogastric cœlom.
Left pharyngeal cœlom	Pharyngeal cœlom.
Pericardial cœlom	Dorsal sac.
Central sinus or “heart”	Head process of axial organ.
Dorsal vessel of trunk*	The gastric hæmal tufts (p. 258).
Left pharyngeal vessel†	Axial organ and and
Ventral vessel of trunk	Oral hæmal ring.

* Afferent to the heart (*cf.* pp. 272, 273 and p. 249).

† The pharyngeal vessels are efferent from the heart in *Balanoglossus*, and a large portion of each is made up of a spongy network of blood channels with distinctly cellular walls which lies in the edge of a fold of the pharyngeal cœlom, a forward extension of the cœlom of the trunk. In *Asterias* at metamorphosis the proximal part of the pharyngeal pocket has a similar relation to the developing axial

ENTEROPNEUSTS.

ASTERIDS.

Left branches of latter vessel	Radial hæmal canals.
Left genital rachis with accompanying space and vessel.	Genital rachis, aboral perihæmal sinus, aboral hæmal ring, etc.

Primitive Characters of the Brachiolarian Larva.—The brachiolaria shows itself to be in all probability the most primitive of existing Echinoderm larval types, in virtue of the following characters taken as a complex :—

(1) In possessing a large preoral lobe ; (2) in showing vestiges of a primitive “protocoelomatous” mode of origin of the posterior cœlom ; (3) in feeding for itself from the gastrula stage right up to metamorphosis ; (4) in having an arrangement of the enterocœlic cavities from which that of the other types of Echinoderms can be derived, and in showing, to begin with, practically perfect bilateral symmetry with regard to the middle or hydrocœlic region of the right and left cœloms ; (5) in having the hydrocœle originating in the left middle cœlomic region as an open crescent ; (6) in having the larval stomach and part of the larval œsophagus and intestine retained ; (7) in having a gut curvature from which the disposition of the alimentary canal in Echinoderms generally can be derived ; (8) in the fact that all the perihæmal pouches originate from the *l.p.c.* ; (9) in having a dorsal pulsating “epicardial” sac ; (10) in acquiring radial symmetry during a fixed stage from which release is obtained by loss of the larval stalk.

Common Ancestor of Balanoglossus and Echinoderms.—We are probably justified in inferring (1) that this ancestor was eleutherozoic ; free swimming or crawling ; with an anterior cœlom* and (paired) middle and posterior cœloms, the anterior and organ, and it will be remembered (p. 275) that the late double-hydrocœle larvæ showed the formation of a pharyngeal cœlom and of an axial organ on the right as well as on the left side.

It is obvious, from its structure, that the axial organ is more than a simple vessel or network of vessels. It contains parenchymatous tissue, and probably has an internal secretion. If it has also an excretory function, the products of excretion could find a way of escape through the marginal madreporic pores (see p. 270). The holothurians which have no external hydroporic canals are unprovided with an axial organ. It is interesting to note that SPENGLER, in 1893 (88, p. 753), while discounting any close relationship between the hæmal structures in *Balanoglossus* and starfishes, stated that from the purely histological point of view the pharyngeal vessels of the former might just as reasonably as its glomerulus be compared with the axial organ of the latter.

* Probably the anterior cœlom was unpaired in the ancestor. The ontogenetic evidence is as follows. Two separate sacs are formed in *A. rubens*, but they take origin from the same expanded portion of archenteron. They remain separate for a considerable time, but finally unite in the preoral lobe. In *Porania* the sacs arise together in the sense that, as a rule, they are not separated from one another previous to their separation from the archenteron. They unite later in the preoral lobe. We have apparently only one ascertained example among bipinnariæ (see p. 242) in which this union does not occur. As regards starfishes with abbreviated development, and all the other orders of Echinoderms, there do not seem to be any instances of a double origin of the anterior cœlom. BATESON (3, p. 525) and DAVIS (15) found an unpaired anterior cœlom in their Tornariæ. The double origin in *A. rubens* and

middle cœloms opening on one or both sides by pores which served chiefly for the adjustment of internal pressure though they were possibly nephridial in their first origin; possibly with the middle or the anterior region bearing "tentacles" which were hollow protrusions of the cœlom; with "epicardial" pulsating sac, "heart," and hæmal system; with a sense organ or organs dorsal to and in front of the œsophagus; with mouth placed antero-ventrally; with sub-epidermal nerve plexus thickened to form tracts which probably included a ring or commissure round the mouth and dorsal and ventral centres, and (2) that a fixed stage following after a creeping stage was present in the evolution of the echinoderm type from the common ancestor, and that it was during the acquirement of the fixed stage that the primitive crinoid stem became separated from that of the Asterids; the primitive asterid stem is the parent of the remaining classes of Echinoderms.

In the above views I agree in the first place with those who reject SEMON'S *Pentactula* (85) theory, and in the second place with those who, like SEMON himself, BÜTSCHLI (10), MACBRIDE (55), BATHER (3A) and MASTERMAN (60) believe that there has been a fixed stage in the evolution of Echinoderms. There are, however, no cogent reasons for thinking that fixation took place by an attaching organ situated elsewhere than in the middle line of the preoral lobe (*e.g.*, right side of body according to BÜTSCHLI, right side of preoral lobe according to BATHER). Very serious ontogenetic difficulties will be introduced if we derive the asterid stock from an Antedon-like one as does MASTERMAN (p. 407) or even from a simple pelmatozoic one as does BATHER (p. 875). It seems to me that MACBRIDE (1896) was right in making the Crinoids an offshoot from the stock which led through the primitive Asterids to the remaining classes of Echinoderms (55, p. 398, 1896). To the characters usually ascribed to the common ancestor I would add the possession of a circulatory "hæmal" system with greater functional activity than in any present day descendant.

(d) *Summary of Development.*

(For paging, see under CONTENTS, pp. 213-216.)

Spawning season from end of April till beginning of July; maturation in progress while eggs are being shed; segmentation total and equal or practically equal; blastula wall a single layer; gastrula by invagination; mesenchyme arises, after gastrulation, from enlarged blind end of archenteron.

The Larva (External).—Gastrula elongates and blastopore migrates ventralwards; stomodæal pit and circumoral depression form near middle of ventral surface; preoral and postoral bands merge at first into an antero-dorsal strongly ciliated area; these bands next continuous as in auricularia, then divided producing bipinnaria type. The typical larval ciliated processes grow out, all relatively long, slender and freely movable, especially the postero-lateral pair. The brachia have the preoral band continued over them, and have truncated ends bearing six to eight papillæ. Sucker well marked with usually two papillæ on each side of it; posterior part of larval body becomes disc-like and shows five arm rudiments in crescentic series; an certain other starfish (*A. vulgaris*, FIELD, 23; and *A. glacialis*, GOETTE, 32), may well be related to the fact that the anterior cœlom has had added on to it the task of forming the paired middle and posterior cœlomic regions (p. 234) in larvæ which are increasing rapidly in length.

interval (aboral brachiolarian notch) between the antero-dorsal and antero-ventral arm rudiments (rudiments II and I).

Ciliation persists from blastula stage onwards, but becomes lessened over general surface; ciliated bands are locomotor except transverse portion of preoral band; special adoral ciliation consists of peristomal ring and œsophageal loop and acts towards stomach except on small ventral segment of peristomal ring; surface between the preoral and postoral bands is a food-gathering area; buccal cavity and first part of œsophagus can be emptied by backward flexion of preoral lobe.

The Larva (Internal).—Two enterocœlic pouches, right and left; hydropore on left side, opening into left pouch; an occasional right hydropore; probable rudiment of posterior coelomic outgrowth from stomach entoderm; enterocœles grow forward, uniting in preoral lobe, and backwards, covering sides of stomach; anterior, middle, and posterior coelomic regions; dorsal sac from mesenchyme near mid-dorsal line; *r.p.c.* and *l.p.c.* cut off; ventral horn of *l.p.c.* crosses to right, opens into *r.m.c.* and grows around rectum; series of five hydrocœle pouches develop in wall of *l.m.c.*; dorsal horn of *l.p.c.* opens into *l.m.c.*; *l.p.c.* gives single outgrowth for pharyngeal cœlom; alimentary canal shows œsophagus, stomach, intestine, and rectum, probably at least a fifth of the œsophagus being stomodœal.

Metamorphosis (External).—Brachia give temporary attachment; definite fixation by sucker through cement formation; retraction of anterior and middle regions of larva and of ciliated processes towards left side of larval disc to form oral surface of starfish; aboral surface from right side of larval disc; aboral notch between arm rudiments I and II closes to form inter-radius I/II which contains hydroporic opening and dorsal sac; part of preoral lobe forms stalk joining disc on inter-radius I/V side of centre of oral surface; hydrocœle lobes project externally; sucker feet develop and first two pairs come into use; stalk becomes slender, drawn out, and finally ruptured near disc; starfish now free, sucker and stalk being left behind; adult mouth appears in centre of oral surface, and adult anus aborally in inter-radius I/V.

Metamorphosis (Internal).—Opening between *r.m.c.* and ventral horn of *l.p.c.*, and that between *l.m.c.* and dorsal horn of *l.p.c.*, become closed; *r.m.c.* disappears; provisional axial sinus formed which includes the *l.m.c.* and the right and left anterior cœloms, and sends cavity into stalk; in the end, *l.m.c.* gives rise to ring canal of hydrocœle, adult axial sinus, stone canal, axial organ, internal oral circular sinus; hydrocœle ring encircles remains of cavity of stalk; stone canal arises as a groove which afterwards closes to form a canal, commencing near inner opening of hydropore and joining hydrocœle ring in inter-radius I/II; internal oral circular sinus is left after fusion of opposite layers preceding formation of adult mouth; axial organ begins by cell proliferation in fold of wall of axial cœlom parallel with the stone canal.

Pharyngeal outgrowth of *l.p.c.* forms pharyngeal cœlom; horns of *l.p.c.* grow round and meet, being separated for a time by mesentery of axial sinus, which

afterwards breaks down; *l.p.c.* becomes hypogastric cœlom and *r.p.c.* becomes epigastric cœlom; mesentery between *l.p.c.* and pharyngeal cœlom (circular hypogastric mesentery) forms ligaments on oral side of stomach; mesentery between *l.p.c.* and *r.p.c.* (circular epigastric mesentery) forms ligaments on aboral side of stomach. Perihæmal outgrowths all from *l.p.c.*, that of I/II arising close to opening from *l.p.c.* into axial sinus; genital rachis and aboral perihæmal sinus from dorsal horn of *l.p.c.*; larval mouth closes early in metamorphosis; larval œsophagus becomes constricted and then divided, the superficial portion along with buccal cavity joining epiderm of oral surface, and the deeper portion becoming incorporated with the stomach. Adult mouth, a new formation without new stomodæum; larval anus closes and terminal moiety of larval intestine degenerates; proximal moiety gives rise to adult intestine and rectal sac; adult rectum, a new formation, growing out from the rectal sac.

CONCLUSIONS.

The following conclusions of morphological or general interest may suitably be appended to the preceding "Summary of Development":—

(1) The presence of a rudimentary posterior enterocœlic outgrowth suggests a principle which goes far to reconcile or explain what seemed extremely divergent modes of origin of the enterocœles in starfish and other Echinoderms, and in Enteropneusts (pp. 233, 234).

(2) There is morphological equivalence between the epigastric (larval right posterior) cœlom and the hypogastric (larval left posterior) cœlom (p. 242, in *development*; pp. 258, 259, at *metamorphosis*; p. 275, in *double hydrocœle*).

(3) In the early larva there is a right middle cœlomic region morphologically equivalent to the region on the left side which gives rise to the hydrocœle, viz., the left middle cœlomic region (p. 242, *development*; p. 230, *double hydropore*; p. 275, *double hydrocœle*).

(4) No rudiments of the right hydrocœlic region are recognisable after normal metamorphosis (p. 254).

(5) The separation of the young starfish from its stalk, and certain other considerations, harmonise with the view that the asterid and the crinoid stalks are morphologically equivalent (p. 255).

(6) The dorsal sac is an "epicardial" pulsating sac homologous with the pericardium of *Balanoglossus* (p. 248). There is detailed morphological and probably also functional correspondence between the hæmal systems of Asterids and Enteropneusts (p. 278). In particular, the axial organ and pharyngeal cœlom of *Asterias* are homologous respectively with the left pharyngeal vessel and the left pharyngeal cœlom of *Balanoglossus*.

(7) A bilateral "starfish" can result from the metamorphosis of a double-hydrocœle brachiolaria (p. 275).

(8) The rays of a starfish should be numbered according to a scheme which makes the anal inter-radius in part the most anterior and in part the most posterior of the inter-radii (p. 276).

(9) There is evidence of the existence in the late larvæ of a sub-epidermal nervous network and of a system of neuro-muscular fibres (p. 264).

(10) Of all known echinoderm larvæ the brachiolarian type has probably retained the greatest number of primitive characters and acquired the smallest number of secondary characters (p. 279).

(11) New data are given regarding a number of points relating to adult structure and function, *e.g.*, regions and curvature of alimentary canal; structure and function of madreporite; the hæmal system, cœlomic and perihæmal ciliation, etc. (see p. 217).

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EXPLANATION OF PLATES.

NUMERALS AND ABBREVIATIONS EMPLOYED.

- 1, 2, 3, 4, 5, 6 are placed respectively on the median dorsal, anterior dorsal, posterior dorsal, posterior lateral, postoral and preoral ciliated processes.
- I, II, III, etc., point respectively by continuous lines to lobes I, II, III, etc., of the hydrocœle, and by dotted lines to the corresponding arm rudiments.
- ant. br.* . . . Anterior brachium.
ant. cœl. . . . Anterior cœlom.
amp. . . . Ampulla of sucker foot.
ax. o. . . . Axial organ.
ax. s. . . . Axial sinus.
b. cav. . . . Buccal cavity.
b. stk. . . . Base of attaching stalk.
cil. prs. . . . The reduced ciliated processes.
circ. s. . . . Circular "lymph" channel (p. 253).
d. h. l. p. c. . . . Dorsal horn of left posterior cœlom.
d. med. pr. . . . Median dorsal process.
epg. c. (r. p. c.) . . . Epigastric or (larval) right posterior cœlom.
ep. mes. . . . Epigastric mesentery.
hy. . . . Hydrocœle: most frequently the ring canal of the hydrocœle, *e.g.*, in fig. 28.
hy. can. . . . Hydroporic canal.
hyp. c. l. p. c. . . . Hypogastric or (larval) left posterior cœlom.
hyp. mes. . . . Hypogastric mesentery.
inf. lab. lp. . . . Inferior labial loop of adoral ciliation.
int. . . . Intestine.
int. or. s. . . . Internal oral circular sinus.
int. or. s.' . . . Remains of provisional axial sinus, in fig. 29, passing out towards the stalk.
l. a. cœl. . . . Left anterior cœlom.
l. entc. . . . Left enterocœlic vesicle.
l. hy. can. . . . Left hydroporic canal.
- l. m. cœl.* . . . Left middle cœlom (or cœlomic region).
l. p. c. hyp. c. . . . (Larval) left posterior, or hypogastric cœlom.
m. . . . Mouth.
m.' . . . Region of former larval mouth in fig. 28.
m. d. l. . . . Middle dorsal lobe or lappet of the posterior ciliated band (p. 235).
nr. or n.r. . . . Part of circumoral nervous tract. (In fig. 27 this identification is not perfectly certain.)
œs. . . . Œsophagus.
œs. lp. . . . Œsophageal loop of the adoral ciliation.
po. pr. . . . Postoral ciliated process.
perih. . . . Perihæmal pouch.
perist. . . . Peristomal ciliated ring.
phar. c. . . . Pharyngeal cœlom.
po. cil. bd. . . . Postoral ciliated band.
po. pr. . . . Postoral ciliated process.
pod. . . . Sucker foot.
pr. cil. bd. . . . Preoral ciliated band.
pyl. . . . Pyloric sac region.
pyl. c. . . . Pyloric or radial cæcum.
r. a. cœl. . . . Right anterior cœlom.
rect. . . . Rectum.
rem. . . . Remains of preoral lobe.
r. entc. . . . Right enterocœle.
r. hy. can. . . . Right hydroporic canal.
r. m. cœl. . . . Right middle cœlomic region (right hydrocœlic region).
r. p. c. epg. c. . . . (Larval) right posterior, or epigastric cœlom.
stk. . . . Attaching stalk.
stom. . . . Stomach.
stone c. . . . Stone canal.
ves. . . . Dorsal sac or madreporic vesicle.
vh. l. p. c. . . . Ventral horn of left posterior cœlom.

DESCRIPTION OF PLATES.

PLATE 18.

- Fig. 1.—Larva about 10 days old from ventral side.
- Fig. 2.—Larva of similar age from left side.
- Fig. 3.—Larva of similar age from ventral side, with preoral lobe bent back in the movement of dorsal flexion described on p. 241.
- Fig. 4.—Larva about 18 days old from dorsal side, showing a right as well as a left hydropore. The preoral lobe is again bent back by the movement described on p. 241.
- Fig. 5.—Dorsal view of larva about 21 days old. The enterocœles have united within the preoral lobe, and separation of the posterior cœlom on both sides has begun.
- Fig. 6.—Larva slightly older than last, from ventral side, showing in particular the growth of the ventral horn of the *l.p.c.* across to the right side between stomach and rectum. The relatively small size of the stomach in the last two figures will be noted. Such variations are of frequent occurrence, but in the larvæ which will afterwards grow best the larger size of the stomach is usual.
- Fig. 7.—Larva about 32 days old from ventral side showing fusion of ventral horn of *l.p.c.* with right middle cœlom, the right posterior or epigastric cœlom having already been separated off. The formation of the folds of the *l.p.c.* which enclose the rectum will be noted, and also the first appearance of the hydrocœle lobes in the *l.m.c.* The specimen is drawn as seen in the contracted condition attended by emptying of the buccal cavity (p. 241). The ciliated processes are now developing, and are shown directed forwards in the position adopted when the larva is sinking.
- Fig. 8.—Dorsal view of same larva as is shown in fig. 7. The dorsal sac is to the right of the hydroporic opening. Hydrocœle lobes are appearing in the *l.m.c.* At this stage the *r.m.c.* will be seen to be almost symmetrical with the *l.m.c.*, though not possessing a hydropore, nor showing hydrocœle lobes. The commencing extension of the dorsal horn of the *l.p.c.* will be noted.

PLATE 19.

- Fig. 9.—Ventral view of larva about 38 days old, showing the ciliated processes still further developed, as well as the brachia and sucker. The *l.p.c.* now forms a complete ring round the rectum. The outline of the food canal is shown by dotted lines.

Fig. 10.—Fully developed brachiolaria shown in balancing position and looked at from left side. As regards the *l.p.c.*, its dorsal horn will be made out, as well as the ventral horn enclosing the rectum. The secondary communication between the dorsal horn and the left middle coelom is a little to the left of the end of the line which indicates the dorsal horn. The terminal ossicles, which have now begun to appear, are not shown in the illustration.

PLATE 20.

Fig. 11.—Drawing from right side of brachiolaria at slightly older stage than in last figure. The ciliated processes have reached their full development and are shown in the position adopted when the larva is rapidly sinking. An attempt has been made to exhibit the arrangement of the coelomic cavities as if the right body wall were transparent.

Fig. 12.—View from aboral side of brachiolaria which is just commencing to metamorphose, having been attached for an hour or thereby. The shortening of the anterior and middle parts of the body will be made out, as well as the prominence of the brachia and sucker. The rotation of disc on rest of larva has begun, as also has the closure of the brachiolarian notch.

PLATE 21.

Fig. 13.—View from ventral side of larva a little further advanced towards metamorphosis than in last figure. It will be noted that the larval vent is now on the oral aspect of the disc (p. 252) and that the larval mouth and the various ciliated processes are being retracted within the crescent of the hydrocoele. The partial want of conformity between the arm rudiments and the radial hydrocoele lobes will also be made out.

Fig. 14.—View from oral aspect of starfish 24 hours after the commencement of metamorphosis. The large sucker and the remains of the brachia will be seen. The ciliated processes have become almost completely retracted while the radial hydrocoele pouches have increased in size and are now five-lobed. The position of the larval mouth is noted, but separation of the oesophagus will have taken place by this time. The sucker is as close as may be to the oral surface of the starfish, the stalk being exceedingly short at this stage.

Fig. 15.—Oral view of starfish four or five days after commencement of metamorphosis. The stalk of the sucker has lengthened, the remains of the ciliated processes have entirely disappeared and the adult mouth is beginning to form. As regards the sucker feet, the first two pairs are coming into functional use.

Fig. 16.—Young starfish two days older than last specimen and ready to crawl off, but still attached by the stalk to the small frond of seaweed on which it had fixed itself at the commencement of metamorphosis. Just prior to separation the stalk is even more slender than is shown in the figure. Near its junction with the body, the slightly broader part, from which the separation will take place, is indicated.

PLATE 22.

Fig. 17.—A stage in metamorphosis 18 hours after fixation, from aboral side. Compare with fig. 12. The aboral brachiolarian notch is practically closed. Retraction of the larval processes, etc., is proceeding rapidly.

Fig. 18.—Cleared disc at metamorphosis, from aboral side, showing the arrangement of ossicles and spines described on p. 265.

Fig. 19.—Young starfish a month after commencement of metamorphosis, showing four pairs of sucker feet and the mouth now formed. The radial cæca are bifid and have grown out beyond the margin of the pyloric sac.

Fig. 20.—Diagram of curvature in food canal of a Crinoid, viewed from aboral side (modified from LANG, 49, vol. 2, p. 475).

Fig. 21.—Diagram to illustrate the extremely modified curvature still recognisable in the adult asterid food-canal, and its relation to the food-canal of the larva. The view is from the aboral (right larval side) and the food-canal of the larva is shown in dotted lines (p. 274).

Fig. 22.—Diagram of adoral ciliation in an advanced brachiolaria. The buccal cavity and œsophagus are represented as looked at from in front. The transverse portion of the preoral band which has to do with feeding is shown in black.

PLATE 23.

Fig. 23.—Transverse section of larva, about 21 days old, in region of the pore-canal, showing cells from which the dorsal sac is developed.

Fig. 24.—Transverse section of larva about 29 days old, showing dorsal sac now vesicular and connected with stone canal by a thin strand of cells. As frequently happens the posterior end of the œsophagus is invaginated into the stomach, forming the smaller inside ring.

Fig. 25.—Transverse section of still older larva, about 35th day, at time when pulsation of dorsal sac begins to be evident. The left and right posterior cœloms are now cut off from the middle cœloms and the ventral horn of the *l.p.c.* has united with the right middle cœlom.

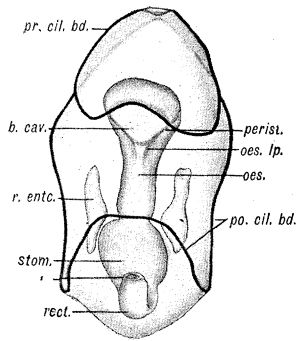
- Fig. 26.—Section somewhat tangential through anal region of larva at commencement of metamorphosis. The anus is still open, the intestine is shortened and the rectum is preparing to separate off from the anal opening. The pharyngeal coelom has not yet grown round as far as the anal inter-radius.
- Fig. 27.—Almost sagittal section through larva about 12 hours after fixation. As regards the oesophagus, what is shown combines the appearances seen in four successive sections which do not singly show the full length of the lumen. The two darkened areas on the disc which are marked *circ. s.* indicate the marginal channel within which fluid mesenchyme or lymph “circulates” at this stage (p. 41). The similarly darkened areas on the preoral lobe, etc., indicate places where there were special aggregations of this lymph. The junction of larval intestine with pyloric region of stomach is shown.
- Fig. 28.—Vertical section through disc, stalk and sucker of young starfish about 36 hours after the commencement of metamorphosis. The provisional axial sinus, mainly made up of the expanded median portion of the anterior coelom (p. 254), surrounds the projecting end of the separated oesophageal cone. The position of the former larval mouth is indicated. The ring canal of the hydrocoele is in part completely cut off from the *l.m.c.*, and in part still communicates with the remains of this cavity. The definitive internal oral circular sinus has not yet been constricted off. This specimen, like that in fig. 27, is shown still attached by its sucker to a thin frond of seaweed.

PLATE 24.

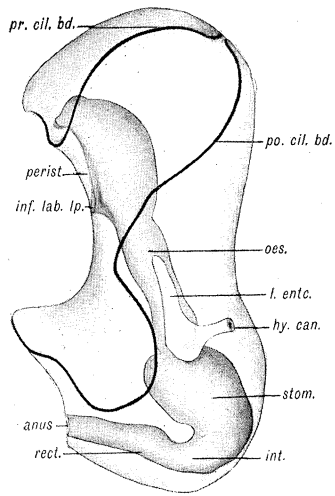
- Fig. 29.—Section vertical to disc of young starfish four days after commencement of metamorphosis. The three regions of the gastric cavity, viz., oesophagus or pharynx, stomach, and pyloric sac, are distinguishable. The internal oral circular sinus now forms a canal in the region of hydrocoele pouches III and IV.
- Fig. 30.—Section from same series as last but passing through insertion of stalk. The junction of the base with the thinner portion of the stalk is seen as a narrow neck. The provisional axial sinus sends a hollow process into the base of the stalk but the stalk itself is solid.
- Fig. 31.—Transverse section through older starfish about six days after commencement of metamorphosis, showing beginning of formation of adult mouth.
- Fig. 32.—From series of a specimen 12 hours after fixation, to show in particular the relation of the pharyngeal coelom to the developing axial organ (pp. 257, 278). The ring canal of the hydrocoele has not yet become separated off from the *l.m.c.*

Fig. 33.—From a series of sections through the madreporite of an *Asterias rubens* of moderate size. The middle of the starfish disc lies on the right of the figure but the sections are somewhat oblique. The stone-canal funnel is cut at the point where it opens into the ampulla and also where its sinistral section (see note on p. 217) has an opening into the axial sinus. As regards these openings the drawing combines the appearances seen in four successive sections, each $10\ \mu$ in thickness. With reference to the axial sinus, it is only the expanded aboral end of its dextral horn which comes into this section (pp. 268, 269). The relation of the ampulla to the underlying dorsal sac will be made out.

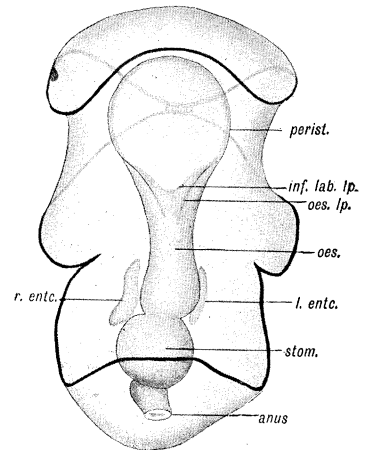
Fig. 34.—From same series as last, but nearer dextral (see note on p. 217) edge of madreporite. The section shows the main primary communication between the dextral section of the stone canal and the expanded aboral end of the dextral horn of the axial sinus. There is seen in the section one of the lobes into which the ampulla of the stone canal is divided. The + on the lining of the stone canal marks a point which, projected aborally, would come opposite the opening from stone-canal funnel into ampulla of stone canal shown in fig. 33. The × on the other side marks a similar point with reference to the opening from stone canal into axial sinus shown in fig. 33.



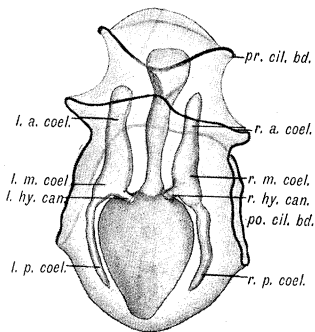
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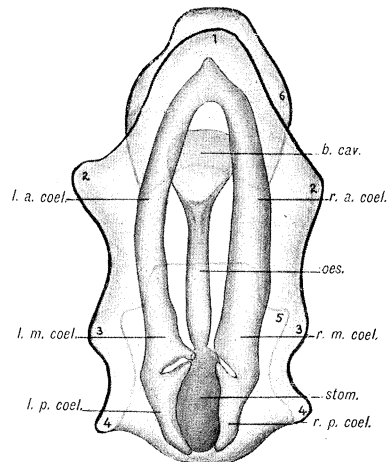
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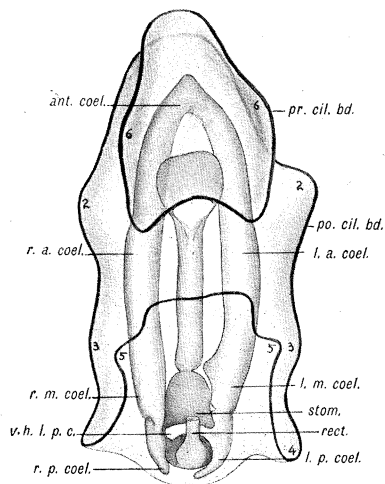
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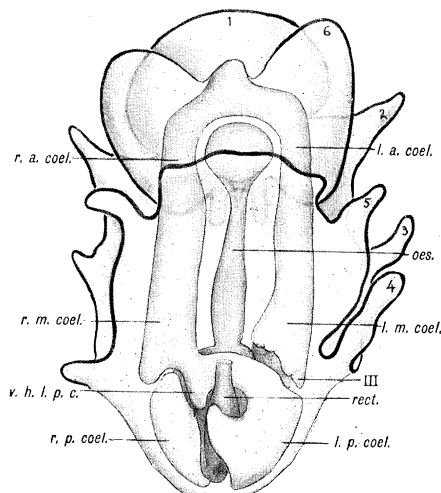
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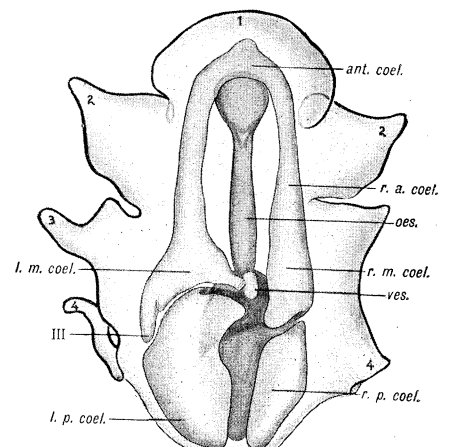
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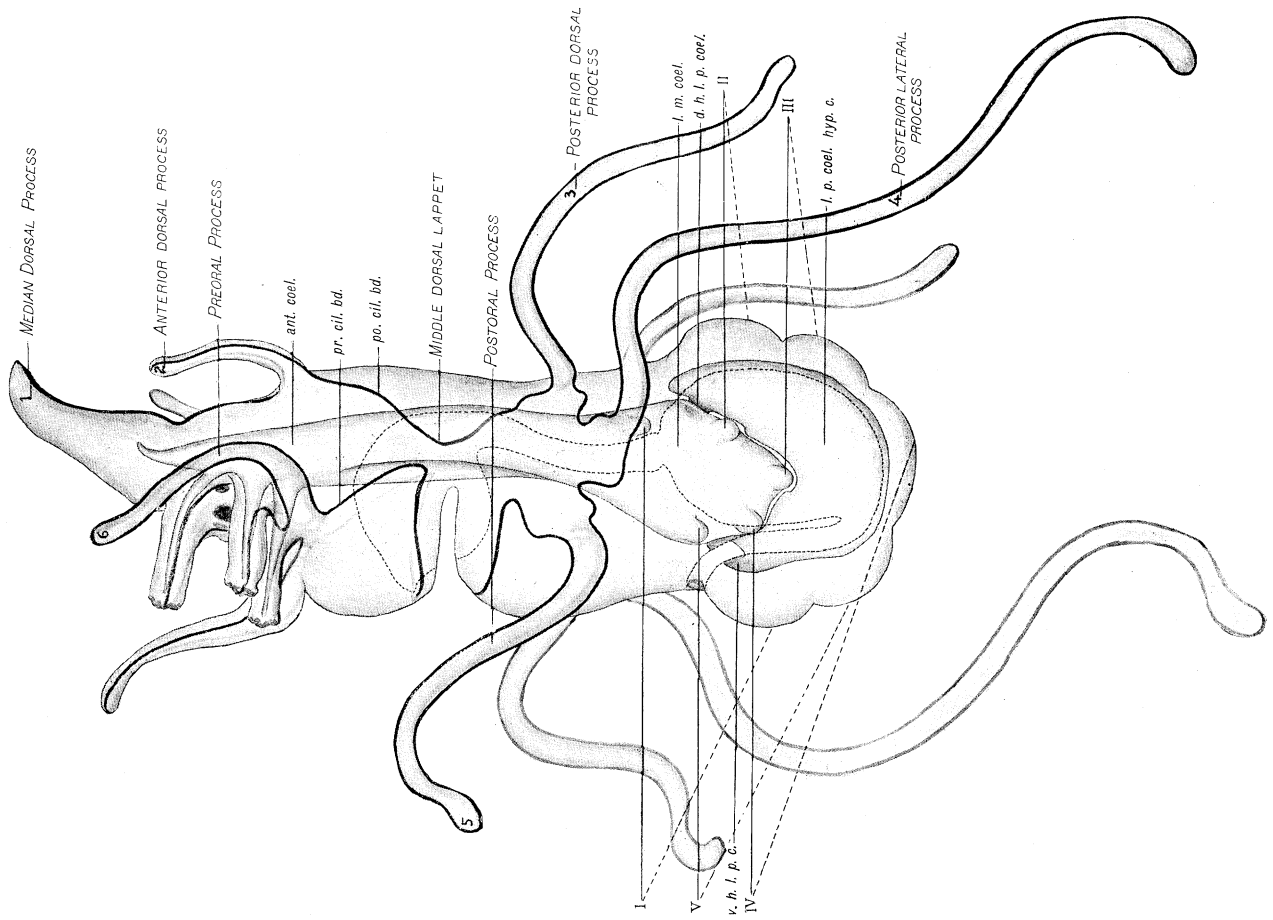
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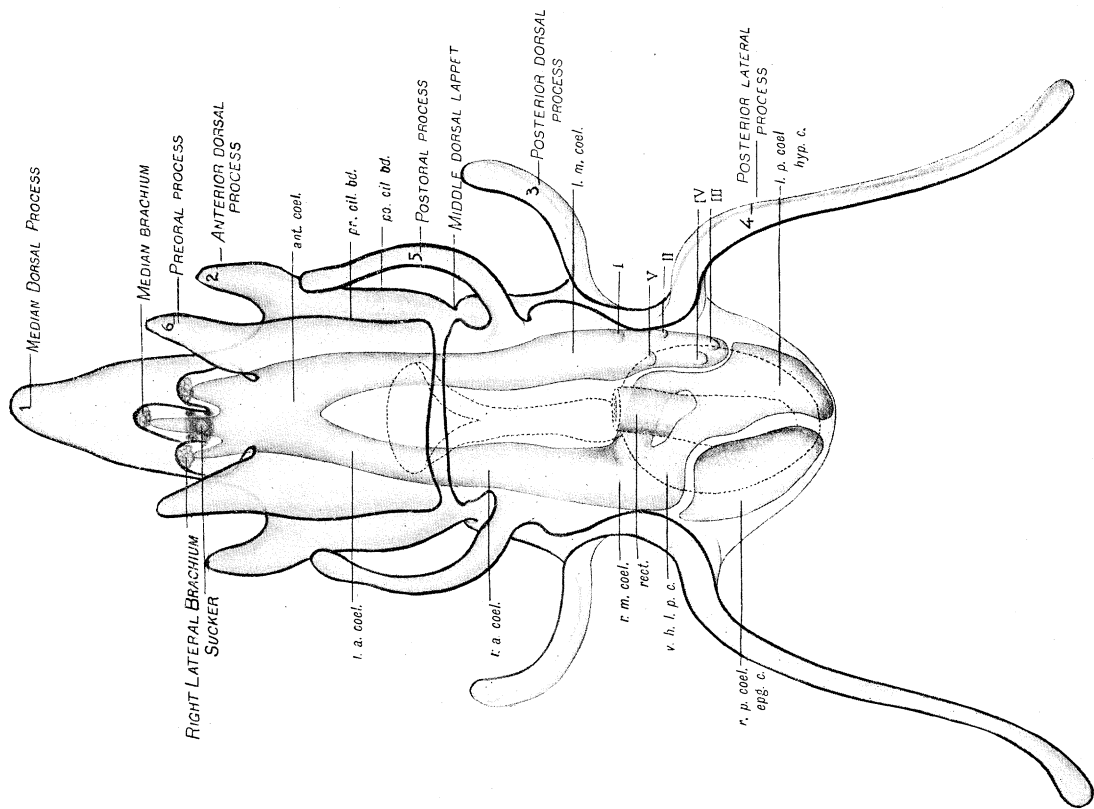
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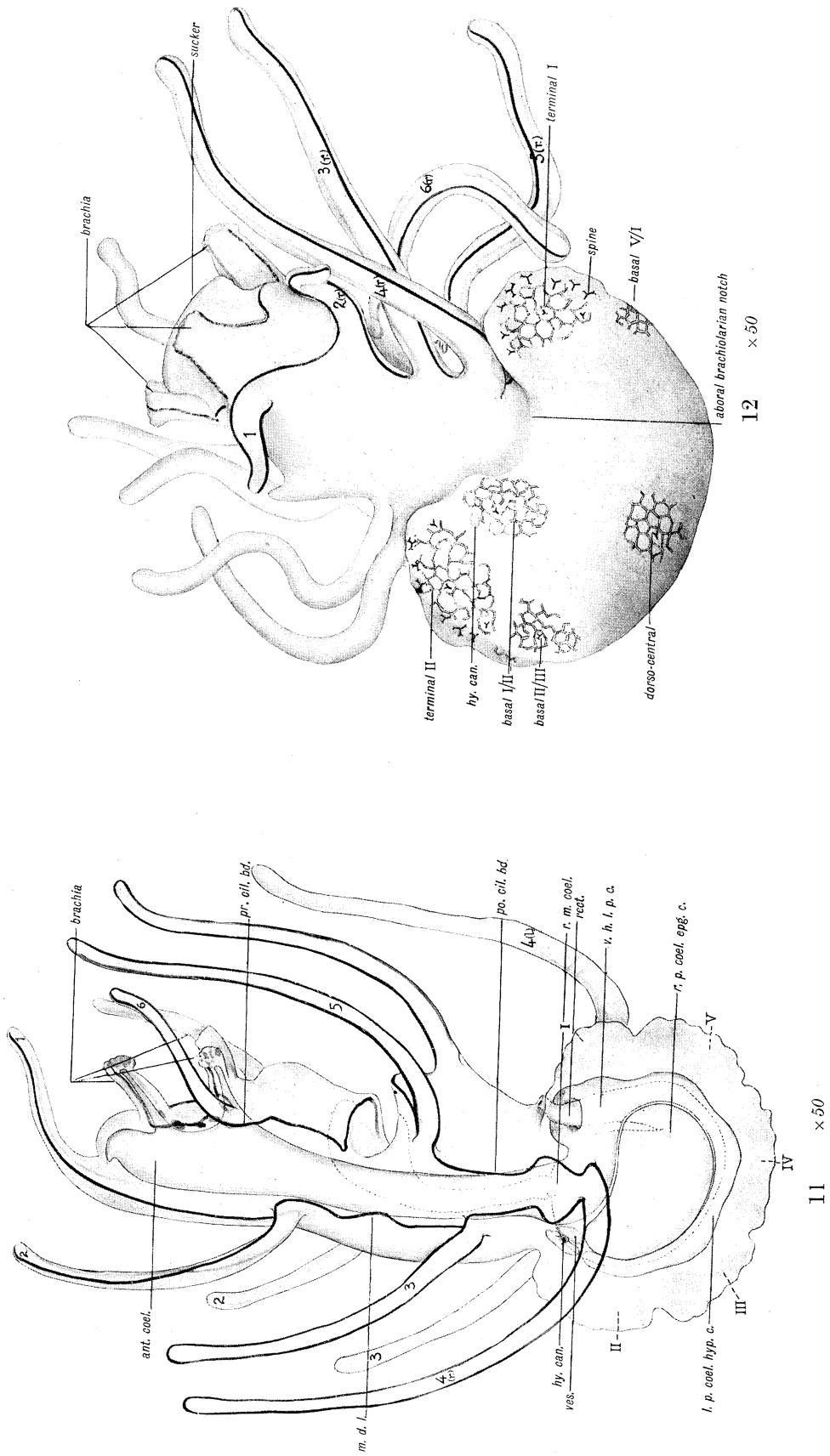
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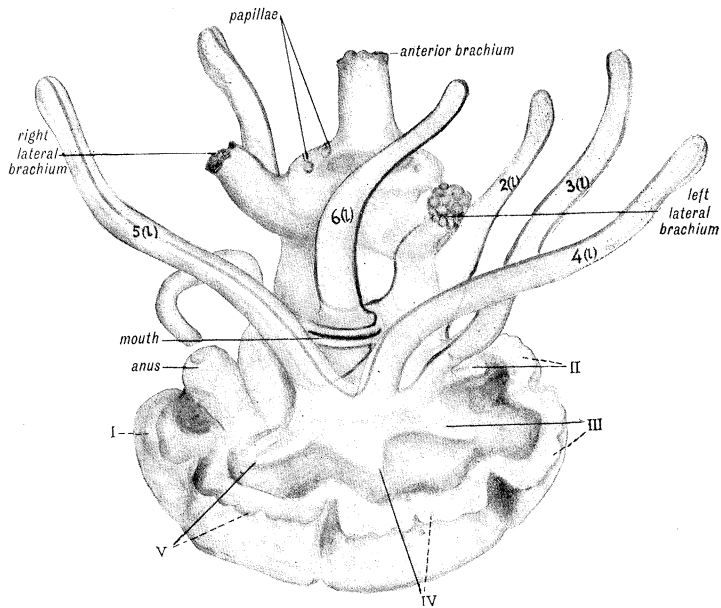


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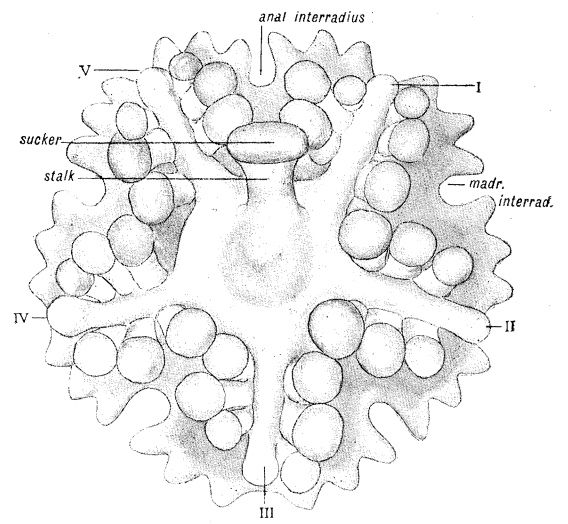


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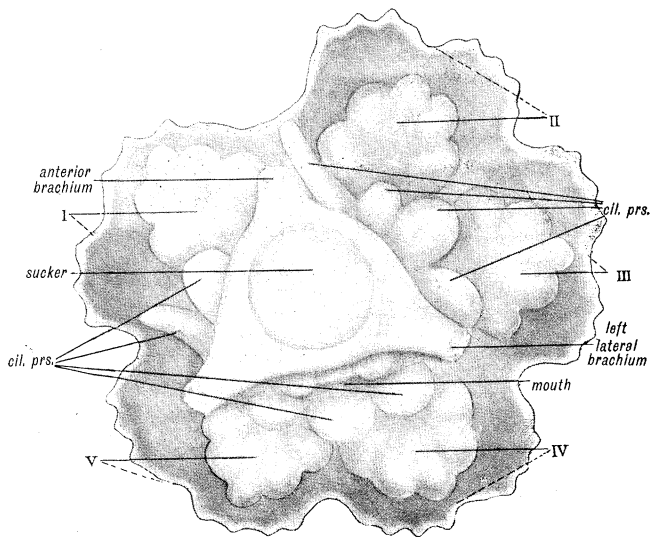




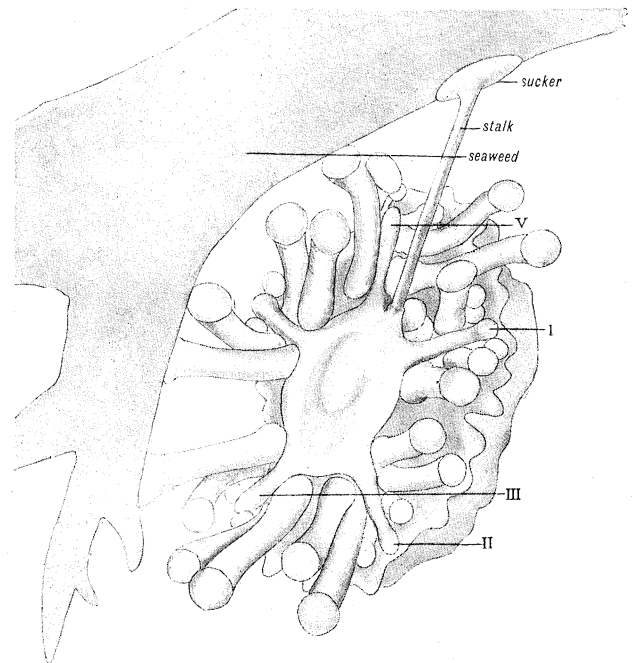
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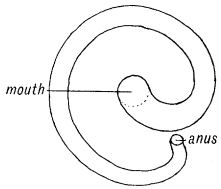
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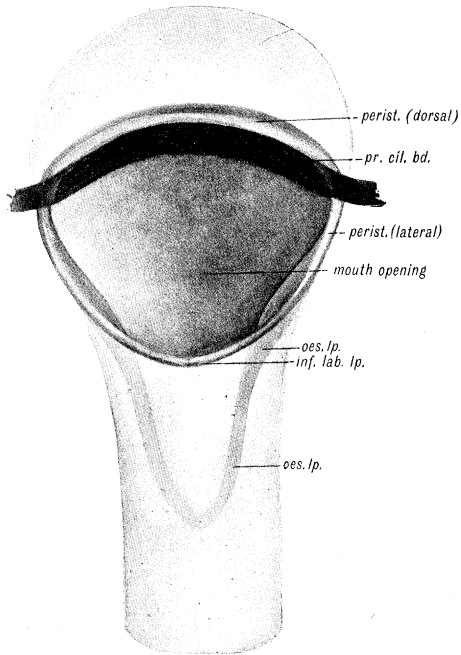
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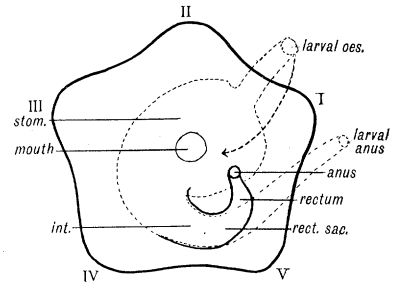
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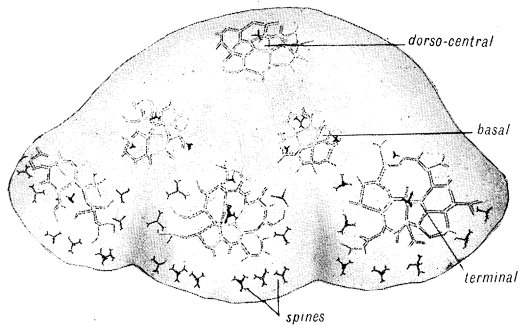
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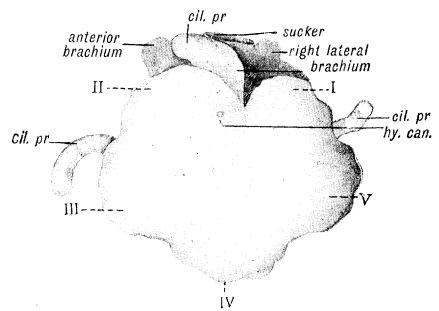
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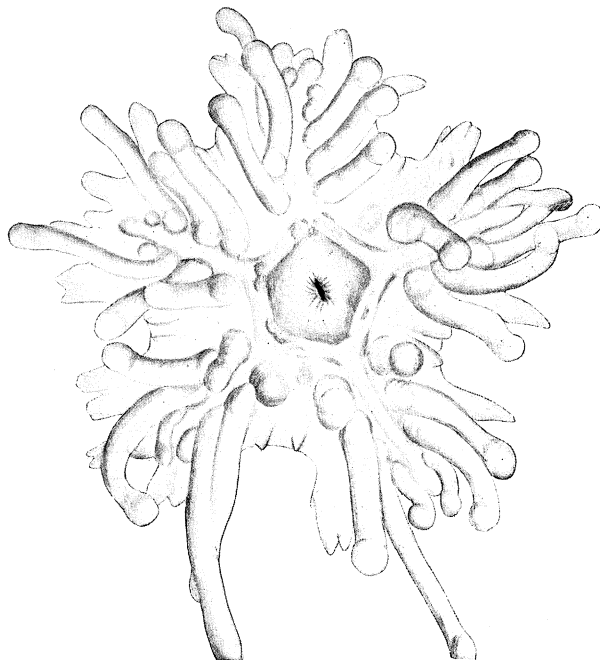
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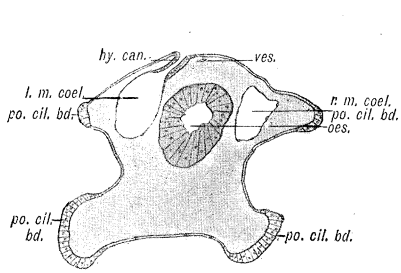
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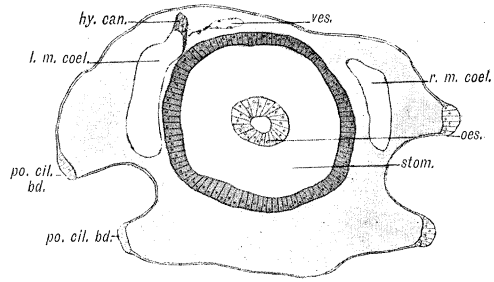
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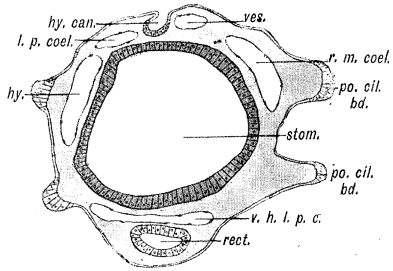
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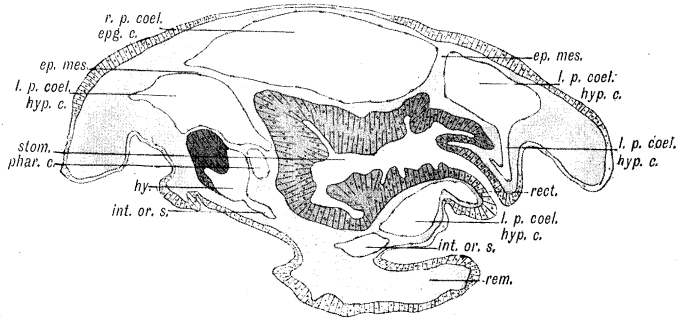
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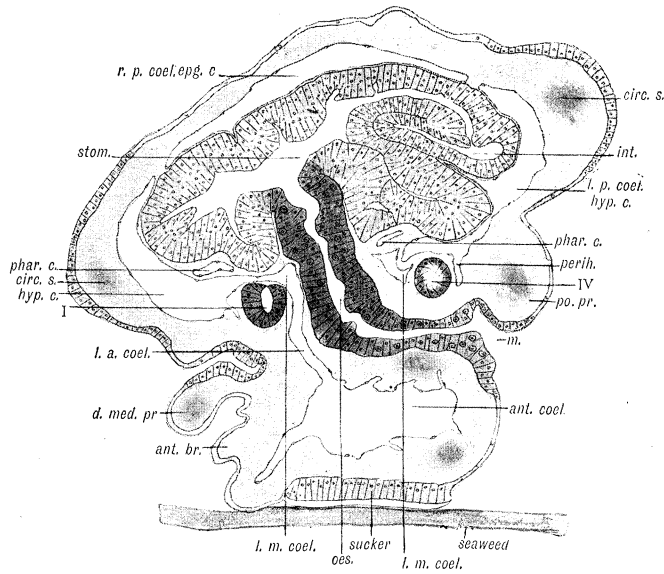
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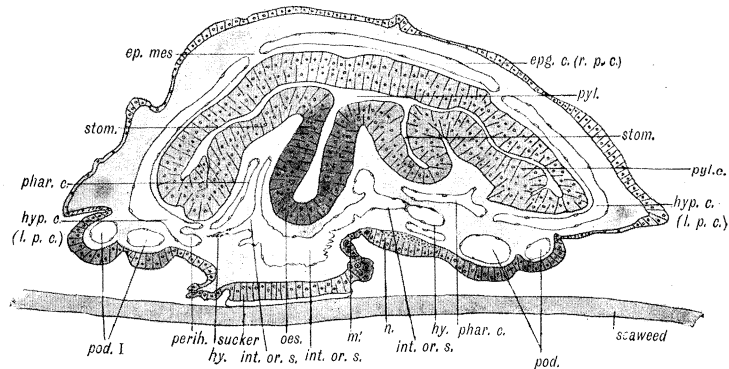
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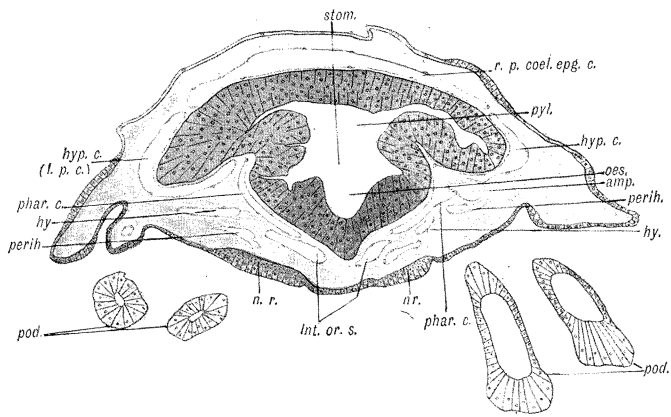
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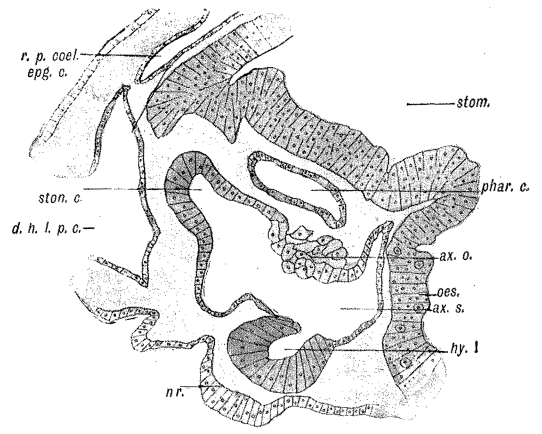
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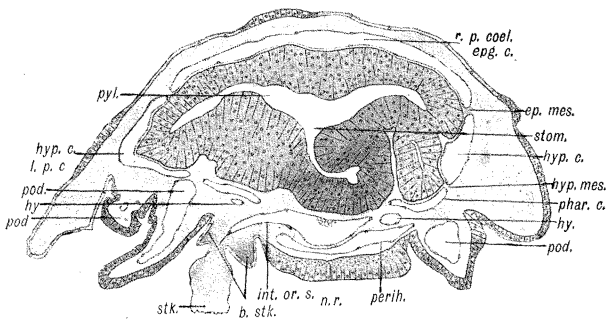
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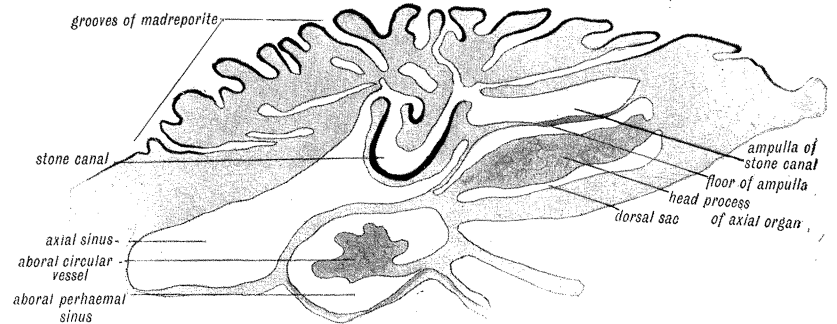
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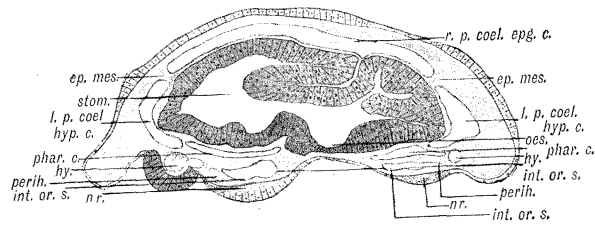
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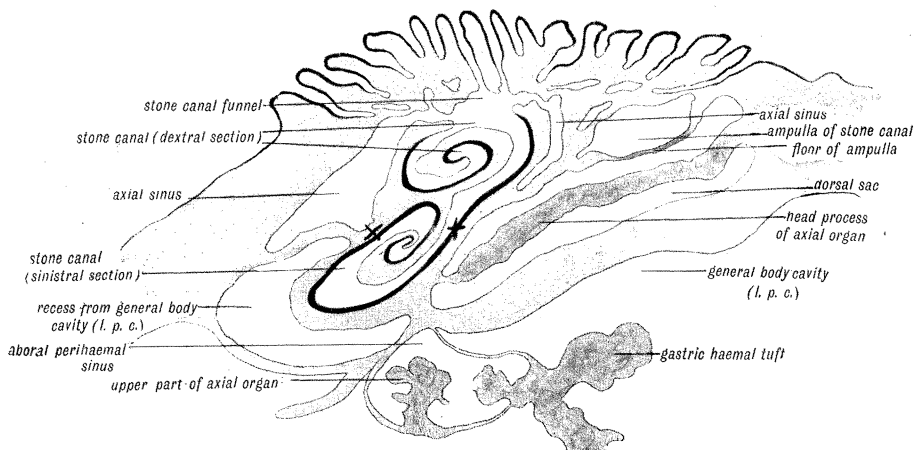
30 × 60



33 × 20

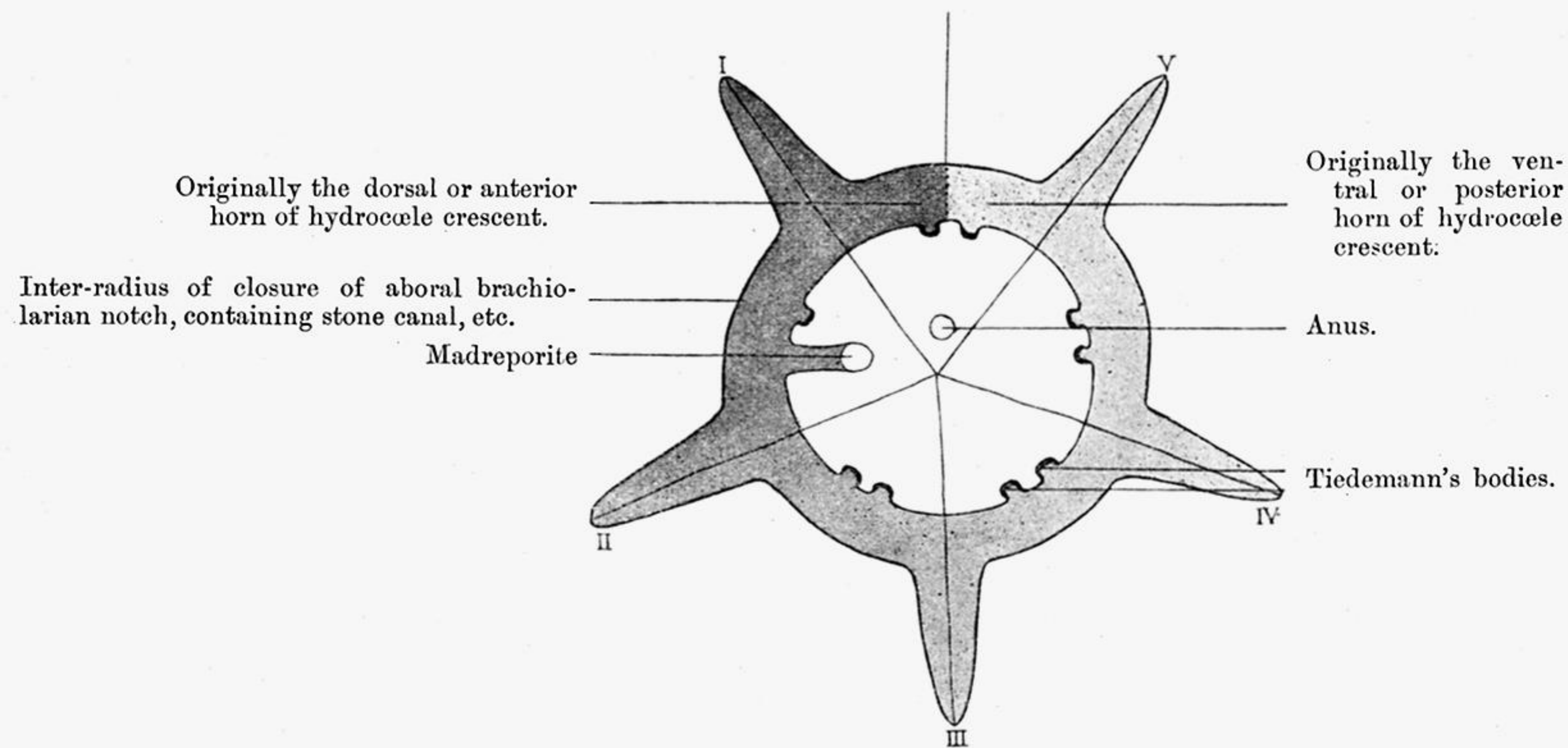


31 × 45



34 × 20

Inter-radius of stalk, anus and hydrocœle-closure.



TEXT-FIG. 1.—Diagram to illustrate the Numbering of the Rays adopted on the developmental grounds explained below. The view is from the aboral side. For purposes of illustration, the original anterior horn of the hydrocœle crescent has been darkened and made to shade gradually into the middle and posterior portions. The point referred to in note on p. 257 is brought out in slightly exaggerated form, namely, that the stone canal opens into the ring canal rather nearer ray II than ray I. The diagram also indicates that stalk, anus, and closure of hydrocœle ring are to be looked for in inter-radius I/V, while the position of the madreporite, and the closure of the aboral brachiolarian notch (p. 252) are in inter-radius I/II.

The numbering is the same as that used by MACBRIDE (55), and exactly the converse of that adopted by LUDWIG (52, 54), GOTO (33), and MASTERMAN (60). SEDGWICK'S (84, p. 120) and DELAGE'S (16, p. 36) numbering makes the anal and the madreporic inter-radii I/II and II/III respectively.

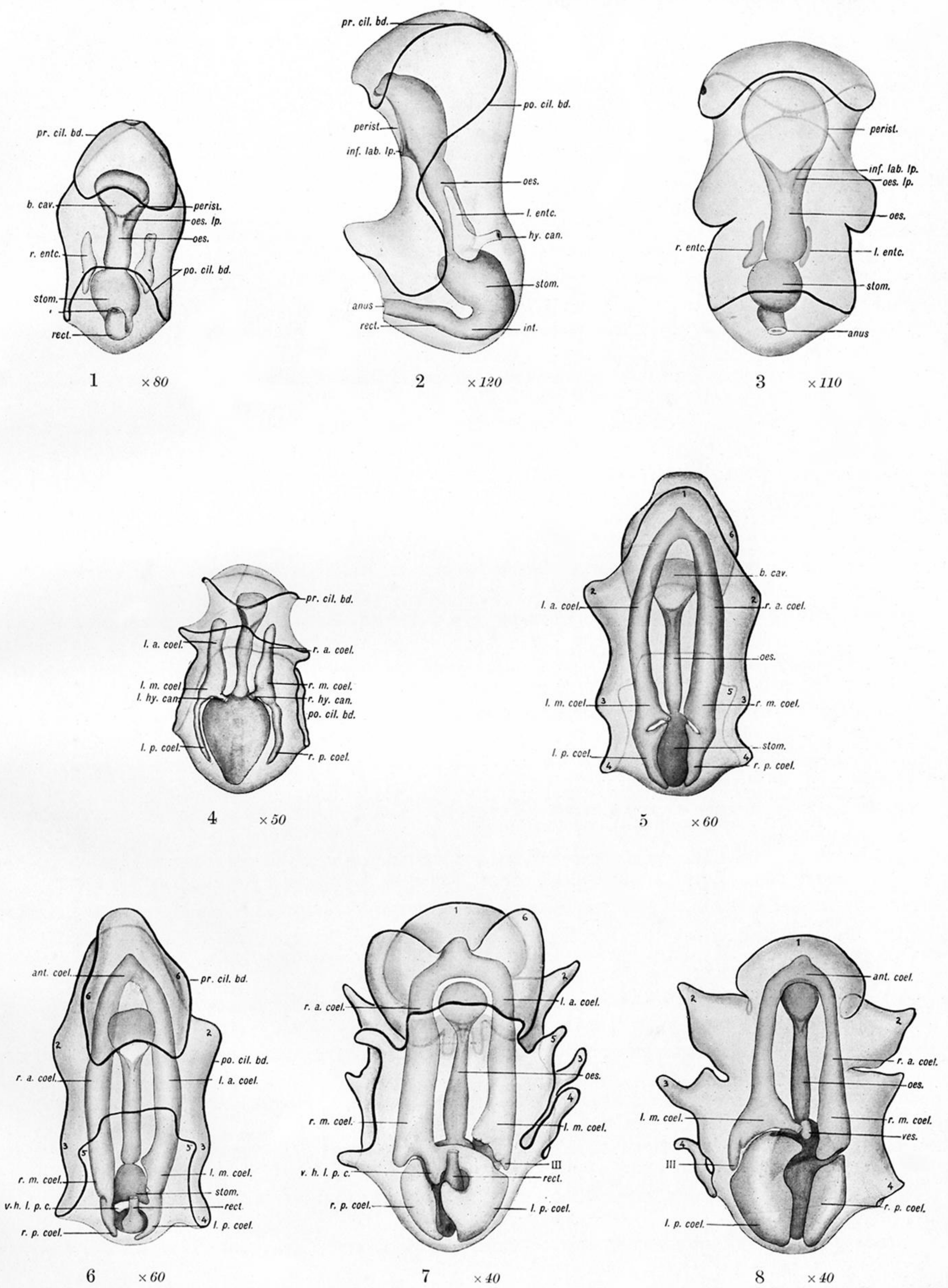


PLATE 18.

- Fig. 1.—Larva about 10 days old from ventral side.
- Fig. 2.—Larva of similar age from left side.
- Fig. 3.—Larva of similar age from ventral side, with preoral lobe bent back in the movement of dorsal flexion described on p. 241.
- Fig. 4.—Larva about 18 days old from dorsal side, showing a right as well as a left hydropore. The preoral lobe is again bent back by the movement described on p. 241.
- Fig. 5.—Dorsal view of larva about 21 days old. The enterocœles have united within the preoral lobe, and separation of the posterior cœlom on both sides has begun.
- Fig. 6.—Larva slightly older than last, from ventral side, showing in particular the growth of the ventral horn of the *l.p.c.* across to the right side between stomach and rectum. The relatively small size of the stomach in the last two figures will be noted. Such variations are of frequent occurrence, but in the larvæ which will afterwards grow best the larger size of the stomach is usual.
- Fig. 7.—Larva about 32 days old from ventral side showing fusion of ventral horn of *l.p.c.* with right middle cœlom, the right posterior or epigastric cœlom having already been separated off. The formation of the folds of the *l.p.c.* which enclose the rectum will be noted, and also the first appearance of the hydrocœle lobes in the *l.m.c.* The specimen is drawn as seen in the contracted condition attended by emptying of the buccal cavity (p. 241). The ciliated processes are now developing, and are shown directed forwards in the position adopted when the larva is sinking.
- Fig. 8.—Dorsal view of same larva as is shown in fig. 7. The dorsal sac is to the right of the hydroporic opening. Hydrocœle lobes are appearing in the *l.m.c.* At this stage the *r.m.c.* will be seen to be almost symmetrical with the *l.m.c.*, though not possessing a hydropore, nor showing hydrocœle lobes. The commencing extension of the dorsal horn of the *l.p.c.* will be noted.

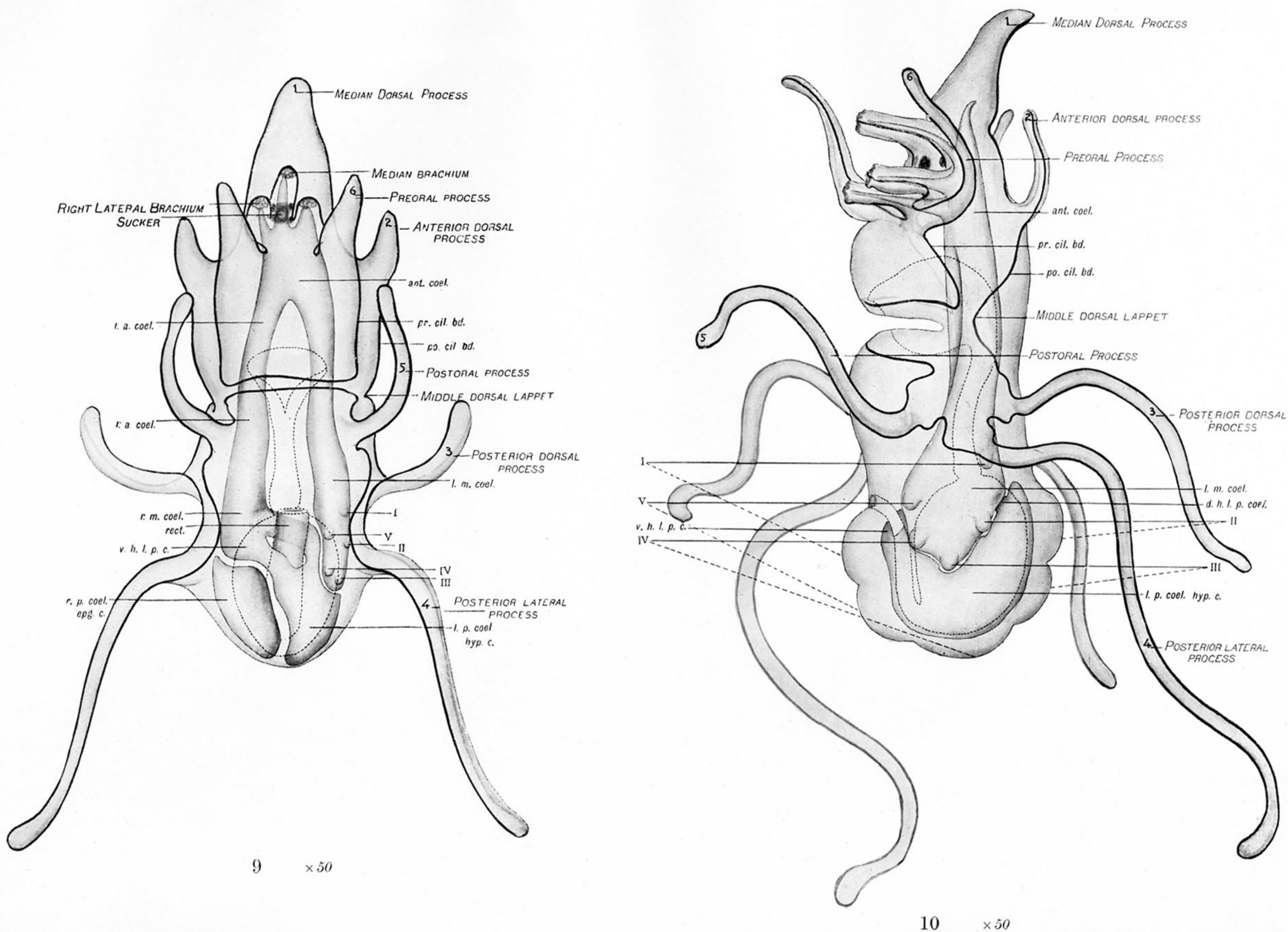
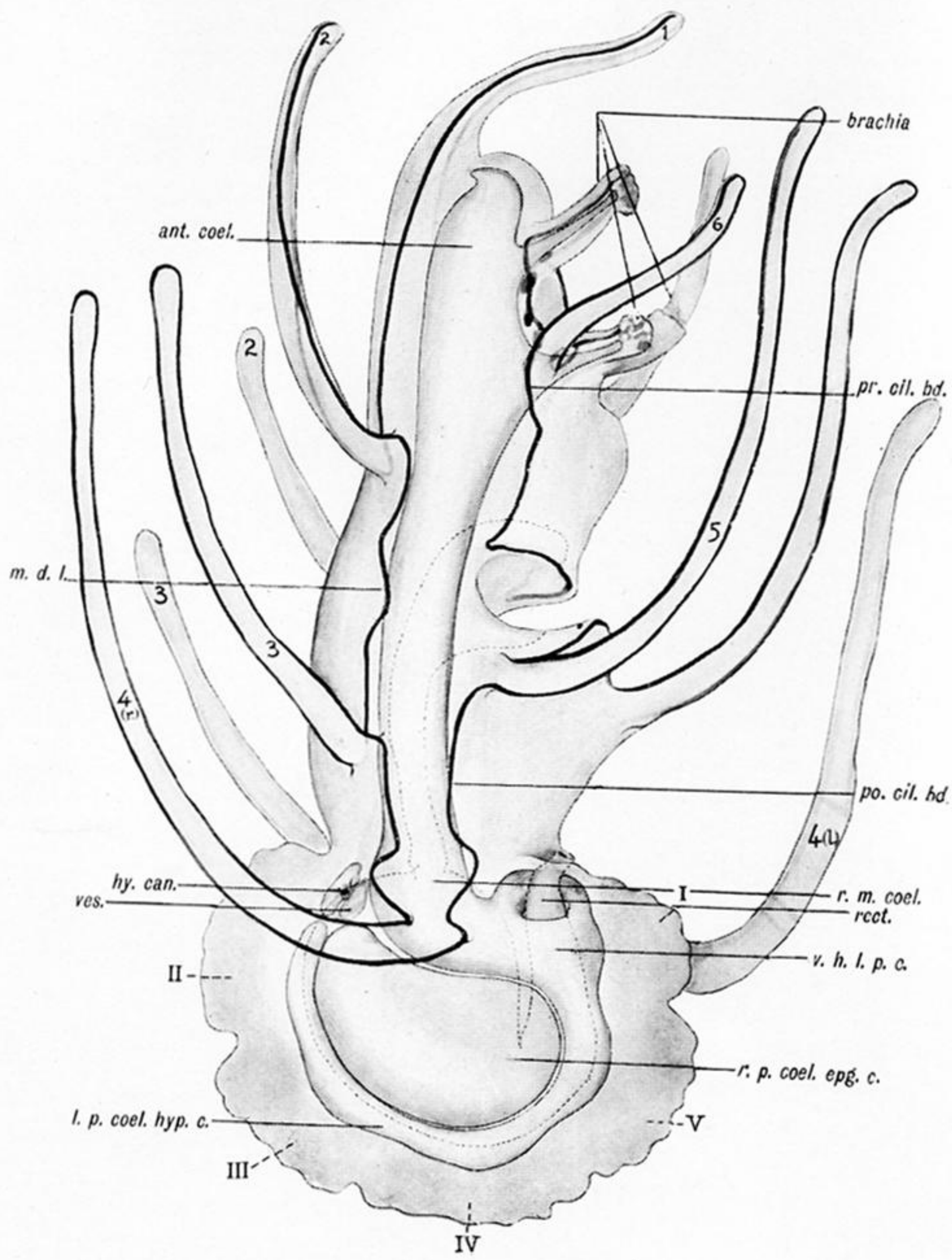


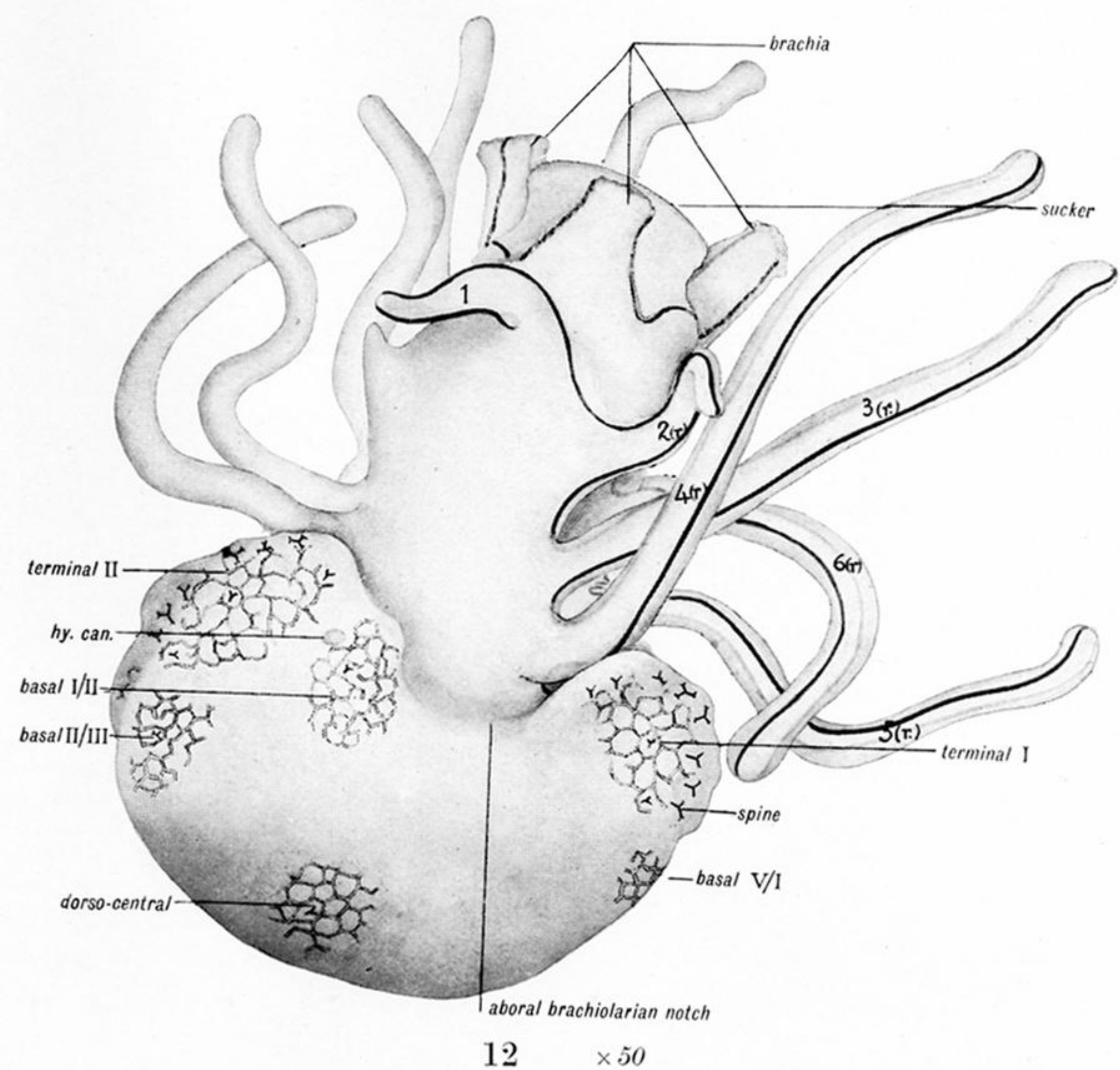
PLATE 19.

Fig. 9.—Ventral view of larva about 38 days old, showing the ciliated processes still further developed, as well as the brachia and sucker. The *l.p.c.* now forms a complete ring round the rectum. The outline of the food canal is shown by dotted lines.

Fig. 10.—Fully developed brachiolaria shown in balancing position and looked at from left side. As regards the *l.p.c.*, its dorsal horn will be made out, as well as the ventral horn enclosing the rectum. The secondary communication between the dorsal horn and the left middle coelom is a little to the left of the end of the line which indicates the dorsal horn. The terminal ossicles, which have now begun to appear, are not shown in the illustration.



11 × 50



12 × 50

PLATE 20.

Fig. 11.—Drawing from right side of brachiolaria at slightly older stage than in last figure. The ciliated processes have reached their full development and are shown in the position adopted when the larva is rapidly sinking. An attempt has been made to exhibit the arrangement of the coelomic cavities as if the right body wall were transparent.

Fig. 12.—View from aboral side of brachiolaria which is just commencing to metamorphose, having been attached for an hour or thereby. The shortening of the anterior and middle parts of the body will be made out, as well as the prominence of the brachia and sucker. The rotation of disc on rest of larva has begun, as also has the closure of the brachiolarian notch.

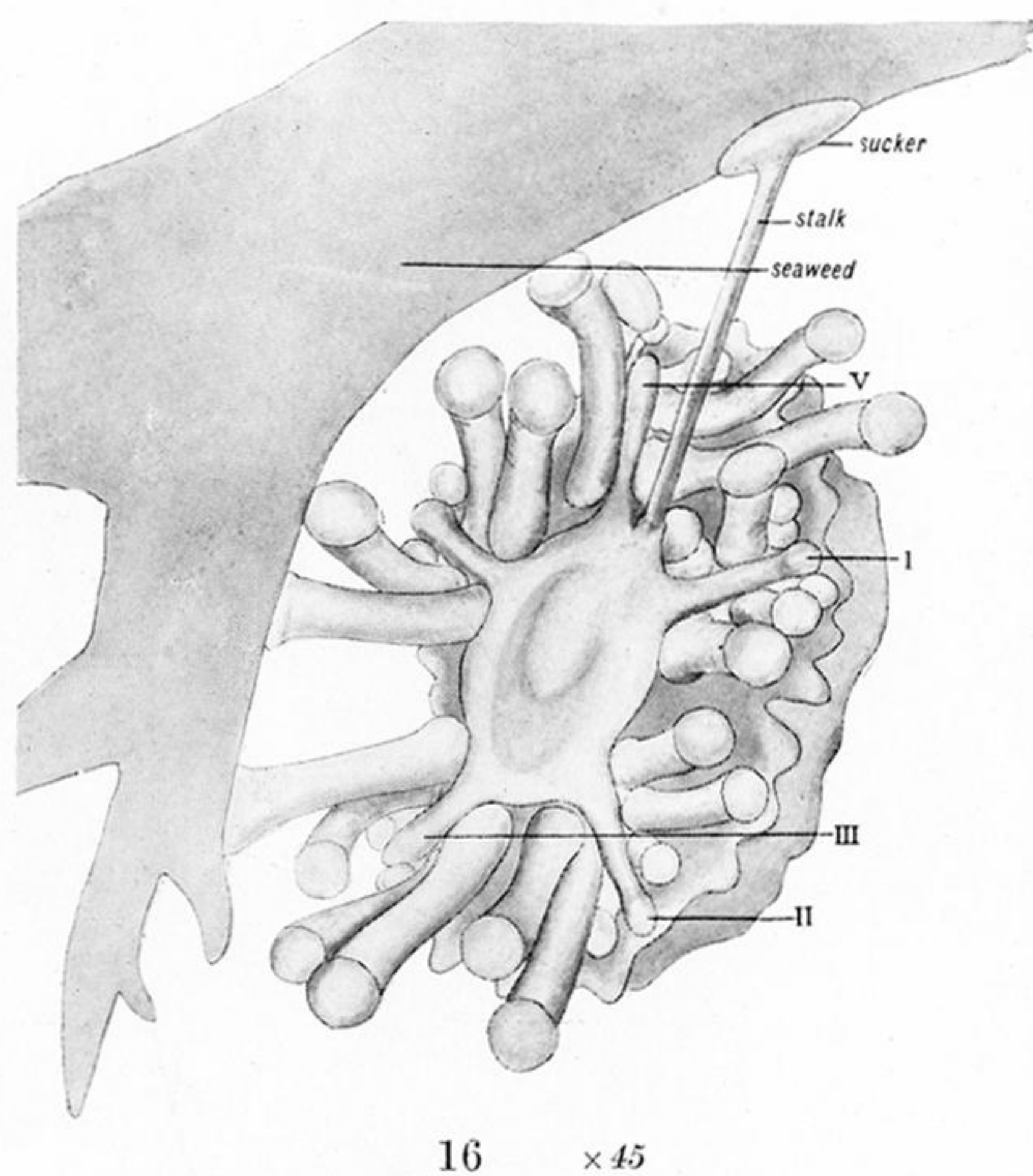
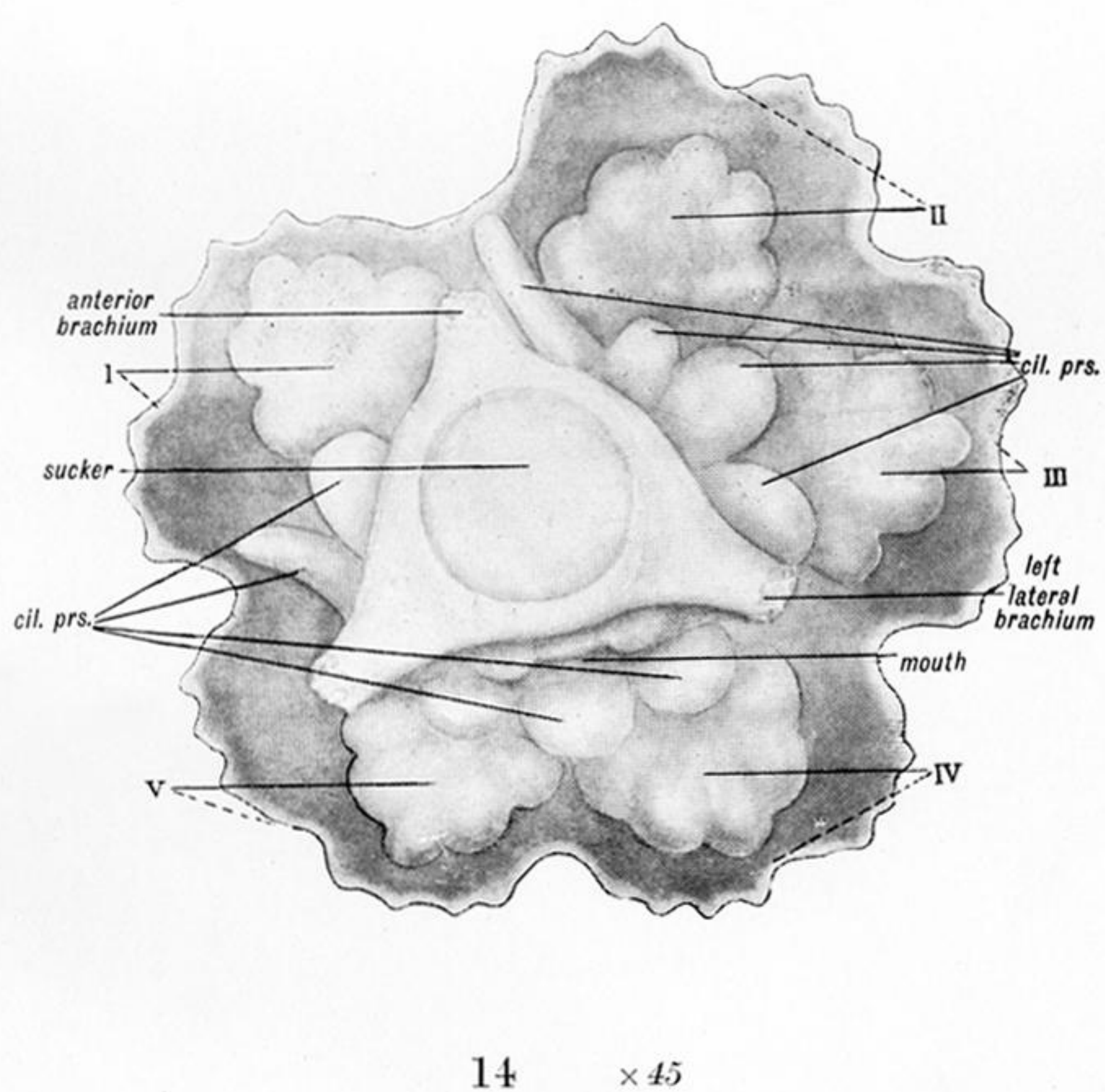
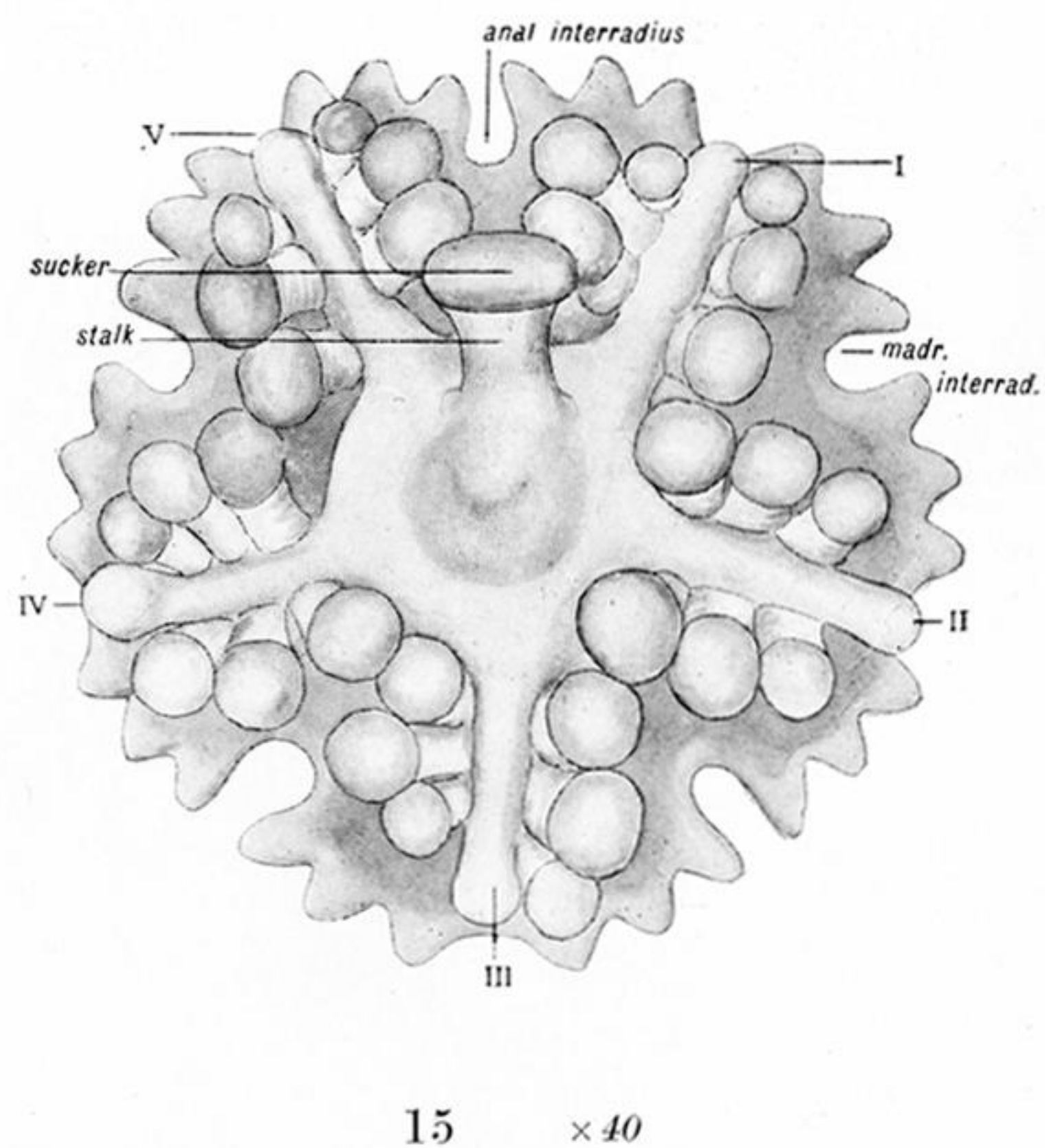
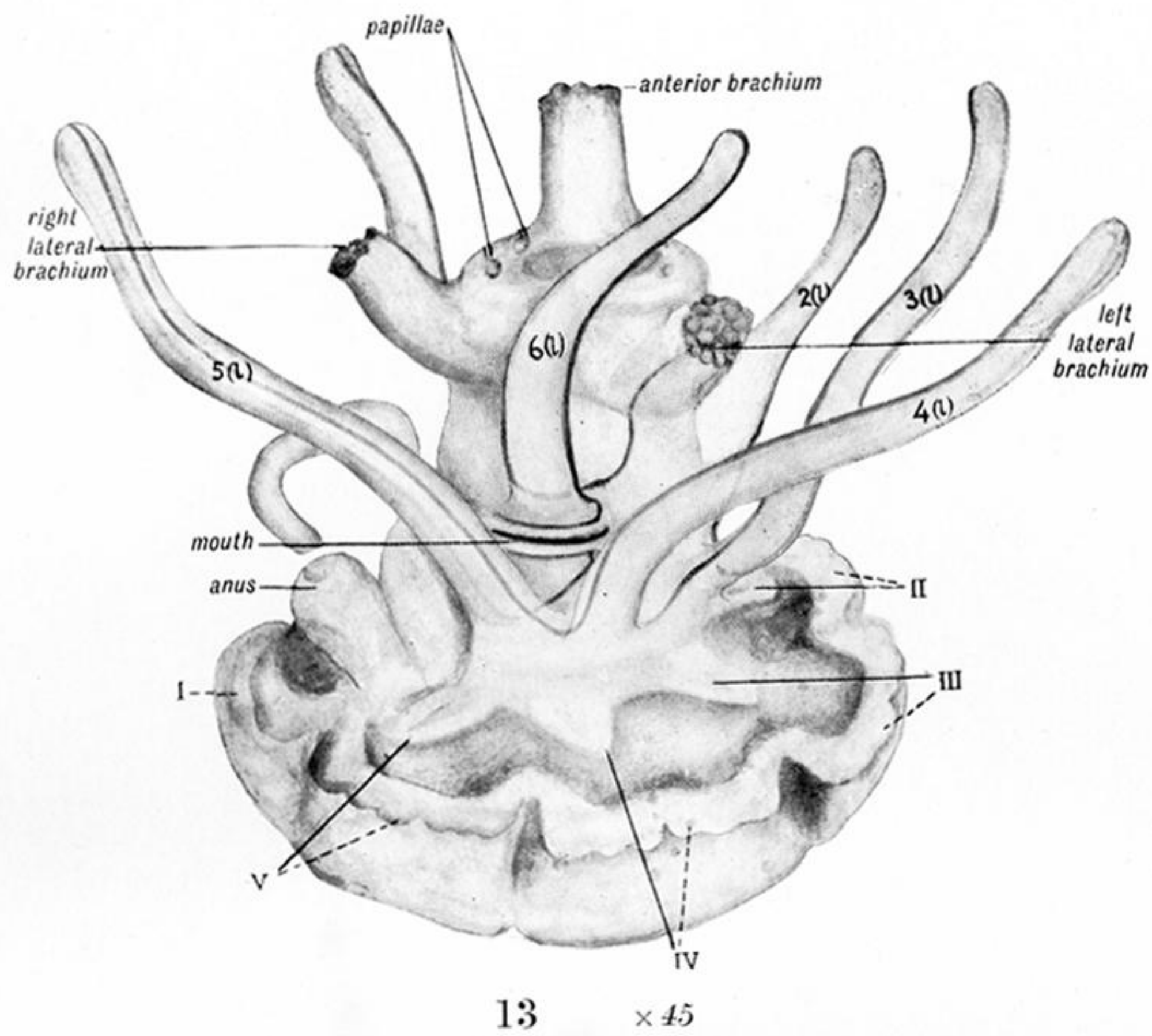


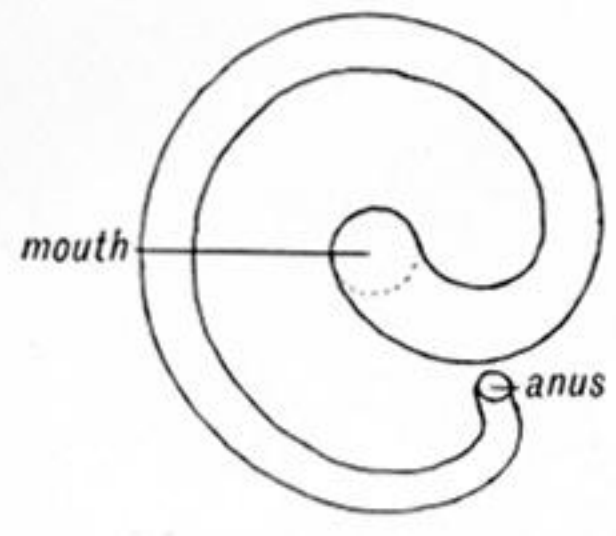
PLATE 21.

Fig. 13.—View from ventral side of larva a little further advanced towards metamorphosis than in last figure. It will be noted that the larval vent is now on the oral aspect of the disc (p. 252) and that the larval mouth and the various ciliated processes are being retracted within the crescent of the hydrocœle. The partial want of conformity between the arm rudiments and the radial hydrocœle lobes will also be made out.

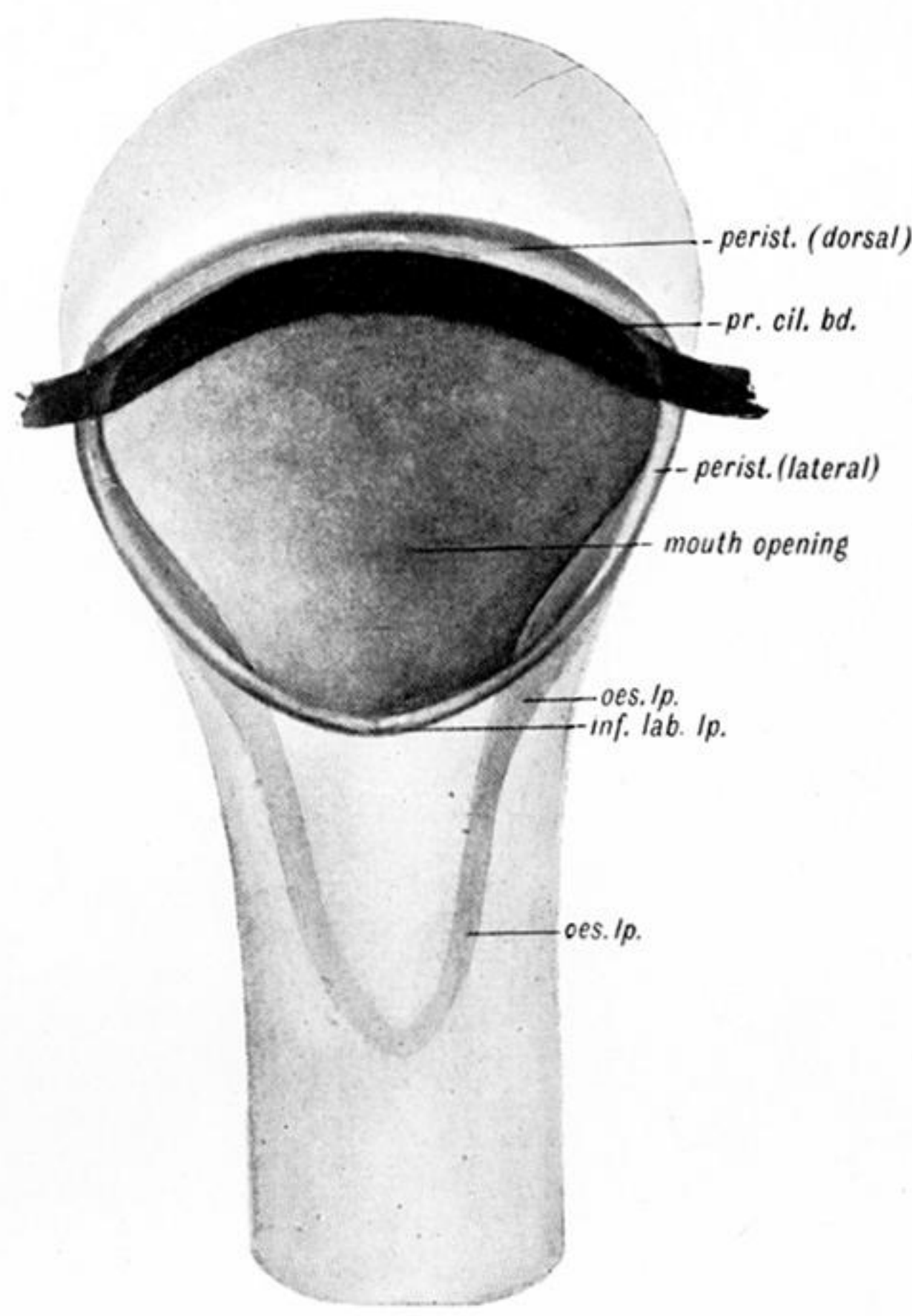
Fig. 14.—View from oral aspect of starfish 24 hours after the commencement of metamorphosis. The large sucker and the remains of the brachia will be seen. The ciliated processes have become almost completely retracted while the radial hydrocœle pouches have increased in size and are now five-lobed. The position of the larval mouth is noted, but separation of the œsophagus will have taken place by this time. The sucker is as close as may be to the oral surface of the starfish, the stalk being exceedingly short at this stage.

Fig. 15.—Oral view of starfish four or five days after commencement of metamorphosis. The stalk of the sucker has lengthened, the remains of the ciliated processes have entirely disappeared and the adult mouth is beginning to form. As regards the sucker feet, the first two pairs are coming into functional use.

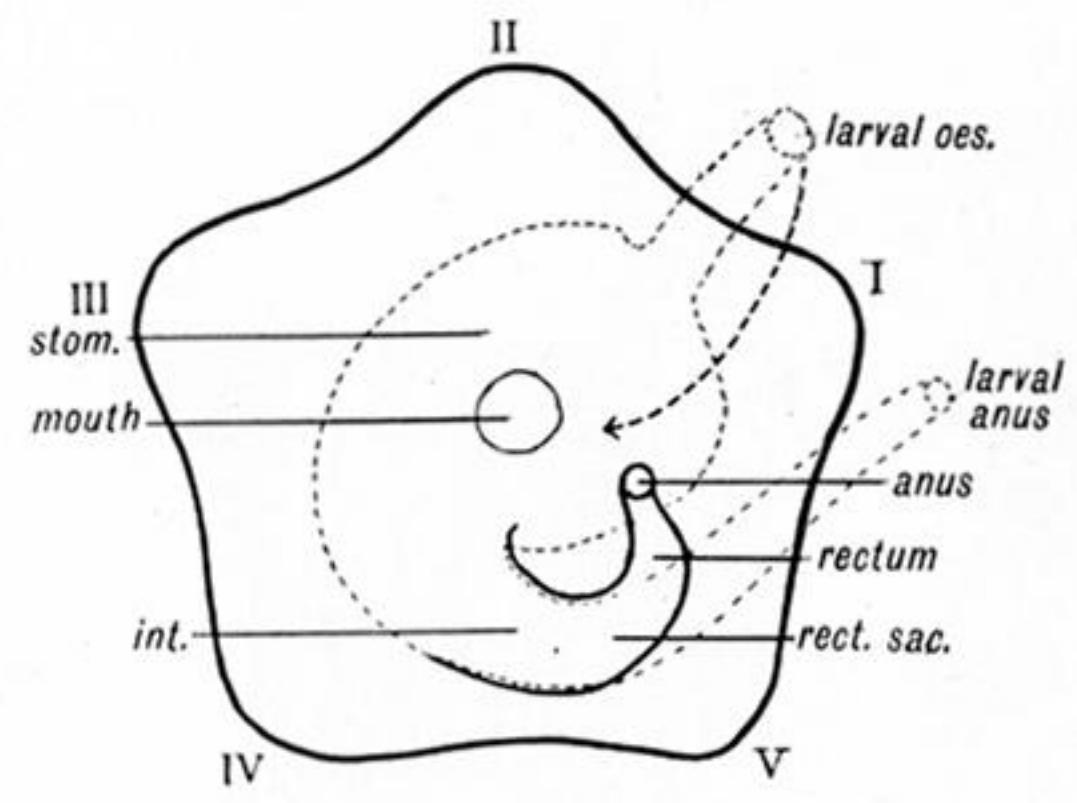
Fig. 16.—Young starfish two days older than last specimen and ready to crawl off, but still attached by the stalk to the small frond of seaweed on which it had fixed itself at the commencement of metamorphosis. Just prior to separation the stalk is even more slender than is shown in the figure. Near its junction with the body, the slightly broader part, from which the separation will take place, is indicated.



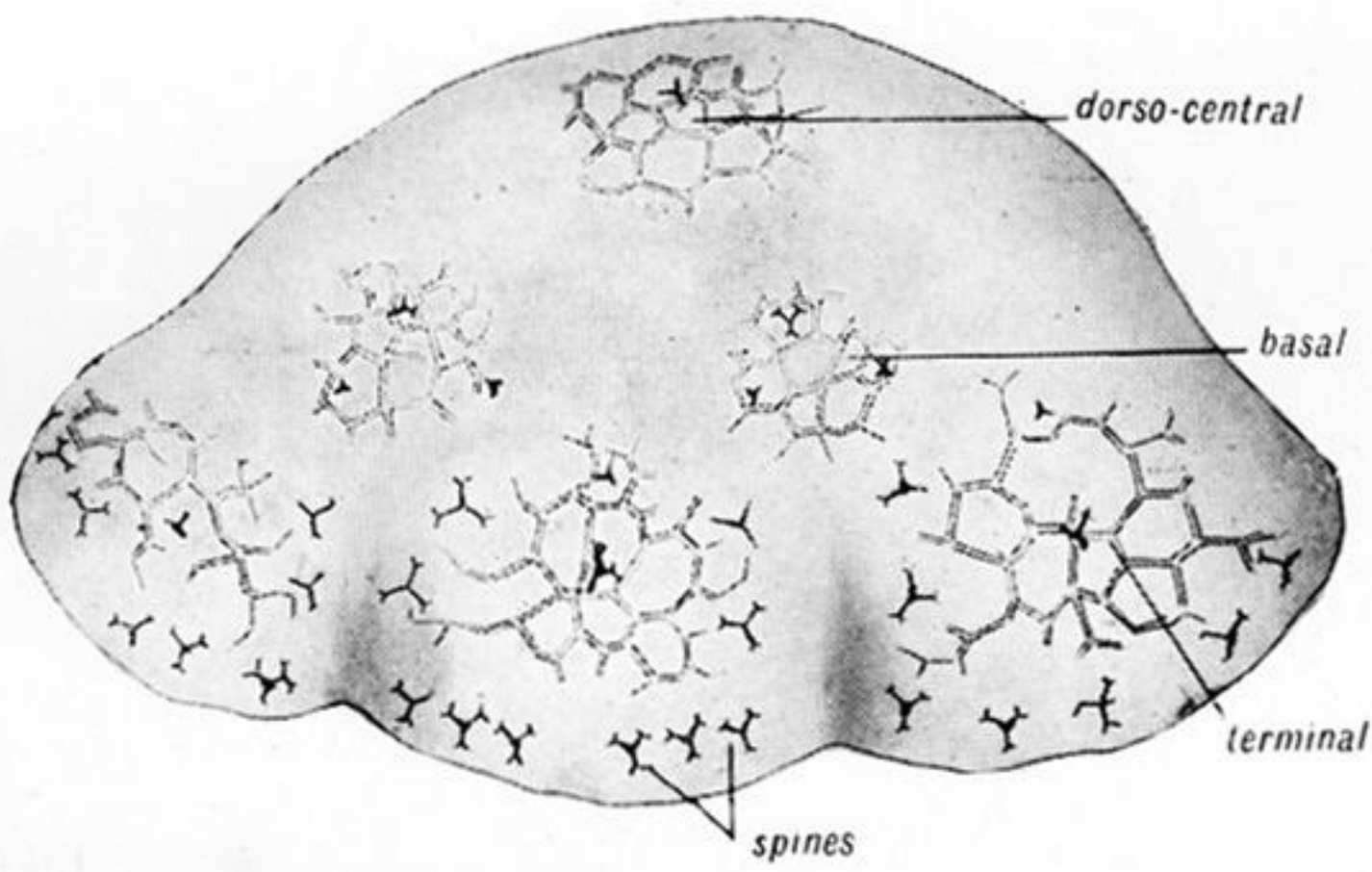
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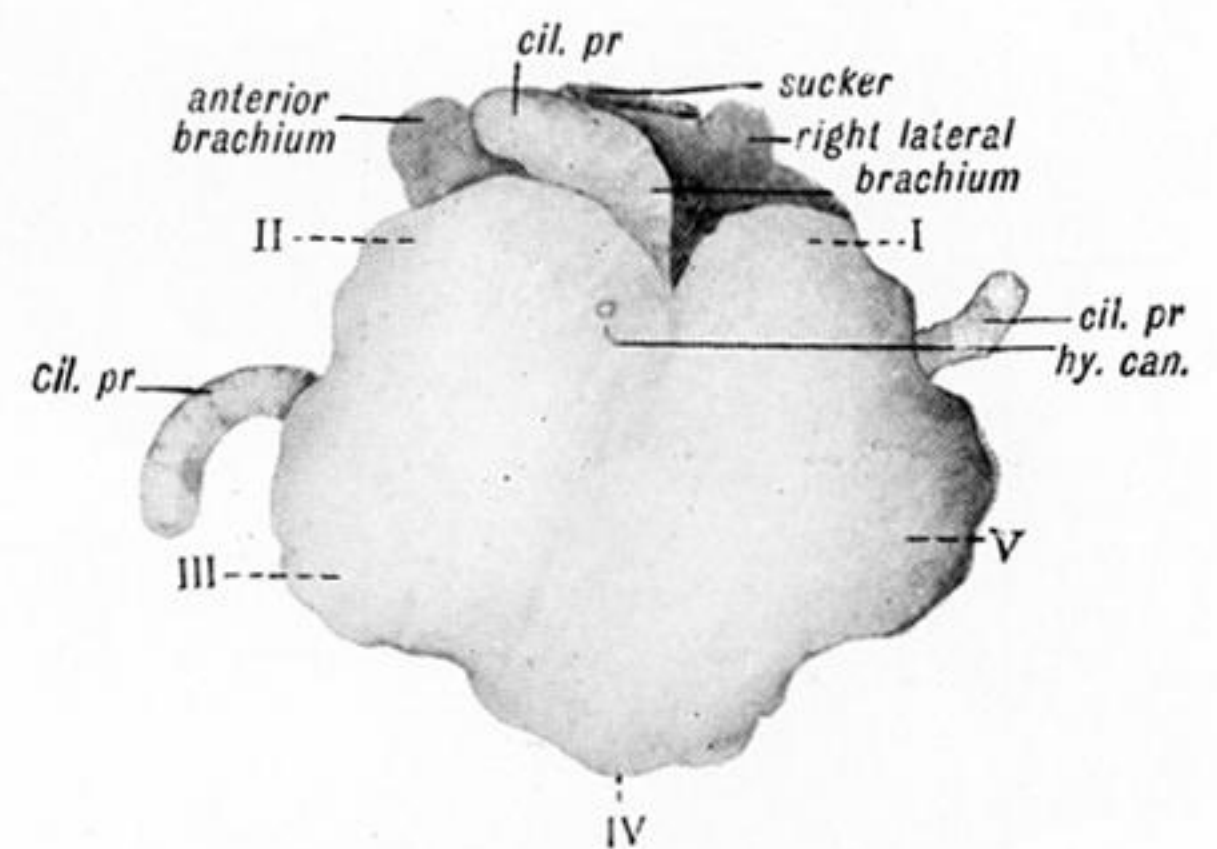
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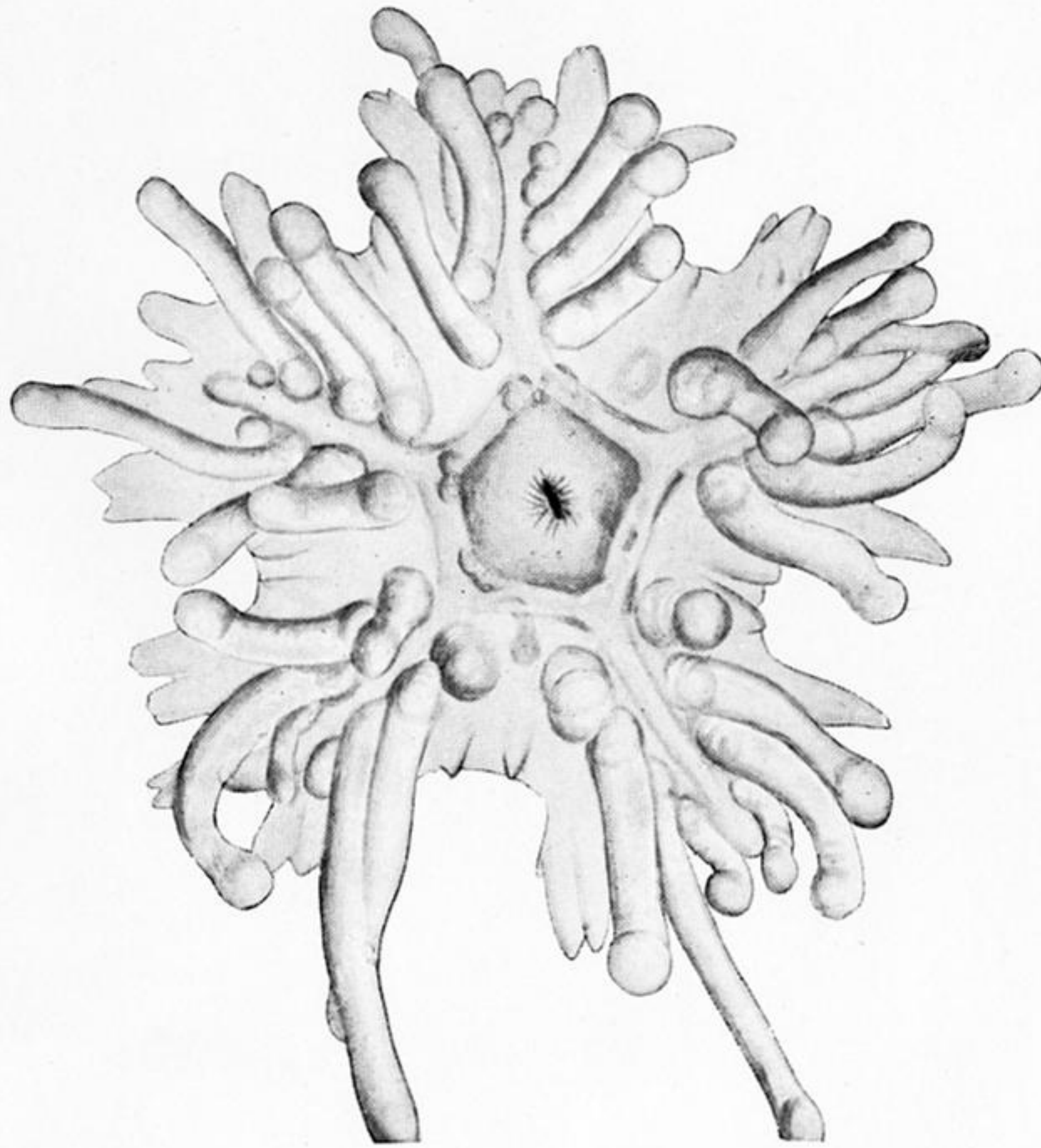
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18 × 45



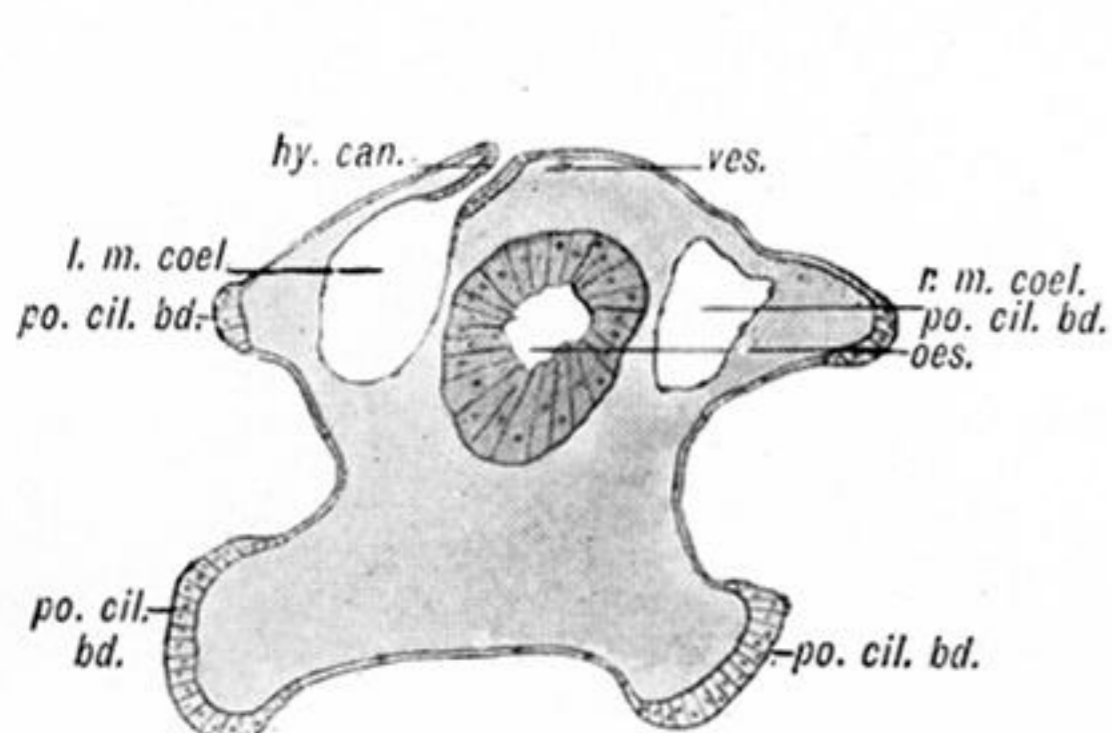
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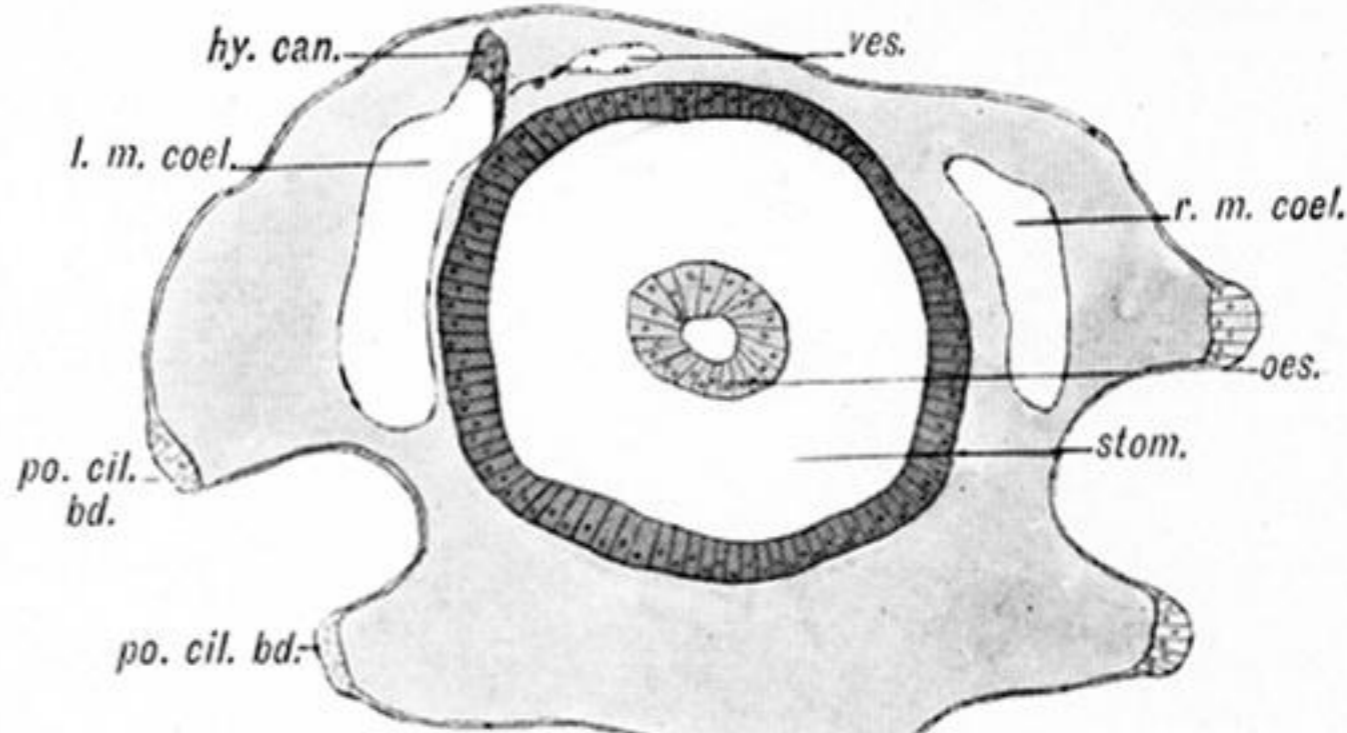
19 × 35

PLATE 22.

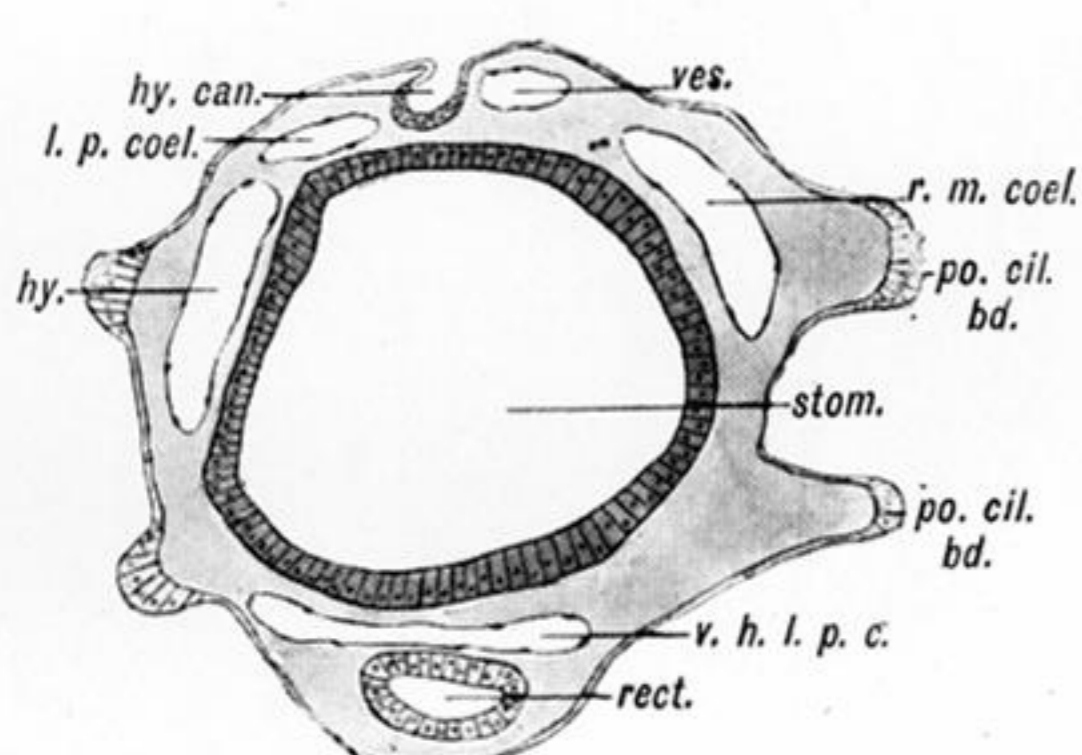
- Fig. 17.—A stage in metamorphosis 18 hours after fixation, from aboral side. Compare with fig. 12. The aboral brachiolarian notch is practically closed. Retraction of the larval processes, etc., is proceeding rapidly.
- Fig. 18.—Cleared disc at metamorphosis, from aboral side, showing the arrangement of ossicles and spines described on p. 265.
- Fig. 19.—Young starfish a month after commencement of metamorphosis, showing four pairs of sucker feet and the mouth now formed. The radial cæca are bifid and have grown out beyond the margin of the pyloric sac.
- Fig. 20.—Diagram of curvature in food canal of a Crinoid, viewed from aboral side (modified from LANG, 49, vol. 2, p. 475).
- Fig. 21.—Diagram to illustrate the extremely modified curvature still recognisable in the adult asterid food-canal, and its relation to the food-canal of the larva. The view is from the aboral (right larval side) and the food-canal of the larva is shown in dotted lines (p. 274).
- Fig. 22.—Diagram of adoral ciliation in an advanced brachiolaria. The buccal cavity and œsophagus are represented as looked at from in front. The transverse portion of the preoral band which has to do with feeding is shown in black.



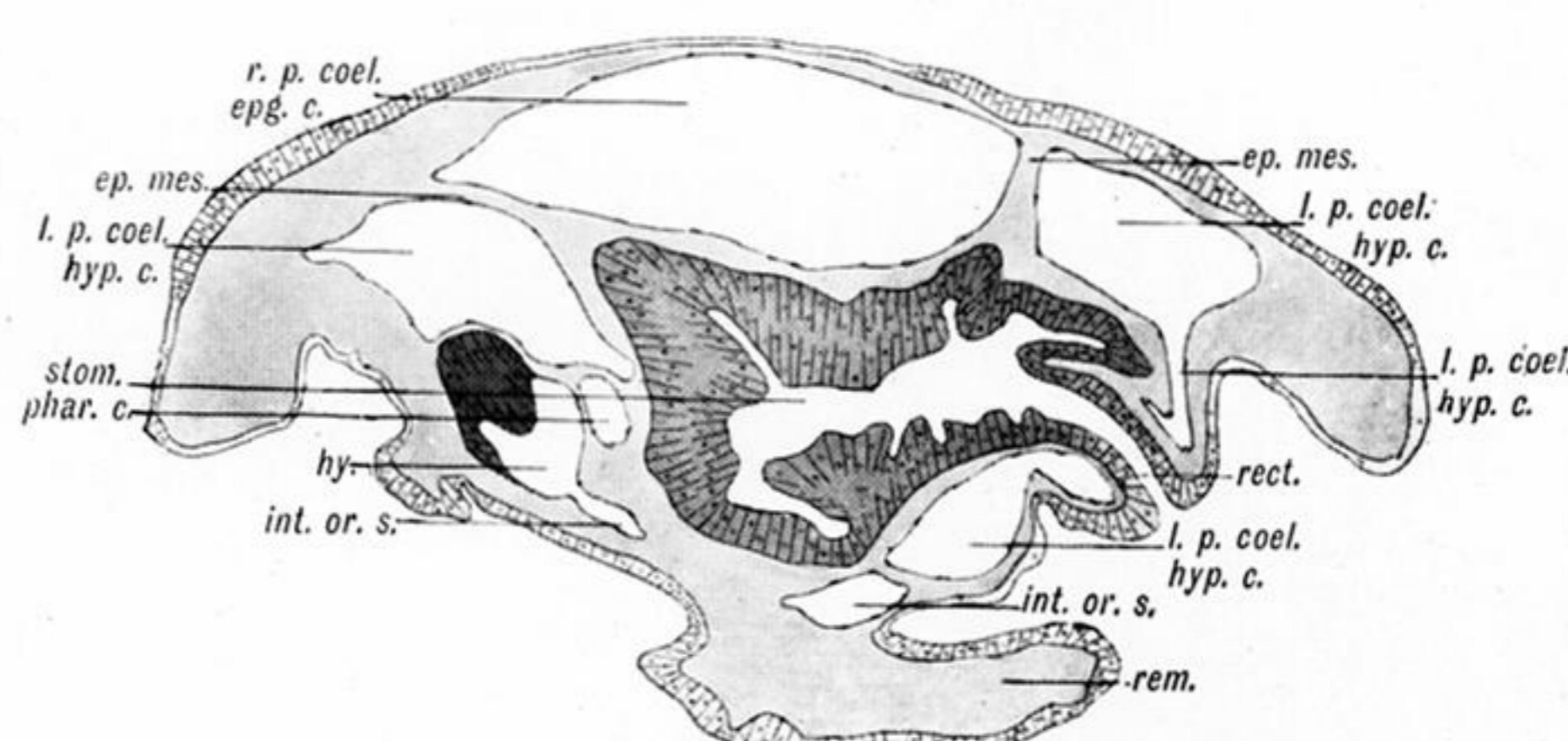
23 × 60



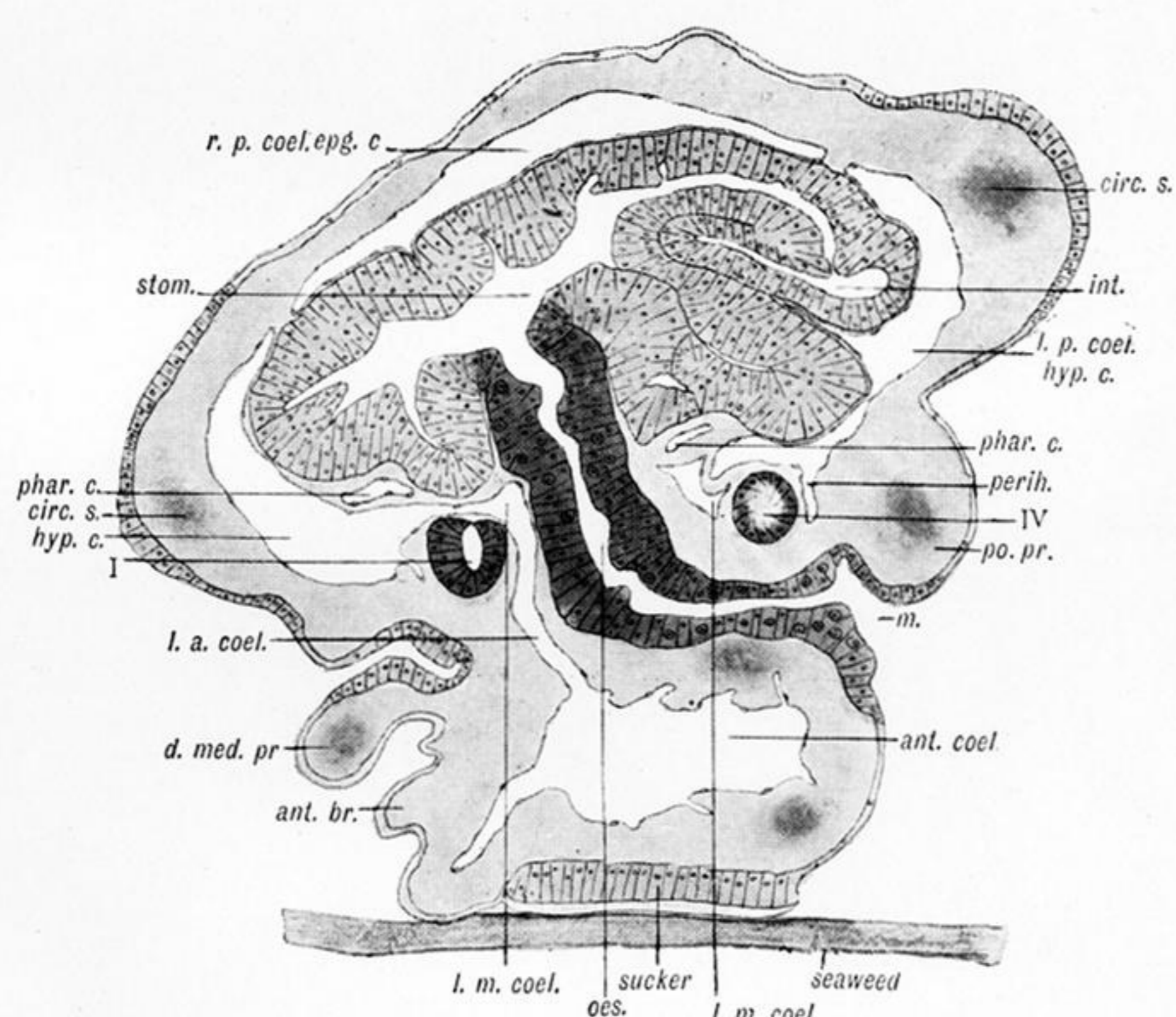
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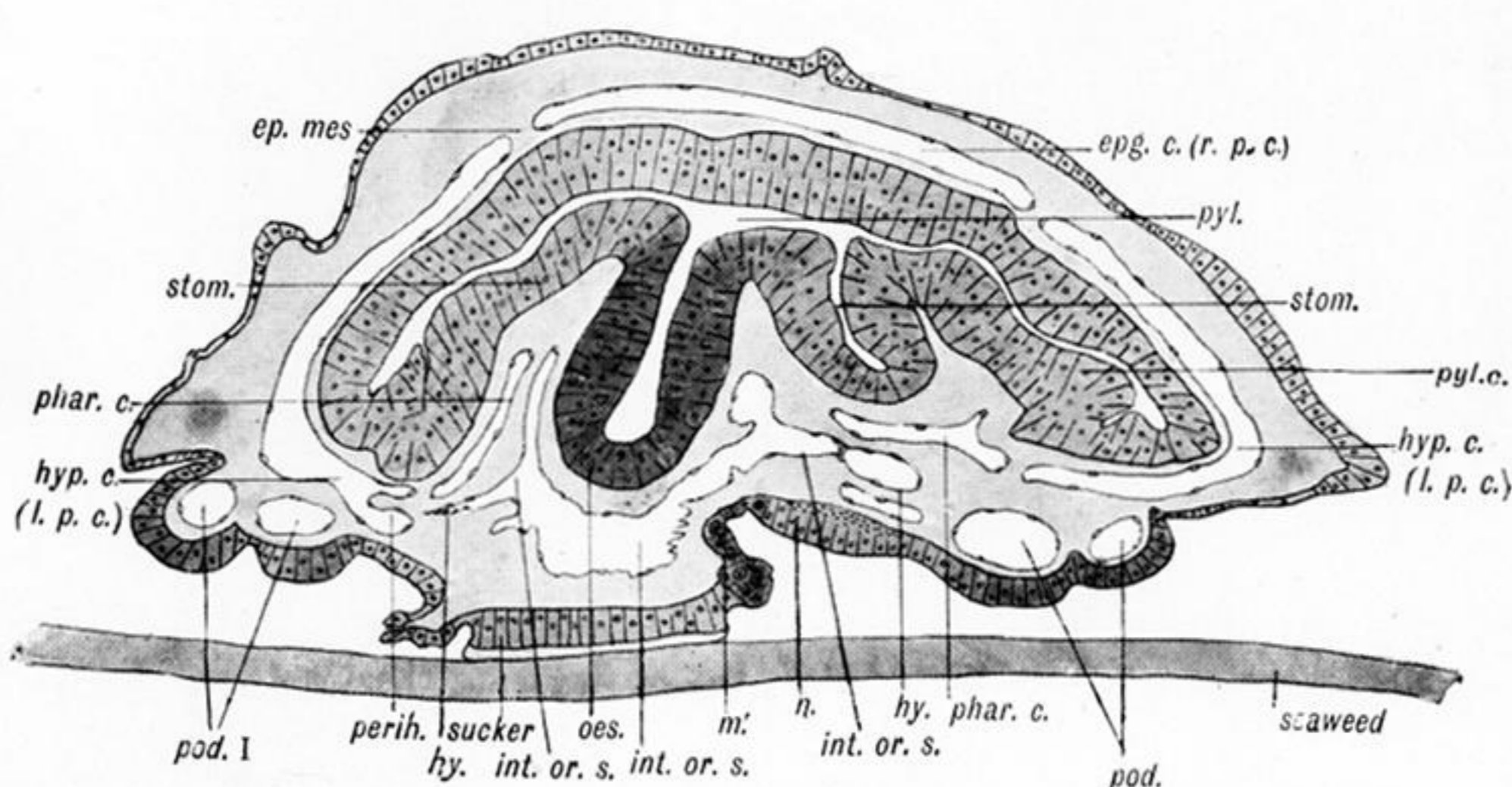
25 × 40



26 × 60



27 × 60



28 × 60

PLATE 23.

Fig. 23.—Transverse section of larva, about 21 days old, in region of the pore-canal, showing cells from which the dorsal sac is developed.

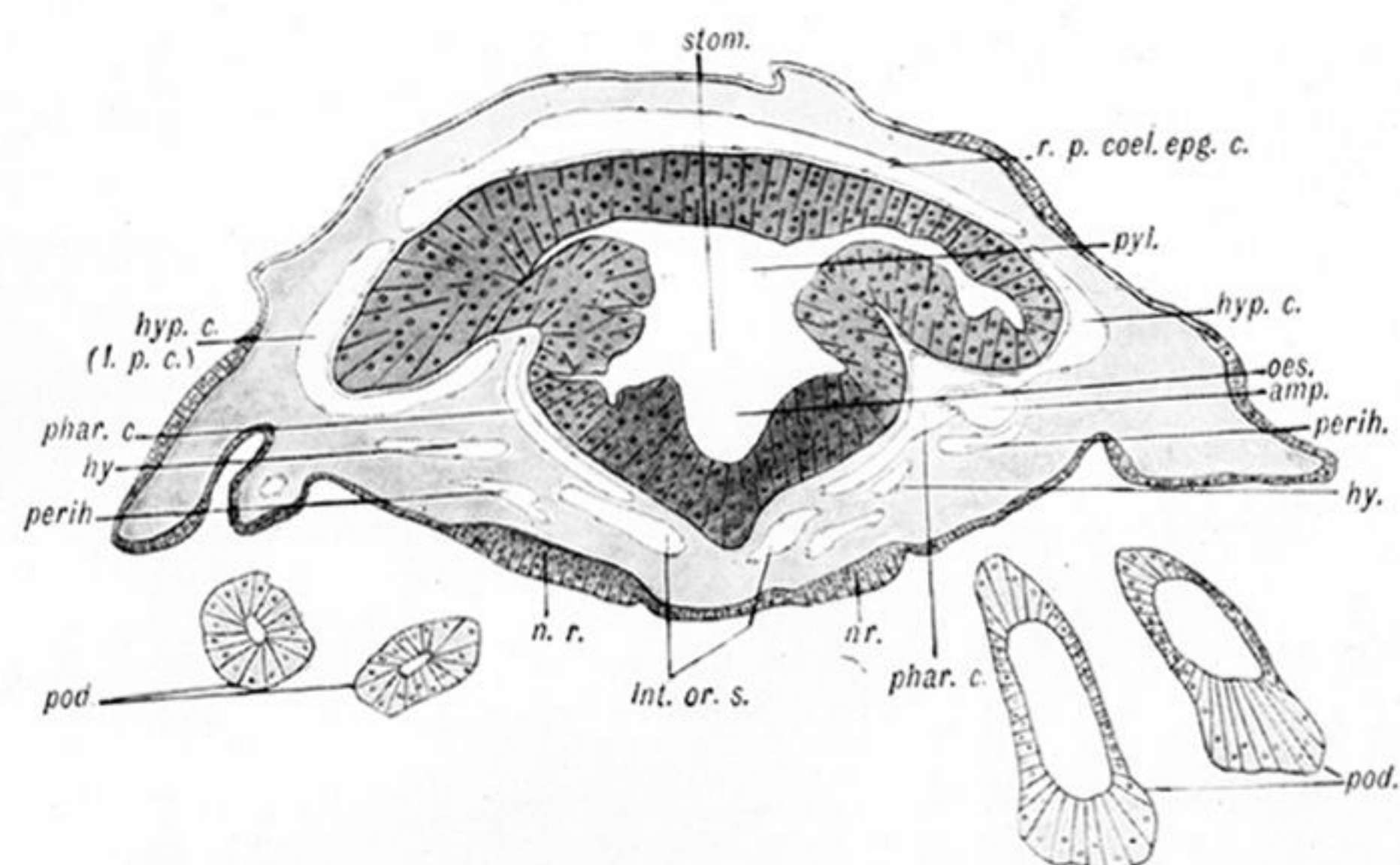
Fig. 24.—Transverse section of larva about 29 days old, showing dorsal sac now vesicular and connected with stone canal by a thin strand of cells. As frequently happens the posterior end of the oesophagus is invaginated into the stomach, forming the smaller inside ring.

Fig. 25.—Transverse section of still older larva, about 35th day, at time when pulsation of dorsal sac begins to be evident. The left and right posterior coeloms are now cut off from the middle coeloms and the ventral horn of the *l.p.c.* has united with the right middle coelom.

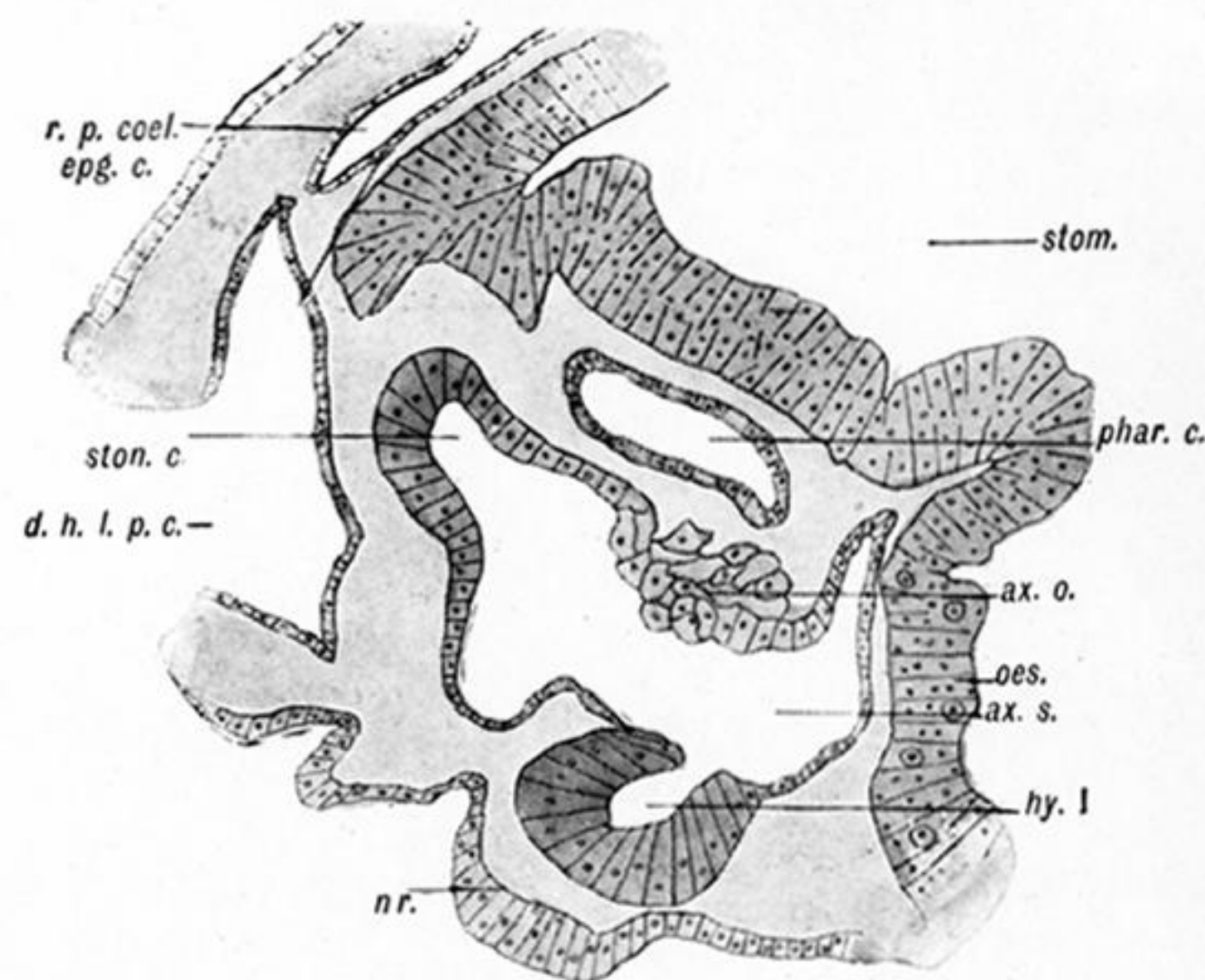
Fig. 26.—Section somewhat tangential through anal region of larva at commencement of metamorphosis. The anus is still open, the intestine is shortened and the rectum is preparing to separate off from the anal opening. The pharyngeal coelom has not yet grown round as far as the anal inter-radius.

Fig. 27.—Almost sagittal section through larva about 12 hours after fixation. As regards the oesophagus, what is shown combines the appearances seen in four successive sections which do not singly show the full length of the lumen. The two darkened areas on the disc which are marked *circ. s.* indicate the marginal channel within which fluid mesenchyme or lymph "circulates" at this stage (p. 41). The similarly darkened areas on the preoral lobe, etc., indicate places where there were special aggregations of this lymph. The junction of larval intestine with pyloric region of stomach is shown.

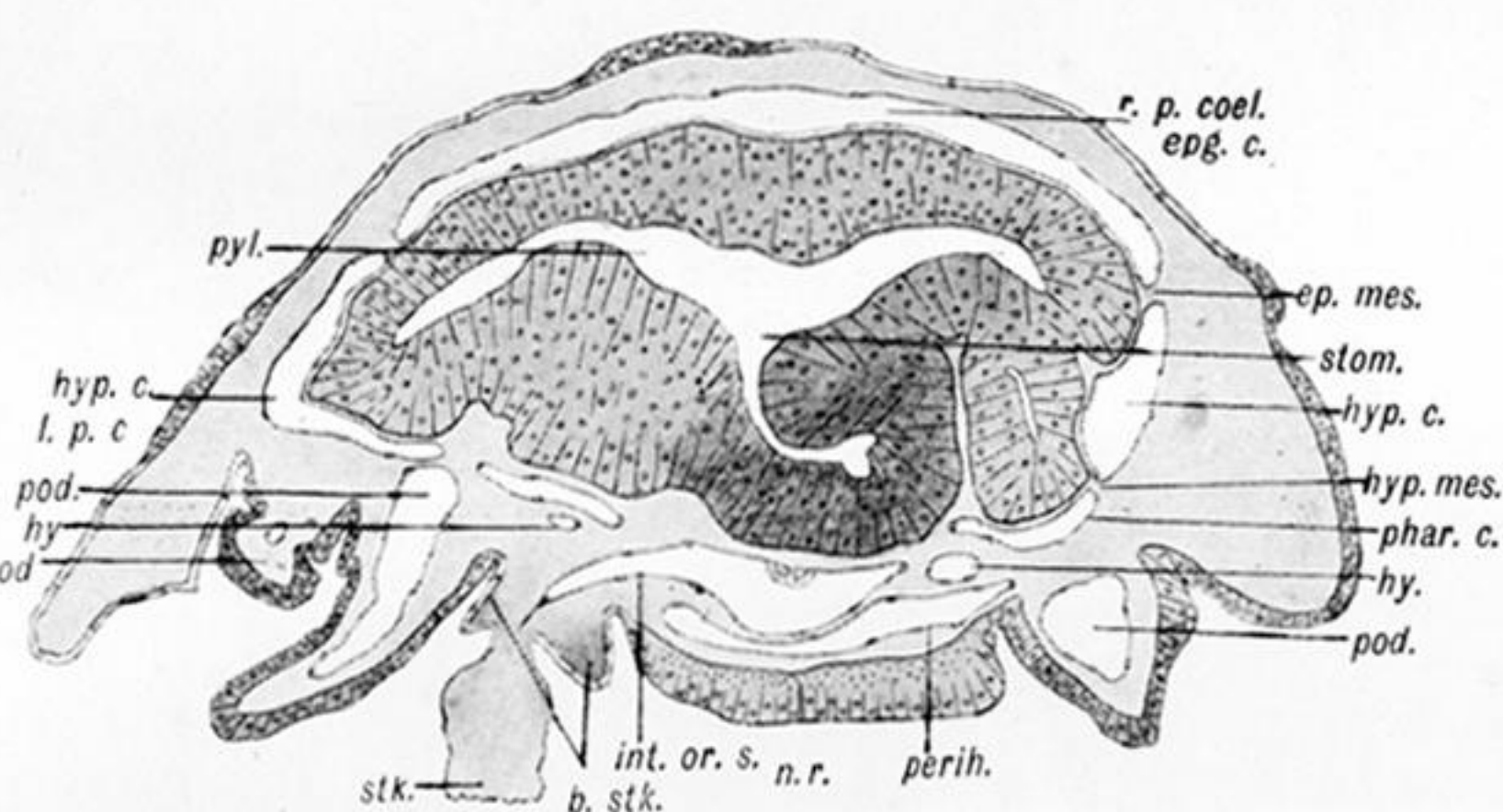
Fig. 28.—Vertical section through disc, stalk and sucker of young starfish about 36 hours after the commencement of metamorphosis. The provisional axial sinus, mainly made up of the expanded median portion of the anterior coelom (p. 254), surrounds the projecting end of the separated oesophageal cone. The position of the former larval mouth is indicated. The ring canal of the hydrocoele is in part completely cut off from the *l.m.c.*, and in part still communicates with the remains of this cavity. The definitive internal oral circular sinus has not yet been constricted off. This specimen, like that in fig. 27, is shown still attached by its sucker to a thin frond of seaweed.



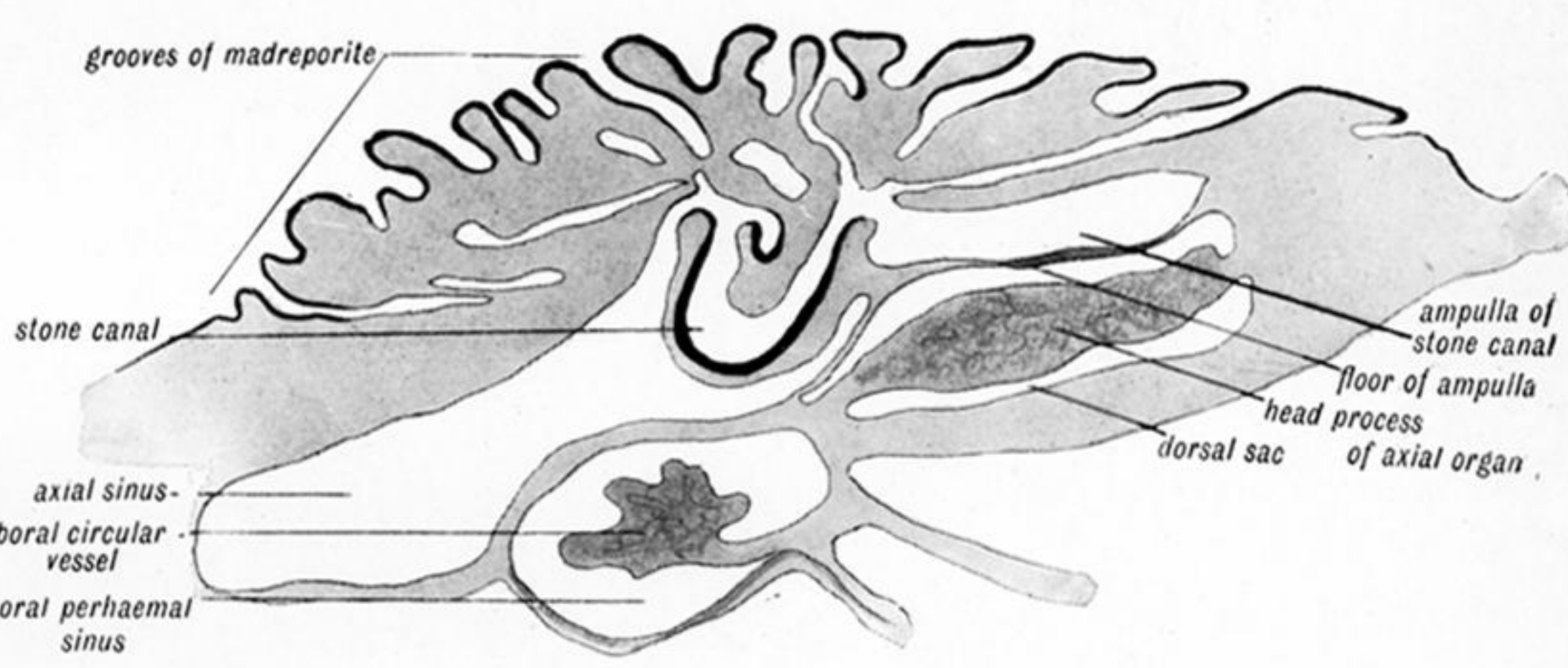
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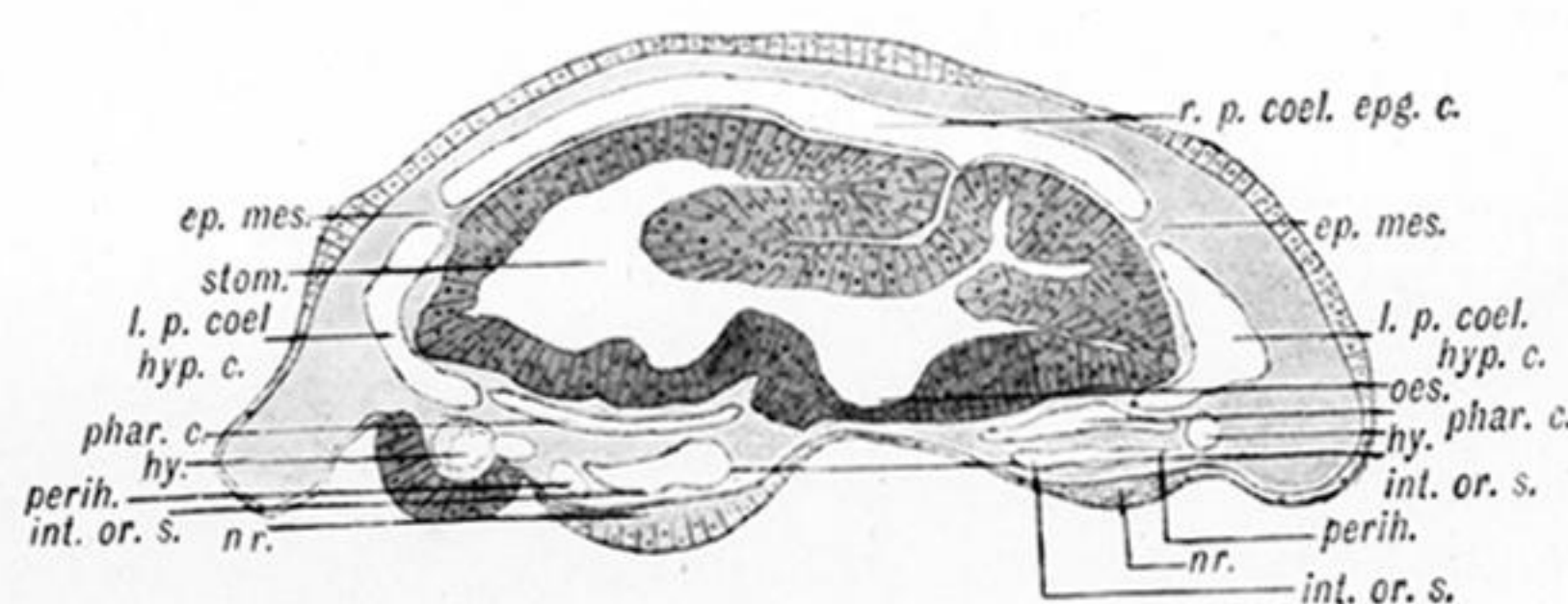
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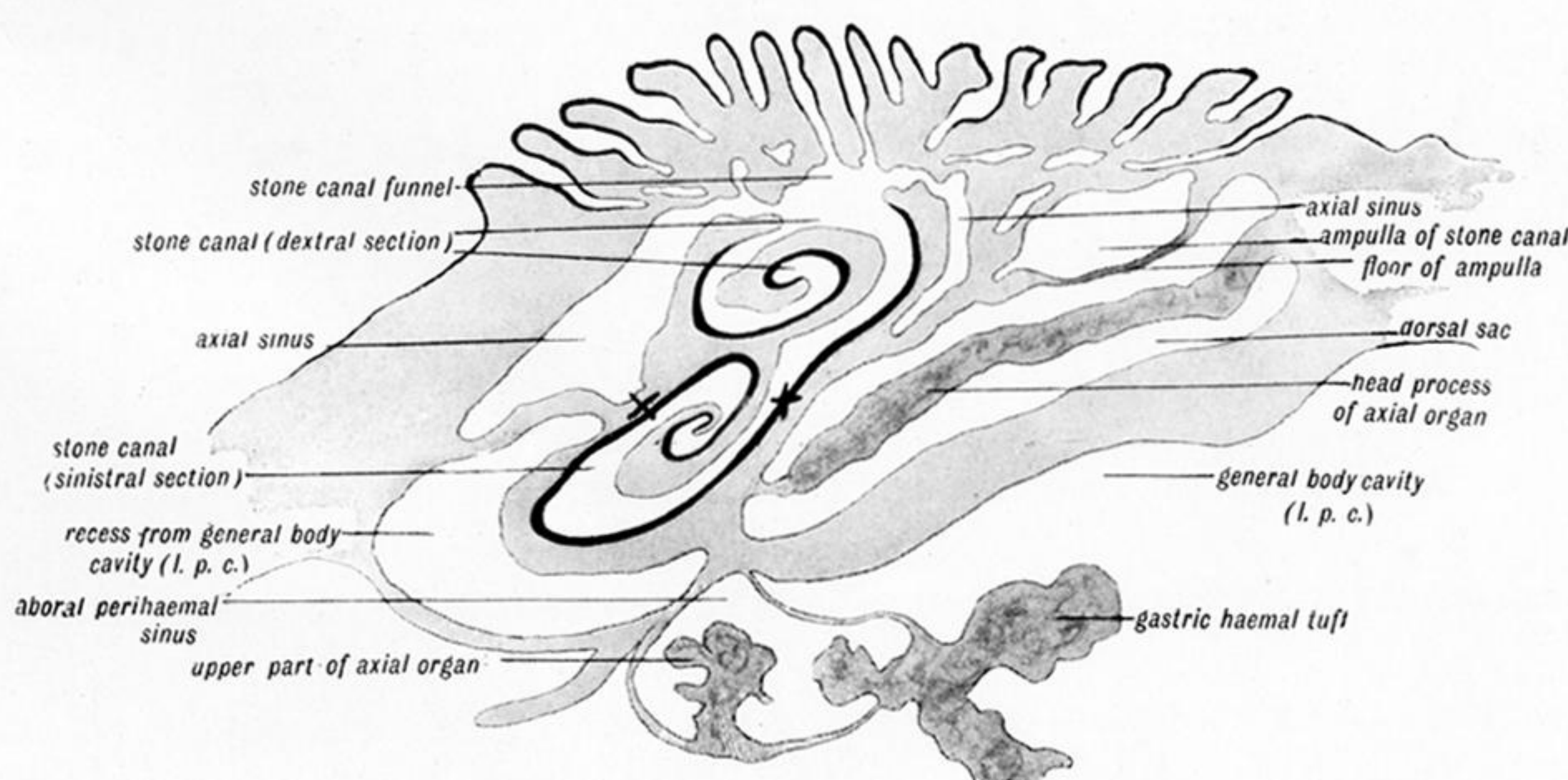
30 × 60



33 × 20



31 × 45



34 × 20

PLATE 24.

Fig. 29.—Section vertical to disc of young starfish four days after commencement of metamorphosis. The three regions of the gastric cavity, viz., oesophagus or pharynx, stomach, and pyloric sac, are distinguishable. The internal oral circular sinus now forms a canal in the region of hydrocoele pouches III and IV.

Fig. 30.—Section from same series as last but passing through insertion of stalk. The junction of the base with the thinner portion of the stalk is seen as a narrow neck. The provisional axial sinus sends a hollow process into the base of the stalk but the stalk itself is solid.

Fig. 31.—Transverse section through older starfish about six days after commencement of metamorphosis, showing beginning of formation of adult mouth.

Fig. 32.—From series of a specimen 12 hours after fixation, to show in particular the relation of the pharyngeal coelom to the developing axial organ (pp. 257, 278). The ring canal of the hydrocoele has not yet become separated off from the *l.m.c.*

Fig. 33.—From a series of sections through the madreporite of an *Asterias rubens* of moderate size. The middle of the starfish disc lies on the right of the figure but the sections are somewhat oblique. The stone-canal funnel is cut at the point where it opens into the ampulla and also where its sinistral section (see note on p. 217) has an opening into the axial sinus. As regards these openings the drawing combines the appearances seen in four successive sections, each 10 μ in thickness. With reference to the axial sinus, it is only the expanded aboral end of its dextral horn which comes into this section (pp. 268, 269). The relation of the ampulla to the underlying dorsal sac will be made out.

Fig. 34.—From same series as last, but nearer dextral (see note on p. 217) edge of madreporite. The section shows the main primary communication between the dextral section of the stone canal and the expanded aboral end of the dextral horn of the axial sinus. There is seen in the section one of the lobes into which the ampulla of the stone canal is divided. The + on the lining of the stone canal marks a point which, projected aborally, would come opposite the opening from stone-canal funnel into ampulla of stone canal shown in fig. 33. The x on the other side marks a similar point with reference to the opening from stone canal into axial sinus shown in fig. 33.