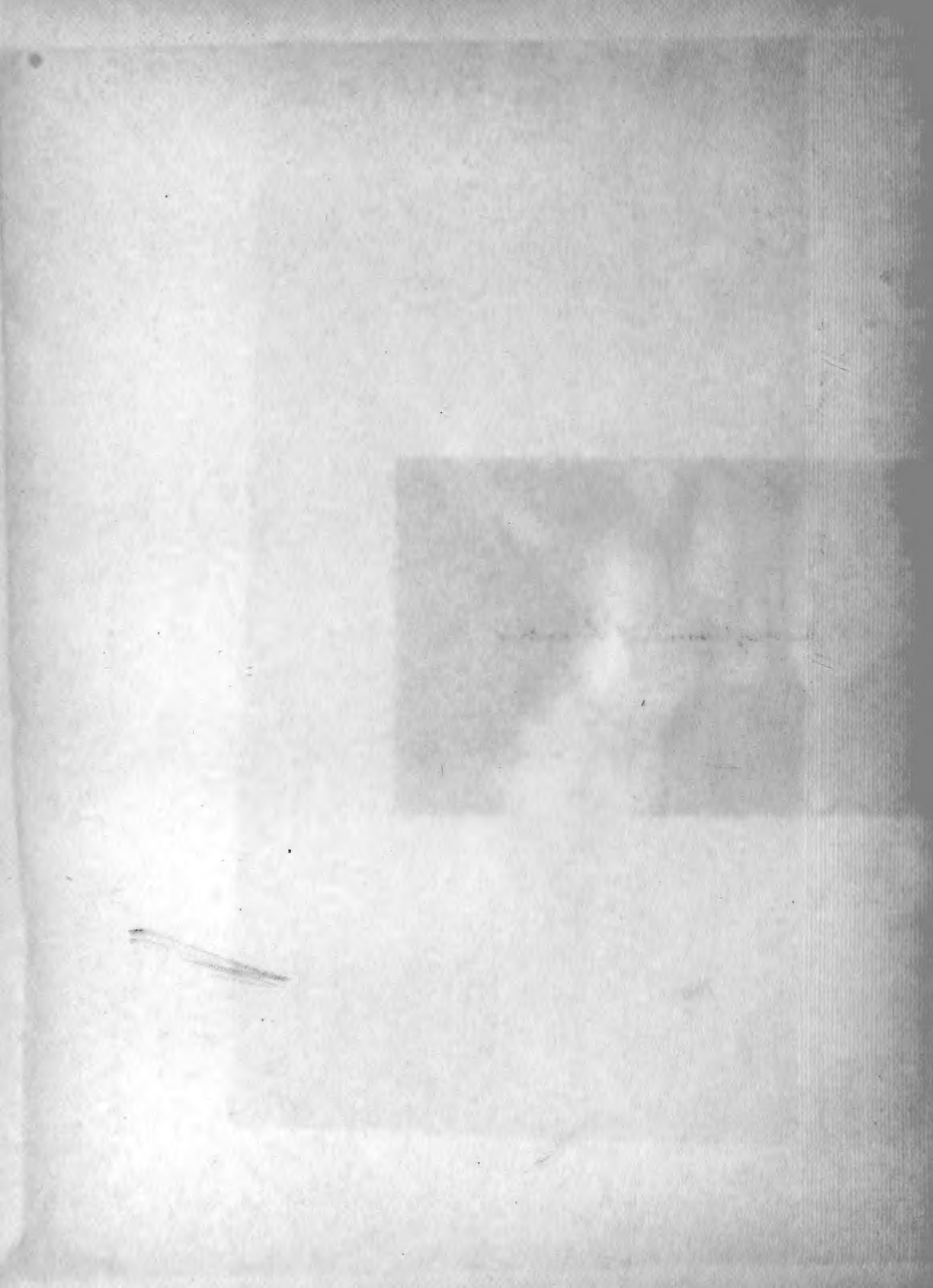

Austin H. Clark

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VOLUME XVI.

STUDIES IN THE DEVELOPMENT OF CRINOIDS

BY
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Of The University of Copenhagen

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STUDIES IN THE DEVELOPMENT OF CRINOIDS

BY
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INTRODUCTION.

During a stay on the island of Tobago, British West Indies, in March and April, 1916, with the expedition of the Carnegie Institution of Washington, I succeeded in rearing the young of the Crinoid *Tropiometra carinata* from the egg up to the fixed stage and also in keeping the Pentacrinoids alive for some time, until the appearance of the first radials. Since our previous knowledge of the embryological development of Crinoids is based exclusively on the European species, *Antedon bifida*, *A. mediterranea*, and *A. adriatica*, all being at least very closely related, it is of no small interest to become acquainted with the embryology of a species belonging to another genus, and even to another family. To generalize from a single type and apply the facts to a whole order is dangerous. It is only through the study of the embryology of different types that we can form a true judgment as to which features are of general and which only of specific value in the developmental history of this and other groups of echinoderms. Although it would be more interesting and important to have the embryology of some stalked Crinoid worked out, I think the facts made known through the present study will be found to be of some value and to represent progress.

I have included in this memoir a report on the development of some other Crinoids, namely, *Compsometra serrata* (A. H. Clark), from Japan, *Florometra serratissima* (A. H. Clark), from the Strait of Georgia, *Isometra vivipara* Mortensen, *Notocrinus virilis* Mortensen, and *Thaumatometra nutrix* Mortensen, all three from the Antarctic Sea. As to the two first named, I succeeded in getting material for the study of their development during my voyage in the Pacific in 1914–15. For the three other species I am indebted to Professor O. Nordenskjöld, of Gothenburg, who sent to me the whole of the collection of Crinoids made by the Swedish Antarctic Expedition (1901–03), including the "*Antedon hirsuta*" of Dr. K. A. Andersson (*Isometra vivipara*), the first truly viviparous Crinoid known. Of this species, material was found for the study of the whole development from the egg until the Pentacrinoid is ready to detach itself from the stalk. Then I had the great pleasure of finding in this material two more new viviparous forms, namely, *Notocrinus virilis* and *Thaumatometra nutrix*.[1] Although only some larval stages were found of the former species and the Pentacrinoid stages of the latter, several important facts were disclosed thereby.

[1] Th. Mortensen: *Notocrinus virilis* n. g., n. sp., a new viviparous Crinoid from the Antarctic Sea. Preliminary notice, Vid. Medd. Dansk Naturh. Foren. Köbenhavn, 68, 1917, p. 205.
—— The Crinoidea of the Swedish Antarctic Expedition. Wiss. Ergebn. d. Schwed. Südpolar-Exped. 1901–1903, vol. VI, 1917, plates I–V.

Thus the present memoir contains the description of the complete, or nearly complete, development of three new types of Crinoids and of part of the development of three other types.

My sincerest thanks are tendered to Dr. A. G. Mayor for the opportunity to take part in the expedition to Tobago, thereby affording me such exceptional advantages for extending my studies in the embryology of Echinoderms.

A short preliminary report on the results obtained in the embryology of Echinoderms during my stay at Tobago was published in the Year Book of the Carnegie Institution of Washington for 1916. The final report on the Echinoderms not included in the present memoir will be incorporated in the report on my researches on Echinoderm larvæ, carried on during my Pacific expedition.

I. TROPIOMETRA CARINATA (Lamarck).[1]

(Plates I to X.)

This Crinoid occurs in fair numbers in places on the coral reef at the western end of the island of Tobago, British West Indies, sometimes in such shallow water that it is exposed at lowest tide. It is a very hardy species, and there was no difficulty in keeping specimens alive in jars, even for several days. Late March and April were just in the breeding-season, and the first lot of specimens gave a few larvæ. After this I succeeded repeatedly in getting cultures of larvæ, never in great numbers, but sufficient to enable me to secure material for a fairly complete study of its development.

As the red-brown larvæ are quite opaque, nothing of the interior structure and its successive transformation could be seen on the living object. Only the first cleavage stages could be studied directly; but from the gastrula stage onwards the whole developmental process, excepting the development of the skeleton, must be studied by means of sections. Not being prepared for preserving material for sections, I had no other preserving fluids than corrosive sublimate and alcohol. The sublimate did not give very good results; the material preserved in alcohol was decidedly better. But upon the whole the preservation is not good enough for studying histological details. Thus, for instance, the larval nervous system could not be studied satisfactorily. However, here and there histological details could be seen which tended to show that as regards the histological development there is

[1] The specific name *carinata* adopted here is used on the authority of H. L. Clark, who mentions the species under this name in his report on the Echinoderms of Tobago. A. H. Clark, who formerly (On a collection of Crinoids from the Museum of Copenhagen, Vid. Medd. N. Foren. 1909, p. 182) held the same view, now (in The recent Crinoids of the coasts of Africa, Proc. U. S. Nat. Mus., 40, 1911) regards the Atlantic species of *Tropiometra* as specifically distinct from the *Tropiometra carinata* of the Indian Ocean, the Atlantic species being designated as *T. picta* (Gay) (*brasiliensis* Lütken). From a zoogeographic point of view I would expect them to be different species, but for want of sufficient material of the Indian form I have no opportunity for forming my own judgment in this case. Accordingly I have thought it my duty here to follow H. L. Clark in using the name *carinata* for the Atlantic form.

complete conformity with what has been made known by Seeliger in *Antedon adriatica*.

The relative scarcity of the material, together with the not very good preservation and the difficulty of the orientation of the embryos in the younger stages, has prevented making a complete study of every detail in the developmental process. Also the very rapid succession of the different stages in the development has added considerably to the difficulties in securing every stage. Accordingly, this report of the development of *Tropiometra* is not quite so complete as that given by Seeliger in his elaborate memoir on *Antedon adriatica*. The previous literature on the embryological development of Crinoids has been so thoroughly revised and criticized by Seeliger that we need not here review it in detail, and subsequently there is only one memoir to be taken into consideration, viz, the "Studii su gli Echinodermi," [2] by A. Russo. Literary discussions thus occupy only a small space of the embryological section of this work. This does, however, not apply to the parts relating to the post-embryonal development.

In his paper "On the origin of certain types of Crinoid stems," [3] A. H. Clark suggests that Crinoids with a very wide distribution, like *Tropiometra*, must have a prolonged free-swimming stage. "Are we justified in saying that the larvæ of *Tropiometra* may not turn out to be plutei or something like them?" This interesting suggestion stimulated interest in the study of the development of this species. The results, however, do not bear out Clark's expectations.

I expect that some day a Crinoid may be found with a truly pelagic larva, resembling a *Pluteus* or *Bipinnaria*, but I think it more probable that we may find it in some stalked Crinoid. In the Comatulids I would expect the case to be the same as in the Dendrochirote Holothurians, all having a simple larva, provided with ciliated rings, but otherwise not specially adapted to a pelagic life. The character of the egg bears a relation to this. In all the numerous Dendrochirotes I have examined, the eggs are large and yolk-laden, and I have no doubt that the larvæ in these, and probably all other Dendrochirotes, will prove to be of the usual simple Cucumarian type. In all the Crinoids I have examined the eggs are likewise rather large and rich in yolk, and I must infer from this fact that their larval form will also be of the usual, simple type. A. H. Clark states that in the Thalassometridæ the eggs are small, and accordingly he expects them to have a long free-swimming stage.[4] It would be of considerable interest to study the development of some species of this group. If the eggs in this family are really noticeably smaller than in other Crinoids, and especially less supplied with yolk, we may

[2] Atti dell'Accad., Gioenia, vol. XII, Mem. VII, 1902.
[3] Proc. U. S. Nat. Mus., vol. 38, 1910, p. 213.
[4] Vid. Medd., 1909, p. 122.

expect their development to afford features of unusual interest. However, the fact that *Ptilometra mülleri* carries its Pentacrinoids on the cirri [5] proves that at least this species has no prolonged free-swimming larval stage. I have not sufficient material of Thalassometrids at my disposal for investigating the character of their eggs; only in *Parametra orion* (A. H. Clark) I find the eggs to be a little smaller than those of *Tropiometra*, namely, 0.15 mm. against about 0.2 mm. in *Tropiometra*.

Now, as regards *Tropiometra*, the larvæ are, as already stated, not plutei or anything like that. Still there is something in the development to account for the wide distribution of this species. First the egg is free, probably pelagic, and then the larvæ, which are very active swimmers (in the jars they generally were found swimming at the surface), may keep up their pelagic existence for quite a long while. If they find a suitable place for fixation they may attach themselves when only 2 or 3 days old; otherwise they may swim for 6 or 7 days, and I had one specimen which did not attach itself until it was 8 days old. Due to this facultative, prolonged swimming period the larvæ may be carried for considerable distances by currents, and this accounts in a natural way for the wide distribution of the species.

An interesting fact to notice in this connection is that none of the specimens from Tobago proved to be infested with *Myzostoma*. This would seem to indicate that the colony living here must be an isolated one, originating from larvæ carried thither by the currents, not in direct connection with the main habitat of the species in American waters, which should probably be sought to the south of the Orinoco and Amazon Rivers. That specimens living there are infested with *Myzostoma* is known from v. Graff, who records *Myzostoma gigas* Lütken from specimens of *"Antedon" carinata* Leach taken by the *Challenger* off Bahia.[6]

A. H. Clark (Vid. Medd., 1909, p. 184) suggests that *Tropiometra carinata* may have extended its range northward from Brazil by passing under the fresh water discharged into the sea by the Amazon and Orinoco, thus surmounting this barrier "by the simple process of gradually increasing the depth of its habitat." This explanation may account for the specimens living in deep water (200 to 300 fathoms) in the West Indian sea, but its littoral occurrence in Tobago (and most probably other places in the southern part of the Caribbean Sea) is more satisfactorily explained through the transportation by means of currents, although there is a possibility that the littoral colony may have come from larvæ of the specimens occurring in the

[5] H. L. Clark (Scientific Results of the Trawling Expedition of H. M. C. S. *Thetis*. Mem. Austral. Mus., IV, part II, 1909) describes such specimens under the name of *Himerometra pædophora*, but A. H. Clark (The Recent Crinoids of Australia, Mem. Austral. Mus., IV, part 15, 1911, p. 785) maintains that they are *Ptilometra mülleri*.

[6] L. v. Graff. Report on the Myzostomida collected during the voyage of H. M. S. *Challenger*. Scientific Results of H. M. S. *Challenger*, vol. X, part XXVII, 1884, p. 35. Though I must doubt the correctness of this identification (*Myzostoma gigas* is otherwise known only from the arctic *Heliometra glacialis*), this proves that *Tropiometra carinata* is the host of a Myzostoma, like other Comatulids.

deep sea, which have risen to the surface and there come under the influence of currents.

It is in accordance with the comparatively long period of active swimming of the larvæ that we do not find the Pentacrinoids attached to the cirri or other places upon the adult. Indeed, I have not found any free Pentacrinoid. Not knowing, then, whether the larvæ prefer any special object upon which to attach themselves, I tried different things—algæ (especially *Udothea* and *Corallina*), coral pebbles, bivalve shells, leaves of Zostera (*Thalassia testudinum*)—which I put into the jars with the larvæ. Although specimens attached themselves to almost all these objects, they did not prove equally favorable. The most favorable attachments were made upon *Udothea* and *Corallina*. A good many specimens attached themselves to the surface film of the water, and here they developed into very fine Pentacrinoids.

The greater number of the specimens which attached themselves to the *Thalassia* leaves, dropped off and fell to the bottom of the jar, but continued developing lying on the side, unattached. This had, however, a curious effect on them: the vestibulary invagination did not close up and the thickened skin of the bottom of the invagination continued to be in contact with the anterior (by this time posterior) end, by which they ought to have been attached. This thickened skin therefore acted as a band keeping the (now) anterior end of the embryo down; the stem-joints keeping on growing normally, the stem became more and more curved, the result being that the embryo assumed a peculiar shape, resembling a pipe (plate IX, figure 6). Even in spite of this abnormal shape, some of these specimens went on growing and at last developed into Pentacrinoids differing from the normal ones only by having the head bent downwards, and I can scarcely doubt that it would have been possible to rear them to full development if time had permitted. A similar aberrant development has been described by Barrois[7] in his "Recherches sur le développement de la Comatule" (p. 640, plate XXX, figure 21, etc.).

On account of the short time of our stay at Tobago I did not succeed in getting the Pentacrinoids very far in their development. On leaving the island I carried some of my cultures along with me, in the hope that they would stand transportation and go on developing. While staying in Port of Spain, Trinidad, waiting for the steamer for New York, I had the cultures placed in one of the laboratory buildings of the Botanical Garden, through the kind permission of the director, Doctor Rorer. During these 5 days everything went well, though there was no opportunity for changing the water. On board the steamer it was difficult to find a suitable place for the cultures, and one night, near New York, the temperature went down too far, so that the Pentacrinoids were chilled. On my arrival at New York I had them

[7] Recueil Zoologique Suisse, IV, No. 4, 1888.

placed in the aquarium, under excellent conditions, suitable temperature, and light. Although some of the Pentacrinoids were still alive, they did not recover from the chilling and did not develop any farther, so that I thought it useless to try to carry them alive with me to Copenhagen and preserved them. I may mention here that I did succeed in carrying some young *Echinometra lucunter*, which I had likewise reared from the egg in Tobago, alive to Copenhagen. I beg to express here my sincerest thanks to Dr. Charles H. Townsend, Director of the New York Aquarium, for his kind assistance. There is no doubt that it would be possible to carry also young Pentacrinoids alive and in good health to New York, if not exposed to too low a temperature, and in such case the New York Aquarium would be an excellent place in which to keep the cultures for further study.

Naturally there is no question of procuring food for the Crinoid larvæ; this trouble does not arise till the mouth has opened in the Pentacrinoid. I used diatom cultures (*Nitschia*), procured in the way indicated by Allen and Nelson,[8] and found this to be a very suitable food for the Pentacrinoids. Also, by simply changing the water every day I found them growing normally. Some of the first Pentacrinoids reared I tried to plant out on the reef in dishes, but without success, the dishes filling with sand, although placed where there was very little surf.

A difficulty in describing the development of a Crinoid arises from the *orientation*, on account of the fact that the larva attaches itself with its anterior end, the posterior end of the larva becoming thus the oral end of the Pentacrinoid. Seeliger orients the Pentacrinoid in the same way as the larva, head downwards. Although there is a morphological reason for this, it seems to me too unnatural. Consequently I adopt the method of Bury, and represent both the larva and the Pentacrinoid in their natural position.[9]

1. CLEAVAGE; FORMATION OF THE GASTRULA. FIRST 6 HOURS.

The eggs (plate 1, figure 1) are rather small, about 0.2 mm. in diameter, opaque, whitish, with a faint reddish tint. On being discharged, they are surrounded by a distinct, clear, follicular membrane. The peculiar structure of the follicular membrane, described by Ludwig in *Antedon mediterranea* (*rosaceus*),[10] I have not observed in *Tropiometra*. It is true I did not look especially for it in the living object, not remembering anything about the structure at that time (and I had, of course, no access to literature); but the fact that I did not notice anything of the kind makes it fairly certain that no such structure of the follicular membrane exists in this species.[11]

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[8] E. J. Allen and E. W. Nelson. On the artificial culture of marine plankton organisms. Quarterly Journ. Micr. Sc., vol. 55, 1910.

[9] By a mistake figures 4–7, plate XXII, have been placed with the anterior end downwards.

[10] Die Bildung der Eihülle bei Antedon rosaceus, Zoolog. Anzeiger III, 1880, p. 470–471.

[11] Ludwig found the structure very distinct also in preserved condition; I have found no trace of such structure in eggs taken from the pinnulæ of the preserved specimens of *Tropiometra*.

While in *Antedon* the eggs remain attached to the pinnulæ during the first stages of development, for a period of 4 to 6 days, in *Tropiometra* they are attached only for a very short time. Almost immediately after the extrusion from the genital opening the follicular membrane dissolves and *the naked eggs sink to the bottom; the fertilization does not take place until after the egg has become free.* Repeatedly I have found the bottom of the jar in which the specimens were kept entirely covered with eggs discharged during the night. Eggs were never found to be discharged during day-time.

The formation of the egg-membrane is very interesting to follow. Immediately on the entrance of the spermatozoön the egg secretes a thick layer of a slimy-looking substance, not regularly limited outwardly. The inner part of this layer at once acquires a harder consistency, thus forming a membrane, the edge of which is sharply defined towards the egg-surface, while outwardly it acquires its final structure only gradually. The formation of this structure starts at one place and spreads from there over the whole egg (plate 1, fig. 2). When fully formed the membrane consists of polygonal areas, slightly sunken, with very distinct, elevated edges. Each corner bears a distinct spine (text-figure 1, *a*). The spines are formed by the outer part of the slimy layer. Sometimes I have observed a radiating striation in it. After the formation of the spines this layer is hardly discernible; still, a fine line may be seen, uniting the points of the spines (text-figure 1, *b*). The whole process occupies 15 to 20 minutes.

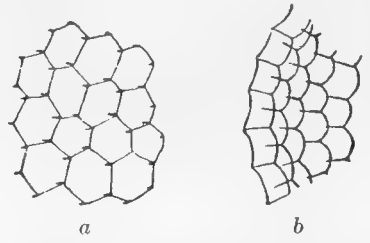

FIG. 1.—Part of the egg-membrane: *a*, seen from above; *b*, side view. ×320.

The fully formed membrane (plate 1, figures 3, 4, 5) is a very beautiful object. It recalls the egg-membrane of *Callionymus*. I would suggest that its peculiar structure is a special adaptation forming a floating apparatus. Although the eggs were always found lying on the bottom in the dishes until the embryo left the membrane, it can hardly be doubted that when free in nature the slightest movement of the water must act on this spiny membrane, causing the egg to drift.

The egg-membrane of *Antedon* has received very little attention; only Wyville Thomson describes it as "perfectly transparent and structureless, with the surface slightly and irregularly echinated." (The Embryogeny of *Antedon rosaceus*, p. 520.) In *Antedon*, therefore, there is evidently nothing like the structure in *Tropiometra*.

The segmentation begins very soon after the fertilization, the blastula stage being reached after about 2 hours. In *Antedon* this stage is not reached till 6 (Seeliger) to 12 hours (Bury) after the fertilization. The first cleavages are quite regular (plate 1, figures 3, 4, 5); in the later stages there is a slight inequality, so that in the newly formed blastula the cells are somewhat

larger at one pole of the embryo (plate I, figure 6). This inequality, however, soon disappears completely and I have been unable to ascertain whether the invagination takes place at the pole, where the larger cells occurred.

When the embryo is about 2½ hours old the *formation of the entoderm* begins. It starts with the wandering into the cavity of the blastosphere of several cells; these cells lie loosely in the cavity and look like mesenchyme cells (plate I, figures 7, 8, 9), which, however, they are not. It appears that they come irregularly from different places of the blastosphere; thus in plate I, figure 8, are seen in one place two elongated cells, in another place one cell similarly elongated and protruding beyond the level of the other cells into the segmentation cavity, apparently being about to wander in; however, I can not ascertain this beyond doubt. When the cavity is nearly full of these cells, the typical invagination takes place, and the loose cells now arrange themselves regularly at the upper end of the invagination (plate II, figures 2 and 3; plate I, figure 10). Probably the formation of the mesoderm cells starts again from these cells, but *at one time all the formerly loose cells have joined the entodermal invagination.*

The formation of the entoderm thus differs considerably from that of *Antedon,* where (according to Seeliger, who has made a most careful study of this process) no such wandering of free cells into the blastocœl takes place before the invagination. However, it must be mentioned that in one case I found the invagination starting before any loose cells had wandered into the segmentation cavity (plate II, figure 1). In this case the formation of the entoderm thus proceeds as in *Antedon.* It is rather startling to find that there can be so great variation within the same species in so important a process as the formation of the entoderm.

The ectoderm cells in the oral half of the embryo have their inner ends turned upwards, making a very characteristic arrangement (plate II, figures 1, 2, and 3); it looks as if they were pushed upward by the invagination. The little space left by the archenteron, together with the considerable elongation of the ectoderm cells at this stage, accounts for this peculiar feature.

In the lower end of the archenteron, near the blastopore, the cells are quite low; in the upper, wider part they are high and cylindrical. The cavity of the archenteron is very narrow and makes a characteristic curve in the upper part (plate II, figures 2 and 3; plate I, figure 10). *The blastoporus is a small, round opening,* not an elongated slit, as in *Antedon.*

The gastrula is fully formed about 5 hours after the fertilization. In *Antedon* this stage is reached (according to Seeliger) about 16 hours after fertilization, but according to Barrois and Bury it is not reached until 24 hours after fertilization, this discrepancy being evidently due to the fact that Seeliger worked on *Antedon adriatica,* while Barrois and Bury worked on *Antedon mediterranea,* as pointed out by A. H. Clark.[12]

[12] A. H. Clark, A new European Crinoid, Proc. U. S. Nat. Mus. 38, 1910, p. 329.

In some cases I have found, instead of an embryo, the whole space inside the egg-membrane filled by a uniform mass of minute spherules, besides a couple of deeply staining protoplasm masses, looking like a pair of cleavage cells, but containing no nuclei. This would appear to be some kind of parasitic organism. It has seemed to me worth while calling attention to this, although I am unable to say more definitely what it is (plate II, figure 8).

When the gastrula stage is reached, the embryo begins to rotate within the egg-membrane, being covered with a uniform ciliation. *About 6 hours after the fertilization the rupture of the egg-membrane takes place and the embryo swims out.* Only a small opening is formed in the membrane, through which the embryo must squeeze itself out. The empty membrane may be found on the bottom of the jar, undisturbed, except for the hole through which the embryo has crept out.

The embryo, just after the liberation, is slightly pear-shaped, being a little pointed at the apical end and a little truncated at the oral end. There is thus no difficulty in seeing directly that the place of the blastopore is the posterior end of the larva; further, this shape of the embryo facilitates the orientation in sectioning, the longitudinal axis being always distinct from the moment the embryo is liberated, while the spherical embryo of *Antedon* can not be oriented with certainty in sectioning until the vibratile bands have been formed, the situation of the archenteron nearer the posterior end and the more numerous mesenchyme cells in the anterior end affording the only means by which to identify the longitudinal axis (Seeliger, pages 171, 200).

The ciliation is still quite uniform, and there is no indication as yet of the ciliated bands. *The blastopore closes immediately after the liberation.* Plate II, figure 4, represents a longitudinal section through an embryo only 6 hours old, immediately after the liberation. It shows the blastopore closed, and the formation of the mesoblast cells from the upper end of the archenteron has already made fair progress.

2. FORMATION OF THE CŒLOMIC VESICLE, SIXTH TO TWELFTH HOURS.

At this stage the *ciliation* is still uniform; in embryos 10 hours old the apical tuft of cilia is distinct, but the ciliated bands do not begin to appear until the embryo is 12 hours old.

The *ectoderm*, which in embryos 6 hours old (plate II, figure 4) is a typical epithelium, with the nuclei arranged fairly regularly in a single series at the basal end of the cells, is considerably thickened with the nuclei arranged pluriserially (plate II, figure 5; plate III, figures 1 to 4); it is, however, still distinctly a single-layered epithelium. At the anterior end under the apical tuft it is more or less thickened (plate III, figures 3 and 4); this part corresponds to the apical pit of *Antedon*, but it is never so conspicuous as in that

form. In embryos 8 hours old the archenteron is nearly separated into an upper and lower part through a median constriction (plate II, figure 5). The blastocœl cavity is completely filled by mesoblast cells; also at the oral end, below the archenteron, a group of mesenchyme cells has made its appearance; that they are derived from the lower end of the archenteron seems beyond doubt.

The *complete separation of the archenteron* into an upper part, the entero-hydrocœl,[13] and a lower part, the cœlomic vesicle, may take place at an age of only 10 hours (plate II, figure 6), though in other cases the two parts may still be in wide connection at this age (plate II, figure 7).

In embryos 12 hours old the lower part of the cœlomic vesicle begins to form two lobes extending somewhat forward and connected by a narrower part (plate III, figures 2 and 4; plate II, figure 9); these two lobes represent the right and left cœlom. In the section of an embryo 12 hours old, represented in plate III, figure 2, is still seen the last trace of the connection between the anterior and the posterior part of the archenteron.

The anterior part, destined to form the intestine and the hydrocœl (the "mesentero-hydrocœl" of Bury and Seeliger), forms a pouch (plate III, figure 3), which is doubtless the rudiment of the hydrocœl. Although its constriction from the entoderm could not be followed, the comparison with what obtains in *Antedon*, as represented by Seeliger, leaves hardly any doubt that this is really the first trace of the hydrocœl. On the other hand, I would not venture to maintain that the pouch seen in a corresponding place in plate II, figure 7, from an embryo only 10 hours old and with the archenteron still undivided, is really the same thing, though it might not seem improbable.

The *entero-hydrocœl* is a simple vesicle, with no posterior prolongations to embrace the narrow middle part of the cœlomic vesicle. The relation between the two primary vesicles is thus quite simple and the complicated structure which occurs in *Antedon* is seen to have no general value in the developmental history of Crinoids.

Concerning the histological character of the two entodermic vesicles, it need only be stated that they consist of a simple, rather low epithelium, distinctly lower than the ectoderm (plate II, figure 7; plate III, figure 4). The formation of mesenchyme cells appears to continue until about the time when the separation of the two entodermic vesicles takes place (plate II, figures 5 and 7); but already at the age of 8 hours the blastocœl cavity may be completely filled up by the mesenchyme cells. The nuclei of the entoderm and mesenchyme cells are generally distinctly larger than those of the ectoderm, a feature which may be observed throughout the embryonic development.

[13] I prefer to use this designation instead of the name "mesentero-hydrocœl" used by Bury and Seeliger.

3. VESTIBULARY INVAGINATION; FURTHER SPECIALIZATION OF THE CŒLOM AND HYDROCŒL, 16 TO 40 HOURS.

In embryos 16 hours old the ciliated bands are fully formed. There are only 4 of them, not 5 as in *Antedon adriatica* and *mediterranea* (plate x, figures 1 and 2). Wyville Thomson figures only 4 ciliated bands in the species which he has studied, *Antedon bifida*, so that it would appear that even within the same genus the number of the ciliated bands may be variable. However, this certainly needs confirmation, as it seems doubtful that so conspicuous a difference would exist in closely related species.

The second band apparently ends abruptly on the sides of the vestibulary invagination, but on closer observation it may be seen to continue along the borders within the vestibulum, around its posterior end, although in the specimen figured in plate x, figure 2, this could not be distinctly ascertained. The first band is pushed slightly upwards, the third slightly downwards, by the vestibulary invagination. The posterior ciliated band lies in a slight depression, as is seen distinctly in most of the sections (*e. g.*, plate III, figures 4 and 6). The anterior or apical pit is not so distinctly circumscribed, as in *Antedon*.

The *vestibulum*, which begins as a flattening of the ventral side of the embryo at the age of 12 hours, now forms a distinct invagination of broad oval outline.

The *ectoderm* is distinctly limited towards the mesenchyme in embryos 16 to 20 hours old, but from the age of 25 hours no limit can be seen. In sections stained with hematoxylin, elements are seen in the ectoderm which stain very strongly and look like glandular cells (plate v, figures 1 to 5, *gl. c.*). Although the histological preservation is not quite satisfactory, I have no doubt that these elements correspond to the "yellow cells" of the *Antedon* larva, which are also supposed to be of glandular nature. In the vestibulary invagination the ectoderm stains very strongly in hematoxylin, a feature which does not depend alone on the fact that the nuclei are here much more numerous than in the other parts of the ectoderm (plate IV, figures 3 and 13; plate v, figure 6). Possibly this indicates a glandular character of the cells of the invagination. Bury (p. 269, plate 44, figure 22) mentions the same feature in *Antedon*, but points out that they lose their color much more readily in acidulated alcohol than do the glandular cells of the ectoderm (*cf.* also Seeliger, p. 246). Bury finds these deeply staining cells only in the anterior, deeper part of the vestibulary invagination. In the *Tropiometra* larva the cells have this character throughout the whole length of the invagination (plate IV, figure 13).

In a specimen 25 hours old (plate IV, figure 2) I have observed very distinctly a feature described by Seeliger in *Antedon* (p. 236), viz, that the ectoderm cells secrete between themselves an intercellular substance, this process being the beginning of the transformation of the ectoderm, which

ultimately results in the complete intermingling of the ectoderm cells in the mesenchyme, so that in the later stages of development there is no separate ectoderm layer. The details of this process could not be followed in *Tropiometra*, but since the first stage of the process and also the end-result are the same in *Tropiometra* as in *Antedon*, there is evidently no reason to doubt that the whole of the process is identical with that obtaining in *Antedon*, as described by Seeliger. An indication of this intercellular substance is also seen in plate IV, figure 1, at the posterior end, as well as in plate IV, figure 3, these figures being likewise from embryos 25 hours old.

In plate IV, figure 13, from an embryo 40 hours old, is seen a depression just in front of the vestibulary invagination, evidently representing the *suctorial disk*, by means of which the larva attaches itself. It is very indistinctly seen, except in sections. The anterior band passes uninterrupted between the disk and the invagination, as is also the case in *Antedon*.

The ciliated bands generally appear in sections as slightly concave structures (plate IV, figure 13); sometimes, however, they are distinctly convex (plate V, figure 3), while at other times they appear to be nearly flat. The differences are evidently due to preservation.

The *nervous system*, first seen by Bury in the *Antedon* larva and described in a detailed way by Seeliger, appears to exist also in the *Tropiometra* larva in at least the same degree of differentiation, or probably even somewhat more strongly developed. In the anterior end, below the apical tuft, is seen a conspicuous layer of an exceedingly fine fibrillary substance, which continues more or less distinctly downwards, below the vibratile bands (plate IV, figures 13 and 14; plate V, figures 3, 4, and 5). The nerve passing along the side of the vestibulary invagination may also be observed (plate V, figure 6, distinct on the right side of the figure only), but not so distinctly as appears to be the case in *Antedon*. Unfortunately the preservation is not so good as to permit the determination of its nervous character from the histological structure, but from the complete analogy of its position with the nervous system of the *Antedon* larva it would appear beyond doubt that this structure in the *Tropiometra* larva represents the nervous system.

The cœlom.—In embryos 16 hours old the right and left cœlomic vesicles have separated completely and are about to assume their final position, the left at the posterior end of the embryo, the right along the dorsal side, covering the entoderm. The series of transverse sections of an embryo 20 hours old (plate III, figures 8 to 11), of an embryo 25 hours old (plate IV, figures 4 to 12), and of an embryo 40 hours old (plate V, figures 7 to 10), combined with the longitudinal sections of corresponding stages represented in the same plates, will show the shape and extent of the two cœlomic vesicles, making a detailed description superfluous. It is seen that the right vesicle widens gradually, so that at the age of 40 hours it occupies the whole dorsal side in the posterior half of the embryo. The epithelium of the vesicles

soon begins to flatten and at the age of 40 hours has completely assumed an endothelial character.

It has not been possible to follow the details of the formation of the *chambered organ,* but plate IV, figure 1, shows the first rudiment of it in the shape of a forward prolongation from the right cœlomic vesicle in an embryo 25 hours old. Whether there are 5 such prolongations, as in *Antedon,* I have been unable to confirm; but there would scarcely be any reason to doubt that the development of a structure so fundamental in Crinoid anatomy as the chambered organ must proceed in the same way, at least in the uniform group of the Comatulids.

The *hydrocœl* has been completely separated from the entoderm at the age of 16 hours (plate III, figure 5). It sends out a forward prolongation, still in open connection with the hydrocœl vesicle (plate III, figure 6). This is the future *parietal canal.* At the age of 20 hours it is completely separated from the hydrocœl. It is only a short vesicle (plate IV, figure 1); I have never found it prolonged anteriorly, as is the case in *Antedon* (Seeliger, taf. 16, figure 68), and as I have found it also in *Compsometra serrata* (plate XI, figures 8 and 9), *Isometra vivipara* (plate XV, figure 11), and *Notocrinus virilis* (plate XXIV, figure 4). The pore canal does not begin to develop until about the age of 40 hours, and there is as yet no exterior opening (plate V, figures 3, 4, and 5).

Russo (*op. cit.,* p. 47) maintains that the parietal canal in *Antedon* remains in open connection with the hydrocœl. In *Tropiometra* this is decidedly not the case, and the same holds good for *Compsometra serrata, Isometra vivipara,* and *Notocrinus virilis.* As for *Antedon,* I would venture to say that Russo's figure 12, tav. II, to which he refers especially as a proof of this statement, does not appear to be a very convincing proof against Seeliger's clear and detailed figures. Certainly the said figure shows a connection between the parietal canal and the hydrocœl, but it would appear to be the stone canal which is here seen to open into the parietal canal, and that does not prove that the parietal canal was always in connection with the hydrocœl.

The *hydrocœl,* which at first is a simple vesicle, sometimes very wide (plate IV, figure 1), gradually curves and assumes the shape of a horseshoe (plate V, figure 3). The opening is at the left side. The primary tentacles have begun to appear already at the age of 40 hours (plate V, figure 2). There is still no trace of a stone canal to be seen at this stage.

The *entoderm* remains a simple sac, distinctly dorso-ventrally compressed towards the end of this period (plate V, figure 9). It should be emphasized only that no cells are observed to wander into its lumen.

4. CLOSING OF THE VESTIBULUM; FIXATION OF THE LARVA.

In accordance with the fact that the fixation may take place at a very different age—some larvæ attaching themselves at the age of 2 or 3 days,

others not till they are 7 or 8 days old—the processes which accompany the transformation from the free-swimming larva to the young Pentacrinoid may pass at very different speeds, and it is thus not possible to say at which age one or another stage of the later development occurs. It may be said only that it is the fixation that hastens the development, while up to that time the developmental processes are going on very slowly or not at all.

As mentioned in the introduction, it often happened that embryos which had attached themselves to unsuitable objects, especially the leaves of *Posidonia*, dropped off and fell to the bottom of the jar. The reason for this evidently was that Diatoms and other micro-organisms growing on the *Posidonia* leaves hindered the fixation to the leaf. Doubtless the suctorial disk secretes some kind of fluid by means of which the fixation takes place, but in this case it would not act, because the disk could not touch the surface of the leaf itself.

The embryos thus lying on the bottom did not die; neither did the developmental processes cease; but the development went on abnormally, resulting in the embryos assuming a peculiar pipe-like shape (plate IX, figure 6). It is the vestibulum which is first affected by the failure of the fixation. The process of closing does not continue till the end; the fold of the epidermis, which normally gradually covers up the invagination, stops growing when it has reached about midway (plate VII, figure 8). The aboral (previously anterior) end of the invagination remains unaltered. When the vestibulum closes normally a remarkable rotation takes place, as is well known through the elaborate researches of Barrois and Seeliger, the vestibulum wandering from the ventral side to the oral (previously posterior) end of the larva, carrying with it the hydrocœl and other internal structures. While at first the vestibulum is contiguous with the disk of fixation, it now lies at the opposite end of the larva. There has thus taken place an enormous prolongation of the part of the epidermis lying between the disk of fixation and the vestibulary invagination—that is, the part occupied by the first (in *Antedon* second) vibratile band. The closure of the vestibulum is, so to say, the sign for the starting of this prolongation. But when the closure is not complete the prolongation of this part of the epidermis does not take place, there is no stimulus to start it, and the vestibulum continues to be contiguous with the disk. Meantime the developmental processes otherwise go on normally, and the stalk-joints of the young Pentacrinoid especially grow rapidly; but gradually there is no room for the stalk and it has thus nothing left but to curve in an arch, and the embryo becomes humpbacked!

In spite of the incomplete closure of the vestibulum, the hydrocœl and other internal structures continue their development normally, and as my material of normal embryos in the fixation stage is very limited, I have found it necessary also to use these pipe-shaped, humpbacked specimens for the

study of the development in the stage of transformation from the free-swimming larva to the young Pentacrinoid.

The fact that these humpbacked embryos may develop into true Pentacrinoids differing from the normal ones only in having the head bent downwards, like a drooping flower, is of no small interest. Using the *Posidonia* leaves for the larvæ to attach themselves to has thus resulted in an unintentional experiment to test the significance of this remarkable embryonal structure, the vestibulum.

Barrois (pp. 642–644, plate xxx, figures 21 to 24) has recorded a similar unintentional experiment with the larvæ of *Antedon*, the result being the same, that the development of the internal organs goes on normally despite the abnormal position. Only it does not appear that Barrois has seen them develop into true Pentacrinoids. Seeliger (p. 266) also has seen abnormal embryos developing their tentacles, although the closure of the vestibulum had not taken place (even less so than in the cases observed by Barrois and the present author), there being in the cases observed by Seeliger no covering up at all of the vestibulary invagination, so that the tentacles are at once free. Seeliger has not seen these abnormal embryos develop into Pentacrinoids. As pointed out by Seeliger, the Crinoid embryo with tentacles developed on the ventral side described and figured by Busch [14] must be such an abnormal embryo.

The main point, or at least the most conspicuous, in the transformation of the embryo from free-swimming to fixed is the *closure of the vestibulum*. This proceeds in the same way as in *Antedon*, so well known through the careful researches of Barrois and Seeliger. An early stage of this process is seen in plate vi, figures 2 and 3, from a specimen 3 days old; it corresponds well with Barrois's diagrammatic figure, plate xxvi, figure 13, and Seeliger's taf. 19, figure 114. The completely closed vestibulum is seen in plate vii, figure 3, representing a longitudinal section of an embryo 8 days old, just attached. To enter on a more detailed description of the process seems unnecessary.

The glandular character of the cells of the vestibulum is indicated by the fact that they retain the hematoxylin as strongly as do the glandular cells of the outer ectoderm, but it disappears with the closure of the vestibulum (compare plate vii, figure 3, with plate vi, figure 2). Also in the epidermis itself the glandular cells disappear; in the stage plate vi, figures 1 to 4, they are still fairly numerous, especially at the anterior end, where previously the apical pit was; also at the posterior end they are still plainly visible. In plate vi, figure 8, and plate vii, figure 5, only a few are still visible; while

[14] W. Busch. Beobachtungen über Anatomie und Entwickelung einiger wirbellosen Seethiere, 1851, p. 87, taf. xiv, figure 6. The embryos represented in his figures 3 and 5 are also abnormal, while the one represented in figure 7 can not possibly be a Crinoid embryo at all, not even an abnormal one, on account of the hooks developed in both ends, on which Busch lays so much stress, taking them to be the future points of the arms. Such hooks do not occur in the Crinoid embryo. What this figure really represents it is hardly possible to ascertain. The hooks recall those of the *Ophiothrix* embryo about to metamorphose, but the figure would certainly be very fantastic for an *Ophiothrix* in metamorphosis.

in plate VII, figure 8, and in the normally fixed stages (plate VII, figures 3, 6, and 7) they have completely disappeared. This is coördinated with the mixing up of the ectoderm with the mesenchyme (cf. p. 11–12), which process has been completed by the time the larva has attached itself. Some few cells may still remain attached to the surface by means of more or less branching prolongations (plate VII, figures 6, 7, and 8). That these "multipolar" cells are the remnants of the ectoderm cells can hardly be doubted, for they are not found in the Pentacrinoid stage.

The suctorial disk loses its special histological character as soon as the fixation has taken place. The same is the case with the larval nervous system.

The exact time when the *hydrocœl* ring closes has not been ascertained, but it takes place during the stage of transformation from free-swimming larva to young Pentacrinoid, and the important organs, *the pore canal and the stone canal,* are formed also during this period. The *pore canal* was seen first in the 4-day-old, free-swimming embryo, from which figures 5 and 6, plate VI, are drawn. It still has no exterior opening. Its appearance in plate VI, figure 6, as a small ring lying within a more spacious lumen must be due to some contraction by the preservation. The stone canal (plate VI, figure 8) is quite short; there are only two sections between its rising from the hydrocœl ring and its opening into the parietal canal (plate VI, figure 9). In the section represented (plate VI, figure 9) a thickening is seen in the left oral mesentery, an ovoid mass of cells lying in the space between the epithelium of the oral and aboral cœlom and separating them from one another. It seems certain that this corresponds to the primary *genital gland* found in *Antedon* by Russo (*op. cit.*, pp. 10–14), a rudimentary organ, which soon disappears, but which, according to Russo, is of great morphological importance, being homologous with the genital gland of the Holothurians, while the axial organ of the Crinoids is a thing apart, and not at all homologous with the ovoid gland of other Echinoderms. I shall discuss these exceedingly interesting and important morphological relations in the general part of this memoir.

Russo has found the first traces of this gland in *Antedon* in Pentacrinoids which had already been attached for some 5 or 6 days and had already a long stalk. In *Tropiometra* it appears somewhat earlier. I have been unable to see this gland in decalcified and stained Pentacrinoids of this species, while in some of the other species studied I have found it easily observable in unsectioned Pentacrinoids (plate XII, figure 5, *Compsometra serrata;* plate XXI, figure 6, *Isometra vivipara*).

The formation of the primary tentacles needs no description. It may be seen directly on the figures (for instance, plate VI, figure 1; plate VII, figure 7); the explanation of the figures gives the necessary details.

The *cœlomic vesicles* have assumed their final position, the left at the oral end, between the hydrocœl and the entoderm, the right at the aboral end

of the entoderm, and they are now distinguished as the oral and aboral cœlom. Their shape and extent is shown in plate VI, figures 1 to 4 and 7 to 9; plate VII, figures 6 and 7. The aboral cœlom has formed the *vertical mesentery* (the details of this process could not be made out) (plate VII, figure 6), and in it the *axial organ* has made its appearance (plate VI, figure 7; plate VII, figure 8). Also the *chambered organ* is assuming its final shape and is seen very distinctly continuing through the whole length of the stalk (plate VI, figure 7, plate VII, figures 4 and 5); but this is already the case previous to fixation, as seen from plate VI, figures 2, 3, and 5.

The *entoderm* undergoes very important changes. First the *rectum develops* after the fixation (plate VI, figure 7), but it does not open outwards; there is not even an invagination of the epidermis to meet it. Then *the mouth opens into the vestibulum*. There is an invagination of the thick ectodermal layer forming the bottom of the vestibulum, which meets the entoderm and forms the esophagus. Plate VII, figures 8, 3, and 7, show the different stages of this process.

A very conspicuous feature in the development of the intestinal tract in *Antedon* is the wandering of cells from the wall of the stomach into its lumen to be devoured there and thus to constitute nourishment for the young Crinoid until its mouth opens and it can procure its own food (Seeliger, pp. 287–291). This very remarkable way of feeding itself is not seen very plainly in *Tropiometra;* in fact, I am not at all sure that it does occur there. It is true that in the specimen from which plate VII, figure 3, is made there is a mass of the fine grains to be seen in the stomach, which might perhaps be such cells about to be digested; but in other specimens I have failed to find anything of the sort—for instance, in plate VII, figure 4, the stomach shows itself as empty as possible; also, these grains which are supposed to represent the residue of cells being dissolved and digested are found not only in the stomach but also in the stalk (on the right side in plate VII, figure 3). In the specimen figured in plate VIII, figures 1 to 3, similar grains are seen in the covering of the vestibulum, but not in the stomach. These facts do not speak in favor of regarding this as a proof that the young *Tropiometra* obtains its food in the same remarkable way as in *Antedon*. Upon the whole, the object of these cells is, certainly, not to be devoured by the larva, as assumed by Seeliger. I think Bury (*op. cit.*, p. 273, etc.) is right in regarding them as phagocytes, which produce an histolysis of the larval tissues, especially the entoderm.

5. THE PENTACRINOID STAGE.

(Plate VIII.)

As mentioned in the introduction, some of the larvæ attached themselves to the surface film of the water, developing into very fine Pentacrinoids. The specimens used for section are from that lot. None of them reached so far as to open up the vestibulum, but (as seen in plate VIII, figure 1) the cover-

ing of the vestibulum is thinning out in the middle and must be very near the time of opening. The other Pentacrinoids that went so far in their development did not afford sufficient material for study by means of sections, but as none of them went much farther in their development (in none of them has the formation of the arms begun) there could hardly be expected any noticeable progress in the internal development beyond the stage figured.

The *ectoderm* has lost the last trace of its original character, and there is henceforth no distinguishing of the former ectoderm cells from the mesenchyme cells; also, the glandular cells have completely disappeared.

The basal disk, which could readily be studied intact in these specimens from the surface film, where no force was needed to loosen the attachment, shows the interesting feature that a rather thick cuticular layer has been secreted. This probably represents the secretion by means of which the attachment is effected. A similar thick cuticula on the base of the stalk was also observed by Seeliger in *Antedon* (p. 337). The upper side of the basal disk contains numerous small grains which stain strongly in hematoxylin, the cell nuclei among them appearing only very lightly colored (plate VIII, figure 1).

In the *vestibulum* the thinning out of the high epithelium of its basal wall has just begun (plate VIII, figures 1 and 2). The formation of the oral nervous system apparently has not yet begun.

The *hydrocœl* ring has just closed (plate VIII, figure 6); in the anal interradius a narrowing of the lumen of the ring is still seen, across which a thin dissepiment goes. This is no trabecule, but the joined end-walls of the two ends of the hydrocœl; it is still intact, so that the lumen of the ring is not yet continuous. The narrowing of the hydrocœl ring seen in the upper left interradius in plate VIII, figure 6, is only apparent and depends on a slight sinuosity of the ring; in the following section it has exactly the same width as in the rest of the circumference, while the narrowing in the anal interradius is continuous through all the sections touching the hydrocœl. The epithelial lining of the hydrocœl ring has taken on an endothelial character and numerous trabeculæ are crossing its lumen. Two pairs of tentacles have developed at the side of each primary tentacle (plate VIII, figure 5; plate VII, figure 1). The outer pair of these represents the interradial tentacles. In the sections through the vestibulum the tentacles are seen to be separated from one another by a fine but distinct line (plate VIII, figure 4), which probably indicates the existence in the vestibulum of a slimy fluid.

The communication between the hydrocœl and the exterior has at length been established. Plate VIII, figure 5, shows the external opening of the hydropore. That it has just been formed is evident from the fact that the hydropore is still closed in the specimen from which plate VIII, figure 1, is drawn, and which is otherwise in exactly the same stage; it ends two sections from the one figured, in a small accumulation of cells just below the skin,

forming a slight elevation; but there is no opening. Apparently there is no outer opening either in the specimen of the same age figured in plate IX, figure 9.

Russo (*op. cit.*, pp. 47, 48) maintains that in *Antedon* the original hydropore and pore canal become obliterated 3 to 4 days after the fixation of the larva; 7 to 8 days after the fixation the definitive hydropore and pore canal develop. In *Tropiometra* I have been unable to ascertain whether this likewise takes place, not having sufficient material of the later stages of the Pentacrinoids; but in any case there has been no exterior opening before this stage.

It should be mentioned that in one series of longitudinal sections of an embryo 10 hours old there is seen a kind of tube or canal visible through 5 consecutive sections. With its outer end it forces itself to some degree in between the ectoderm cells, pushing their basal ends aside. But it does not reach the surface and there is no outer opening. One might be inclined to see in this a primary pore canal; but so far as can be judged from the somewhat unsatisfactory preservation of the interior of this embryo (the ectoderm and the said tube are very well preserved), the entoderm is in a very primitive stage of development, not yet separated into its two main parts, and there is, of course, no trace of the parietal canal as yet. Furthermore, it is impossible to discover any connection between the entoderm and the inner end of the tube. It is, then, hard to see how this could represent a pore canal. In *Antedon* Seeliger has found the porus in the fully formed larva, not in a stage so young as this.

Russo does not distinguish between the stone canal and the pore canal, designating both as "canale petroso." He certainly distinguishes the "canale petroso interno o primario" and the "canale petroso esterno o secondario," but as, according to Russo, there is also a primary external "canale petroso," this nomenclature is confusing. The distinction between the stone canal and the pore canal is of great morphological importance, as is well emphasized by Bury, and should certainly be upheld clearly.

In plate VIII, figure 2, is seen the opening of the pore canal into the parietal canal, and in plate VIII, figure 7, the stone canal is seen to open into the latter. Finally, plate VIII, figure 3, shows the parietal canal in direct communication with the cœlom. Thus the final arrangement of the interrelations between the hydrocœl and the cœlom has been established. But there is still only the one (primary) stone canal and pore canal. This is seen *in toto* in plate IX, figure 9; but it was impossible to follow the stone canal very distinctly in its entire length in this specimen.

The oral cœlom appears to be in open communication with the aboral cœlom.

The stomach is empty, showing no cells in its lumen. The rectum is now well developed and about to open to the exterior (plate VIII, figure 8). The epidermis shows a slight invagination over it, but there is still no anal opening formed. The place of the future anal opening is seen to be near the

adjoining radius, not in the middle of the interradius. When it has been formed the young Crinoid is ready to open the vestibulum and the embryonic life proper is ended.

6. THE DEVELOPMENT OF THE SKELETON; THE PENTACRINOID.

(Plates IX to X.)

The first rudiments of the skeleton appear at the age of 24 hours (plate IX, figure 1); here the basalia and oralia are seen lying in two half-circles, which are open ventrally. The plates of the two half-circles do not correspond exactly to one another; there is some shifting, as is also the case in *Antedon*. It is evident that the plates do not all appear at one and the same time. The oralia I and II are slightly larger, and therefore older, than the other 3 oralia, and the basale V has just appeared as a minute grain, while the other 4 have already begun to form small processes. The terminal stem-plate has appeared and 5 stalk-joints. It is noticeable that the joint nearest the terminal plate is smaller than the next one, showing that it is not the first formed.

FIG. 2.—Three stages in the development of the stalk-joints. ×320.

In plate IX, figure 2, which also represents a larva of 24 hours, the skeleton is somewhat more developed; the terminal stem-plate and some of the basalia and oralia are distinctly branching; the stalk-joints still number only 5; here, however, the one nearest the terminal stem-plate is the largest, so that it would appear to be also the first formed in this case. Then an important new skeletal element has appeared. At the upper (oral) end of the stalk 3 very small calcareous grains are seen, which are the first traces of the *infrabasalia*. Their definite number can not be stated from this young stage, but the following stages afford the proof that there are only 3 of them.

A later stage is shown in plate IX, figure 3, representing a larva 30 hours old. The oralia and basalia, as well as the terminal stem-plate, have considerably enlarged and are now more or less fenestrated plates; their relative position has changed somewhat, so that they are no longer arranged in the form of a horseshoe. The vestibulum could not be made out in this specimen, but judging from the curvature of the stalk the specimen must be drawn in the same position as figure 1. Only two of the infrabasalia are seen in the figure, below one of the basals; the third was probably quite concealed by this plate. The stalk-joints have grown considerably in breadth, assuming the shape of a half moon, their transformation into the ring-shaped joints occurring in the same way as in *Antedon*. In this stage some very small calcareous grains are seen between some of the normal stalk-joints, especially between the fifth and sixth and between the sixth and seventh joints. This might perhaps represent new joints interpolated between the first formed. However, it is by no means certain that they are really intercalated joints.

On some of the joints small separate pieces are seen apparently soldered to the main piece of the joint, and I am inclined to think that this is the destiny of all these small separate calcareous pieces, even the fairly large one lying between the sixth and seventh joints, counting from the terminal plate. Seeliger (pages 229 and 324) finds such intercalation to occur in *Antedon*, but only between the second to third upper (younger) joints, and only where the distance between the joints is larger than usual. This evidently means that there is only a shifting in the time for the first appearance of the joints, as is actually the case with the first joint in plate IX, figure 1.

In plate IX, figure 4, is figured an embryo 40 hours old, seen from the ventral side, the stalk lying thus directly under the vestibulary invagination. The skeletal plates have grown considerably, forming large fenestrated plates. A comparison with plate IX, figure 3, shows one of the basal plates apparently in quite a different position from what is seen in that figure, reaching nearly to the terminal stem-plate. The difference is, however, only apparent; on turning figure 3 to the same position as figure 4, the basals will occupy a corresponding position, and what change has occurred is due mainly to the increase in size. The infrabasals are fairly large, fenestrated plates, hidden by the overlying basal plates, but quite distinctly seen on close observation. They do not appear to be of different size. The number of stalk-joints appears to be 10.

Plate X, figure 3, represents a normal embryo shortly after the fixation. The oral and basal plates have assumed their final position, forming the calyx, and the stalk-joints have begun to grow in length. There are 10 of them, the upper one mostly hidden by the basal plates. The infrabasalia can not now be seen, on account of the opaqueness of the embryo. Figures 4 and 5, plate X, show only growth-changes, depending mainly on the prolongation of the stalk-joints; new joints have not appeared. The vestibulum has not yet opened; there is only a depression, showing the place of the future opening.

The fully formed young Pentacrinoid is shown in plate X, figure 6. The oral valves have separated and the tentacles are protruding. No new stalk-joints have appeared as yet. The terminal stem-plate has developed into a fairly large, irregular, roundish disk consisting of a thick, reticulate network. The oral and basal plates begin to form reticulations. It is a conspicuous feature that the upper edge of the basal plates embraces the lower edge of the oral plates.

The oldest stage reached is that seen in plate X, figures 7 and 8. The anal plate has been formed, but there is as yet no trace of the radials. The basalia are still seen to have at their upper edge a wider circumference than that formed by the oralia, so there is a characteristic offset between the two circles of calyx plates, a feature which does not appear to be due to the preservation. The plates are already considerably thickened, strongly reticu-

lated, their surface looking coarsely thorny when seen in profile. Upon the whole this Pentacrinoid is by no means such a beautiful, delicate-looking object as are several other Pentacrinoids—for instance, that of *Hathrometra prolixa*. The oralia are but very slightly concave, as seen in figure 9, representing the calyx seen from above. The stalk-joints now are 13 in number, 3 new ones having formed at the upper end. These upper joints are conspicuously thickened in the middle, a feature which gradually disappears on the lower joints; from the seventh to eighth there is no thickening in the middle of the joints, which are now simply cylindrical; a dark line across the middle of the joint still indicates the originally formed plate, from which the joint develops by means of vertically growing processes, which unite by cross-beams, as described by Seeliger in *Antedon* (pages 325, 326). The final shape of the stalk-joints, as well as their definite number in the full-grown Pentacrinoid, remains, of course, unknown. The terminal stem-plate is an irregular disk with some short, rounded prominences (plate x, figure 10). The dark plate at the upper end of the stalk (plate x, figure 8) represents the infrabasalia, now considerably thickened, and destined to form, together with the upper stalk-joint (not the upper joint seen in this figure), the centrodorsale.

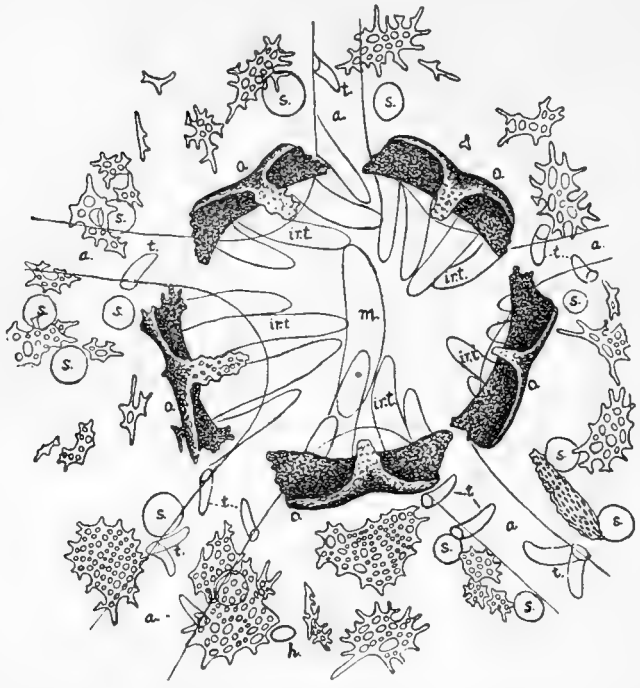

FIG. 3.—Oral region of a specimen of *Tropiometra*, 2 mm. in diameter, ×175. *a*, ambulacral furrow; *h*, primary hydropore; *ir. t*, interradial tentacles; *m*, mouth; *o*, oralia; *s*, sacculi; *t*, tentacles.

A discussion of the infrabasalia will follow in the general part.

While no later stage in the development of the Pentacrinoid was obtained, a young specimen, which was found by Dr. H. L. Clark, and which he most kindly gave me, gives some valuable information respecting the further development. The specimen had an arm-length of 10 mm., the diameter of disk being 2 mm. There are 10 pinnulæ to each arm and 13 cirri. It would appear from this specimen that the order of appearance of the oral pinnules is the same as that found in *Compsometra serrata* (see page 28). The tentacles are studded with small, simple spicules, generally lying in a series along one side of the tentacle.

As seen in text-figure 3, the oralia are still fairly large and of a very peculiar shape, with a prominent point, bent towards the mouth. The skin of the oral disk otherwise contains numerous fenestrated plates, among which is a large anal plate (not in the figure). The primary hydropore is seen in the anal interradius; each of the other interradii has some 5 to 10 hydropores (situated outside the part figured), while in the anal interradius there is still only the primary pore. A larger plate is found in the lower part of each interradius, in the corner between the costals. The basalia have already completely disappeared from the outside of the calyx and formed the rosette, as may be seen from the inside. The first cirri are seen to be radial in position.

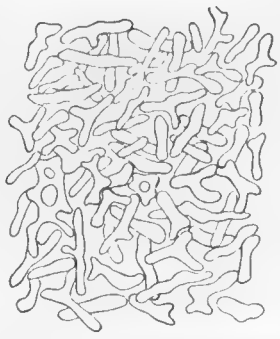

FIG. 4.—Spicules from the oral disk of a grown *Tropiometra*. ×200.

In the grown specimens the oral plates as well as all the other fenestrated plates have disappeared, and instead the skin has been studded with small, more or less bone-shaped spicules (text-figure 4), inextricably entangled.

II. COMPSOMETRA SERRATA (A. H. Clark).[15]

(Plates XI to XIII.)

This species was found to be fairly common on the rocky shores near the biological station at Misaki, from about low-tide mark to somewhat deeper water. It was often found on the under side of rocks which one could turn over, and also among the roots of Laminarians and other algæ. Although I examined many specimens very carefully and kept them in jars for some time, I did not succeed in finding any with eggs or embryos on the pinnulæ. Then, to my great surprise, I found, on my return, on examining the preserved specimens, a few with a good number of embryos on the pinnules. They proved to be of only two different stages, no intermediate stages being represented. This proves that in this species, as in *Antedon*, the eggs are laid contemporaneously by different individuals, apparently on account of the stimulating effect of the sperm emptied by some male specimen. I had at that time never studied the embryology of any Crinoid, otherwise I would probably have succeeded in getting specimens to discharge their eggs, so that the complete developmental history would have been obtained. However, the two stages obtained give such valuable information of the embryology of this species that a description seems worth while, the more so as I secured good material for the study of the postembryonal development of the species. With the exception of the very youngest stages of the embryological development, I can thus give the developmental history of this species almost completely.

[15] I am indebted to Dr. A. H. Clark for the identification of this species.

I. THE EMBRYOS.

The *egg* is, judging from the ripe eggs within the pinnulæ of the preserved specimens, rather small, only about 0.25 mm. The eggs remain attached in clusters to the pinnules around the ovarian opening, as in *Antedon*. The egg-membrane does not appear to have any structural peculiarities, but is simple, as in *Antedon*, serving only as means of attachment, not as a floating apparatus as in *Tropiometra*. It appears to be very spacious, affording ample room, so that the embryo is not globular, as is the case in *Antedon*, but while still lying within the membrane has its natural, elongate shape—a circumstance very fortunate for the study, the orientation of the embryo by sectioning being fairly easy, whereas the *Antedon* embryos are very difficult to orient while they remain within the egg-membrane.

From the material in hand it is evident that the embryos remain within the egg-membrane until fully formed and ready to attach themselves and transform into Pentacrinoids. It may then be concluded with a fair degree of certainty that they have only a very short free-swimming period, and this supposition is strengthened by the fact that the Pentacrinoids were found very close to the localities where the Crinoids were obtained.

The cleavage, the formation of the archenteron, and the formation of enterocœl and hydrocœl has not been observed. The youngest stage represented is that figured in plate XI, figures 1 to 4.

The *hydrocœl* has occupied its place on the ventral side and the *parietal canal* is about to separate from it (figure 3, plate XI). The two enterocœl vesicles have separated completely from one another and occupied their usual position, the left at the posterior end, the right at the dorsal side of the entoderm. Unfortunately this stage is too far progressed to show whether the entoderm sends out posterior prolongations to embrace the middle part of the enterocœl vesicle, as is the case in *Antedon* but not in *Tropiometra*. The anterior end of the right enterocœl is more thick-walled than the rest of the vesicle (plate XI, figures 1 and 4); it would appear that this has something to do with the formation of the chambered organ. I was at first inclined to think that it might be the parietal canal which was being formed in this case from the right enterocœl vesicle instead of the hydrocœl, which would certainly be astonishing. But at length the question was settled by the oblique sections, from which figure 3 has been drawn, which proves that the formation of the parietal canal is in conformity with what obtains in *Antedon* and *Tropiometra* and what must evidently be regarded as the rule in Crinoids.

The *vestibulary invagination* and the *suctorial disk* have begun to form, as seen in figure 1 and, in a slightly more advanced stage, in figure 4. Also the vibratile bands have begun to develop, as is evident from the arrangement of the cells in the ectoderm, especially in figure 4. There are no glandular cells seen in the ectoderm. The apical pit I have not found distinct. As in

Tropiometra, I find the nuclei of the ectoderm distinctly smaller than those of the rest of the embryo.

The next stage represented is the fully formed larva (plate XII, figures 1 and 2). The length is only about 0.3 mm.; the shape is elongate, the hind end slightly pointed. The vestibulary invagination is broadly oval; the suctorial disk is distinct, as is also sometimes the apical pit. There are 5 ciliated bands, but the anterior one is rudimentary and seen only on the dorsal side. The third band appears to be interrupted by the vestibulary invagination; it is only slightly bent downwards. I have been unable to trace the continuation of it inside the edge of the vestibulary invagination. The fourth band is hardly bent downwards on the ventral side, and neither is the band at the anterior end of the vestibulary invagination bent upwards.

The interior organization of the larva shows considerable progress from the former stage (plate XI, figures 5 to 10). The *hydrocœl* has formed the 5 lobes representing the primary tentacles; the *parietal canal*, which is large, with a conspicuous anterior prolongation (figures 8 and 9), *communicates with the exterior through the pore canal* which opens between the third and fourth vibratile band (figure 10). The outer end of the pore canal is somewhat widened. The shape and arrangement of the two enterocœl vesicles appears from a comparison of the transverse sections (figures 5 to 7) with the longitudinal sections (figures 8 to 10). The chambered organ is seen to continue towards the anterior end (figures 5 and 8). The stomach may be a large sac (figure 9) or flattened, so that the lumen can hardly be discerned (figure 7). The nervous system is very well developed (figures 8 and 10) and as usual it continues as a distinct nerve along each border of the vestibulary invagination (figure 5). In the ectoderm glandular cells are numerous in the anterior end, in the region of the apical pit. Also in the vestibulary invagination they are fairly well developed, though very much less so than in *Tropiometra*. In the rest of the ectoderm glandular cells are hardly present at all. The nuclei of the ciliated bands are beautifully arranged in arcs, the surface showing a corresponding concavity, more or less distinct.

In plate XII, figure 5, is represented a young Pentacrinoid, decalcified. The pore canal is remarkably short and its outer opening apparently closed. This seems to be in conformity with Russo's observation that the hydropore of the *Antedon* larva disappears, and a new, secondary pore develops in its place.[16] I must, however, say that I do not venture to assert that this is also the case in *Compsometra*, the histological character of the material, preserved in alcohol, not being sufficiently clear to reveal such minute details with all desirable distinctness. The pore really appears to be closed, but it may perhaps be due to contraction. In any case this deserves closer investigation.

The stone canal appears to have the shape shown in the figure quoted, but it could not be made out with certainty. The inner half of the parietal

[16] Russo (*op. cit.*, pp. 47, 48).

canal is thicker-walled than the other part; I have not been able to make out the meaning of this structure satisfactorily. Upon the whole, these structures in the young Pentacrinoid would deserve to be very carefully worked out on material preserved specially for histological study. On the inner side of the parietal canal is seen a small body, which apparently represents the primary genital gland (comp. under *Tropiometra*, p. 16). It may still be mentioned that the pharynx in the specimen figured was very distinctly compressed. In another specimen sectioned this was, however, not the case, so that it is not safe to state that this is a characteristic feature of the Pentacrinoid. The axial organ was found to be only slightly developed.

The *formation of the skeleton* is just beginning in the first of the embryonal stages represented (plate XII, figure 3). As in *Antedon* and *Tropiometra*, the oral and basal plates do not lie exactly opposite one another. At this stage 8 to 10 stalk-joints are present. In the figure quoted is seen a single very small plate, just a small grain lying inside the circle of basalia. This is, as becomes evident from a comparison with the following stage, the first rudiment of the infrabasalia.

In the next stage (plate XII, figure 4) the skeletal plates have enlarged considerably and have the usual fenestrate structure. In this stage 4 plates much smaller than these and with only one or a few holes are seen inside the basalia. These are the infrabasalia. Generally there are 4 of them, but sometimes only 3, or more rarely 2, and in no case were 5 found. They are about equal in size, and there is no indication that one of them might be double, so that the number would virtually be 5. About 18 stalk-joints are present in this stage, when the embryo is ready to leave the egg-membrane and swim out to find a place for attaching itself and transforming into a Pentacrinoid.

2. THE PENTACRINOIDS.

The Pentacrinoids were found attached to Corallines growing on the rocks in the same localities where the grown specimens were found. Although they were not reared, there can be no doubt that they are really the Pentacrinoids of *Compsometra serrata*. This was the only species of Crinoid found in this locality; only once a single specimen of another species was found, but this was a 20-armed form, a young example of *Comanthus japonica* (?), which occurs abundantly in other localities near the biological station at Misaki. That the Pentacrinoids can not belong to a 20-armed species is proved by the later stages, which are 10-armed. One more species of Crinoid is common in the same localities as the large *Comanthus*, viz, *Tropiometra macrodiscus*.[17] But the Pentacrinoids can not belong to that species, as is shown by the remarkable spicules of the Pentacrinoids, described below, which do not occur in the *Tropiometra*, while they are identical in the grown *Compsometra*.

[17] I am indebted to Dr. A. H. Clark for these names.

In the youngest Pentacrinoids found (plate XIII, figure 1) the basal plates embrace the lower end of the oralia; the latter are distinctly concave along their middle line, the edges being prominent. The infrabasalia can no longer be seen distinctly, but on dissolving the calyx very carefully with dilute hypochlorite of sodium they are seen lying inside the basal plates, around the upper stalk-joints, where they are found also in the following Pentacrinoid stages. There are still only 18 joints in the stalk. The first (lowermost) 3 to 4 joints are very short, nearly spherical; the middle ones are more elongate. In all of them the middle ring is very prominent.

In the next stage, represented in plate XIII, figure 2, the radials have appeared; the anal plate, which appears shortly before the radials, lies almost in the radial midline, the corresponding radial lying almost in the middle between the oral and basal plates. The oral plates are no longer embraced by the basal plates, and their lower end is beginning to acquire an outward twist. A pair of small, new-formed joints are seen at the upper end of the stalk, which is now composed of 20 joints.

In the stage represented in plate XII, figure 6, the oralia have been separated from the basalia, so that a piece of naked skin is seen between the adjoining ends of the two plates. The radial plates have become large, with a prominent knob at the upper edge, to which the costal is attached; at the upper end of the costal the axillary has appeared. The small joints at the upper end of the stalk have widened somewhat, but not grown in length. Apparently no new joints have been formed. (The stalk is incomplete in the specimens of this and the next stage.)

FIG. 5.—Part of tentacle of Pentacrinoid of *Compsometra serrata*, showing spicules. ×290.

The Pentacrinoid is especially characterized by its tentacles, which are long and slender and provided with calcareous spicules, thin, bow-shaped, finely thorny bodies, which are generally arranged in a single series in each tentacle (figure 5). In specimens mounted in Canada balsam these serially arranged spicules make a very conspicuous and curious object. They are found equally well developed in the tentacles of the grown specimens.

The stage represented in plate XII, figure 7, is slightly more advanced; the axillary is distinctly two-lobed and the costal is more elongate. The anal plate is seen to encroach upon the oral; the lower part of the oral plate has partly undergone absorption, and is partly covered by the anal plate; also, the radial to the right of the anal plate is unsymmetrical, the side joining the anal plate being less developed.

In the stage represented in plate XIII, figure 3, the arms have already grown to some length and consist of about 5 to 6 joints; the exact number of joints can not be made out distinctly because they are somewhat overlapping and have no such prominent middle plate as the stalk-joints. The

radials, which are still widely separated from one another, have assumed a characteristic heart-shape, while the costals still remain slender. The orals are widely separated from the basals; they have a very characteristic shape, having a deep furrow along the middle line, the sides being gracefully bent outwards, as is also the basal part. The stalk is now composed of 27 joints. The 5 upper joints are very short, but wider than the rest and with prominent middle plate; then follow 2 equally short but much narrower joints. The eighth joint is slightly longer, the next about twice so long, and from the tenth they have assumed their final shape, as described for the following stages.

Plate XIII, figures 4 and 5, represent the fully formed Pentacrinoid. In figure 4 the cirri have just begun to appear; in figure 5 the first pinnule has been formed. The oralia have, on account of the growing of the disk, shifted their position, so that they lie now entirely on the ventral side of the disk and separate from the calyx proper. The anal cone has developed in the space between the anal plate and the adjoining oral plate, so that there is now a large plate both on the outer and the inner sides of the anal cone (plate XIII, figure 5). The radialia have enlarged considerably, and join with their lateral edges. The costal has enlarged laterally and the axillary has assumed its characteristic shape, with the two oblique articulating surfaces. The arm-joints are short and broad, somewhat thickened at the ends. The pinnule is attached to the twelfth joint, which means that the first pinnule to develop is the first true arm-pinnule, the oral pinnules developing later. In a newly detached young specimen, with 6 to 7 arm-pinnules, the oral pinnules are just about to develop, and it is seen therefrom that of these latter the first and the fifth to sixth are the larger and of about the same size; they must, accordingly, develop first and contemporaneously, while the second to fourth are much smaller and must appear after these, and also about contemporaneously. Generally the fourth would seem to be the last of them to develop, but in one arm of the specimen mentioned this is slightly larger than pinnules 2 and 3. The pinnules 7 and 8 have not yet appeared, which is the more remarkable, as later on these become larger than the other oral pinnules except the first. Although the 4 outer oral pinnules contain genital organs in the grown specimens, they are true oral pinnules, without tentacles.

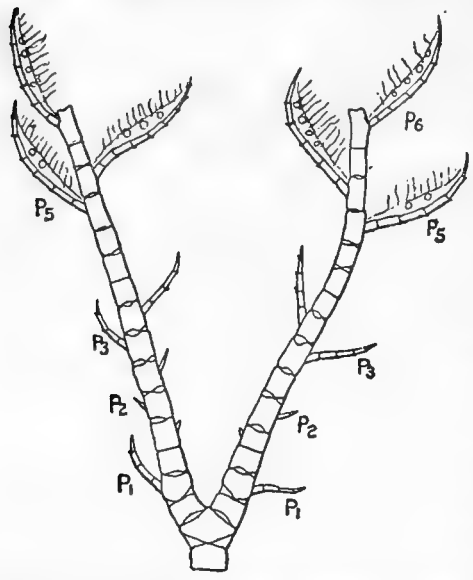

FIG. 6.—Arm of a young specimen of *Compsometra serrata* showing order of appearance of oral pinnules.

W. B. Carpenter,[18] in describing the development of the pinnules in his memoir on the development of *Antedon rosaceus* (p. 735), is inclined to think that it takes place "rather after the manner of the joints of the stem and dorsal cirri than after that of the segments of the rays and arms; that is, to commence with a complete ring which extends itself longitudinally into a hollow cylinder rather than a cribriform plate which wraps itself (so to speak) around the extension of the sarcodic axis." This is not the case in *Compsometra;* both arm-joints and pinnule-joints begin as a simple transversally lying rod, from which extensions grow out to each side. These extensions very soon unite and thus a cribriform plate is formed, in which the original rod can be distinguished for some time, although it is not nearly so conspicuous as the middle plate of the stalk-joints. It is true that the joints of the young pinnule may show this original structure more distinctly than the arm-joints, but this is evidently due to the fact that the rolling-up of the point of the arm makes it difficult to see the structure of the young arm-joints, while the young pinnule is generally straight, showing the structure of the growing joints distinctly. This would appear to be the usual type of development of the arm and pinnule joints; at least I have found it also in *Isometra vivipara* and essentially so in *Antedon bifida.*

The first cirri are distinctly radial in position (plate XIII, figure 5); and this is in accordance with what is the case in *Hathrometra sarsii,* as described and figured by M. Sars (p. 53, tab. v, figure 11);[19] also, in *Tropiometra* the first cirri appear to be radial in position. As pointed out by M. Sars, this is a remarkable difference from *Antedon rosaceus* (*bifida*), in which the first cirri are stated by W. B. Carpenter to be interradial in position, which is also confirmed by M. Sars (*loc. cit.*). I must, however, maintain that in *Antedon bifida* also the first cirri are really radial in position, as is also distinctly seen in one of Carpenter's own figures (plate XLII, figure 3). Here four of the first cirri (those with the terminal joint fully developed) are very distinctly radial, while the fifth is slightly out of position, which may perhaps be due to a slight error in the drawing. Upon the whole it is not quite easy to determine the exact position of the first cirri; but when observed in a stage while still growing (as in plate XIII, figure 5) their exact position can easily be ascertained.

In the younger of the two specimens (figure 4) the stalk consists of 29 joints; in the larger (figure 5) of 33 joints. As the cirri are developing on the upper joint of the younger specimen, the number of its stalk-joints would not have been augmented; there is thus some variation in the definite number of the stalk-joints of this Pentacrinoid. Some of the upper joints, evidently varying in number (3 to 5), are wider than the rest of the stalk-joints and

[18] W. B. Carpenter, Researches on the structure, physiology and development of *Antedon* (*Comatula* Lamarck) *rosaceus*, part I, Philos. Transact., 1856.

[19] M. Sars. Mémoires pour servir à la connaissance des Crinoïdes vivants, 1868.

apparently remain quite short, as was also found by M. Sars in *Hathrometra sarsii*. Also in *Antedon bifida* a few of the upper stalk-joints are somewhat wider than the rest of the stalk-joints, as is shown distinctly in plate XXXIX, figure 2, of W. B. Carpenter's memoir; but it is not so prominent a feature here as in *Hathrometra* and *Compsometra*, and less constant; in some specimens there is hardly any widening at all discernible in the upper joints.

The shape of the fully formed joints appears from figure 5, plate XIII. While in the joints of the young Pentacrinoids the middle plate is wider than the rest of the joint, and thus appears as a prominent ring around the middle of the joint, the fully formed joints are a little narrowed in the middle, slightly hourglass-shaped, and the middle plate appears only as a more or less distinct line across the middle of the joint. The ends of the joint are a little widened. The articulating surfaces are alternating, as usual in Pentacrinoids, whereby the impression is produced that the joints are united two and two. Sometimes, however, the articular surfaces at both ends of a joint may be identical, not alternating; this is the case, for instance, with the upper joint in the small piece of the stalk shown separately in plate XIII, figure 5. The joints are smooth and short, the longer of them only about 0.25 mm. The terminal stalk-plate is small, slightly lobed.

The young Crinoid is detached very soon after the stage figured in plate XIII, figure 5. I have found a detached specimen with only two pinnules developed and a third beginning. There are only 8 cirri, viz, the 5 of the primary whorl and 3 of the second, one about as long as the primary ones, the second half as long, and the third quite small; the second is in the anal interradius, the first to the left, the third to the right of it. The oral plates and the anal plate are still distinct, but the absorption has begun. That the specimen has just been detached is evident also from the fact that a small hole is still seen in the middle of the centrodorsal.

In another young specimen, the above-mentioned one with the oral pinnules about to develop, the anal and oral plates have entirely disappeared and the skin of the disk is quite naked, as is also the case in the grown specimens.

A Pentacrinoid of the Australian *Compsometra loveni* (Bell) was figured by A. H. Clark in his monograph of the existing crinoids (Bull. U. S. Nat. Mus. 81, 1915, p. 317, figure 410). It appears to be a stage where the radials have just begun to form, slightly younger than the stage of *C. serrata* figured in plate XIII, figure 2. The difference between these two Pentacrinoids would at the first sight appear to be very great—still this is probably mainly due to the different way in which the figures have been drawn, that of *C. loveni* being apparently somewhat diagrammatic. It appears, however, that in this species also the basalia embrace the lower end of the oralia. The latter would seem to be more rounded than is the case in *C. serrata*.

III. ISOMETRA VIVIPARA Mortensen.

(Plates XIV to XXIII.)

In 1904, Dr. K. A. Andersson published an account of a viviparous Crinoid found in the Antarctic Sea by the Swedish South Polar Expedition.[20] This was the first instance of care of the brood known among Crinoids. K. A. Andersson referred the species to *Antedon hirsuta* P. H. Carpenter. A. H. Clark,[21] however, pointed out that it was more closely related to Carpenter's *Antedon angustipinna*, for which the genus *Isometra* was established, and in my report on the Crinoidea of the Swedish Antarctic Expedition I described it under the name *Isometra vivipara*.[22]

Dr. K. A. Andersson gives only a short account of the development of the species and expected to write a more detailed report later, but, not finding opportunity for so doing, he kindly left the interesting material to me for study, for which I thank him very cordially

The preservation of the material simply by means of alcohol is, of course, not of the best, but it suffices except for the finer histological details.

For a more detailed account of the viviparous habit and the way in which the care of the brood is carried out reference must be made to the papers by K. A. Andersson and the present author as quoted here.

1. CLEAVAGE; FORMATION OF ENTODERM.

The *egg* is about 0.3 mm. in diameter. The reticulated structure of part of the egg mentioned by K. A. Andersson (*op. cit.*, p. 4) I believe to be the result of preservation instead of a normal structure. It is very rich in yolk and quite opaque. As pointed out by Andersson, the eggs are found in various stages in the ovary, not ripening all at the same time, as is the case in other Crinoids, and they are not emptied all at the same time as normally in Crinoids, but gradually as they become ripe. This accounts for the fact that the embryos are in all different stages of development—one may find fully formed larvæ together with embryos in the first cleavage stages in the same marsupium—a very fortunate circumstance for the study of the development, as there is thus no difficulty in finding all stages of development in this species, such as was the case in *Compsometra serrata* and *Notocrinus virilis*. On the other hand, there is no possibility of ascertaining how long a time is required for development, and the direct age of the different stages can not be given, as it was for *Tropiometra* and by Seeliger for *Antedon*.

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[20] K. A. Andersson. Brutpflege bei *Antedon hirsuta* Carpenter. Wiss. Ergebn. d. Schwed. Südpolar-Exped. 1901–3, vol. v, 1, 1904.

[21] A. H. Clark. Die Crinoiden der Antarktis. Deutsche Südpolar Exped., XVI, Zoölogie, Bd. VIII, 1915, pp. 106, 146.

[22] Th. Mortensen. The Crinoidea of the Swedish Antarctic Expedition, Wiss. Ergebn. d. Schwed. Südpolar-Exped. 1901–3, vol. VI, 8, 1917, p. 10–15, plate I, figures 6 to 10; plate II, figures 5 to 7.

Andersson did not find more than 5 embryos in a marsupium, generally only 3. I have, however, found as many as 8 eggs and embryos together in one marsupium.

The *fertilization* probably takes place within the ovary itself. Andersson discovered the remarkable fact that there is a space filled with spermatozoa in each ovary, from which it must evidently be concluded that a sort of copulation must take place in this species. It can scarcely be doubted that the fertilization then must take place within the ovary, before the eggs are emptied into the marsupium. It may, however, be stated that I have failed to find any fertilized egg within an ovary, nor does it appear that Andersson has found this. On the other hand, I have not found any unfertilized egg in the marsupia.

The *egg-membrane* is very thin and quite simple, without any special structure (plate XIV, figure 1). The embryos remain within the membrane during their whole development and do not leave it until they leave the marsupium as fully formed larvæ. In the figures the membrane has been omitted, except in the very youngest stage of development (plate XIV, figure 1).

The *cleavage* is very remarkable and thus far unique among Crinoids (plate XIV, figures 1 to 3), corresponding to the superficial cleavage typical in Arthropods. The egg does not divide at all; only the nuclei divide and spread irregularly in the yolk-mass. In the youngest stage found some few nuclei are seen lying in the middle and a few near the surface (plate XIV, figure 1). Gradually they multiply, and then a number of nuclei are found lying irregularly spread in the mass of yolk with no trace of cell limits (plate XIV, figures 2 and 3). The nuclei are here beginning to arrange themselves along the surface, while another, less distinct, group occupies the middle of the embryo. Whether an actual wandering of the nuclei towards the surface takes place, or whether the outer nuclei descend exclusively from those lying near the surface in the youngest stage, the inner ones from those lying in the middle, can not be determined.

The next stage is represented in plate XIV, figures 4 and 5. Here the *ectoderm and entoderm have been differentiated.* The nuclei at the surface now form a fairly regular layer, and cell limits have begun to appear, so that there is now a distinct ectoderm of typical form, clearly delimited from the entoderm. The cells are high, cylindrical, and full of round yolk-grains (plate XV, figure 3). The nuclei in the middle of the embryo have collected in a more definite group and in the middle of this group the archenteron begins to appear as a small, narrow slit (plate XIV, figure 5). It soon grows in size and the nuclei range themselves more regularly around it; then cell limits begin to appear and *thus the entoderm is formed; accordingly, there is no blastoporus, as no invagination takes place* (plate XIV, figure 4).

It is interesting to notice that there is some inconsistency in the order of appearance of the developmental process, as appears from a comparison of

figures 4 and 5 of plate XIV. In figure 4 the nuclei of the ectoderm still form a simple, nearly regular layer, while the entoderm is fairly advanced in development; in figure 5 the nuclei of the ectoderm are already much more numerous, and not arranged in a simple layer, while the entoderm is in a considerably younger stage of development, the cavity having just appeared. Also, the limitation of the ectoderm cells is more advanced in figure 4 than in figure 5.

In an embryo in a stage corresponding exactly to that represented in figure 4 there was a distinct indication of cilia in one place. An important differentiation is also beginning to take place in the yolk substance; while the whole of the entoderm and ectoderm is uniformly filled with yolk-grains, some of these are collecting into distinct balls of varying size, lying between the ectoderm and the entoderm (plate XIV, figure 4). These groups of yolk-grains remain a very characteristic feature in the following stages of development; they generally stain intensively red with eosin, and thus are very conspicuous in sections otherwise stained with hematoxylin.

This corresponds in some degree to what has been described so very carefully for *Ophiura brevispina* by Caswell Grave.[23] In this case, however, nearly all the yolk material is transferred from the cells to the segmentation cavity, while in *Isometra* it is only a smaller part of the yolk that is lying free in the cavity which corresponds to the segmentation cavity, while the cells themselves are still filled with yolk granules.

This remarkable cleavage-modus (the superficial cleavage) is not unique among Echinoderms. I described in 1894 a similar development in *Cucumaria glacialis;*[24] though the material was insufficient for a complete study of the development (the formation of the entoderm could not be made out), there is no doubt that this is a case quite analogous to that of *Isometra vivipara*. Furthermore, I can ascertain that there are still more such cases among Echinoderms. In a viviparous Ophiurid, *Amphiura vivipara* H. L. Clark, observed at Tobago, British West Indies, during the Carnegie expedition, the development is of the same type as that of *Isometra vivipara*. Later I hope to give a full report of its development, but this may serve as a preliminary notice of this very interesting case, hitherto unknown among Ophiurids.

Having thus found three cases of this peculiar type of development, so different from the total, regular cleavage otherwise found in all Echinoderms, so far as hitherto known, I expect that it will be found in several other cases, especially in viviparous Echinoderms. That it is not the rule for all viviparous Echinoderms is proved by the fact that *Amphiura squamata*,

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[23] Caswell Grave. *Ophiura brevispina*, II. An embryological contribution and a study of the effect of yolk substance upon development and developmental processes. Journ. Morph., vol. 27, 1916, p. 426.

[24] Th. Mortensen, Zur Anatomie und Entwicklung der Cucumaria glacialis (Ljungman). Zeitsch. f. wiss. Zoöl., Bd. LVII, 1894, p. 721–23, taf. XXXII, fig. 32–36.

the classical object for the study of the development of Ophiurids, has total cleavage. However, the cleavage is irregular and the entoderm is formed by delamination.[25] We have thus here a deviation from the normal process of cleavage and entoderm formation tending towards the type occurring in *Isometra vivipara*, *Amphiura vivipara*, and *Cucumaria glacialis*. Another somewhat intermediate type is found in *Henricia sanguinolenta* (O. F. Müller), in which some nuclei may be found lying free in a larger part of the yolk not yet limited into cells (*cf.* plate I, figure 11, in Masterman's[26] memoir). No case quite analogous to what is found in the above-named forms of Crinoids, Ophiurids, and Holothurians is known as yet among the Asteroids. In Echinoids it would appear that the superficial cleavage is of quite general occurrence among the forms which protect their young. I have been able to ascertain it for *Hypsiechinus coronatus* Mortensen, *Abatus cavernosus* (Philippi), and *Amphipneustes kœhleri* Mortensen.

In Caswell Grave's paper on *Ophiura brevispina*, quoted above, it is stated (p. 428) that the eggs of "practically all species of Echinoderms" are minute bodies, containing only a small amount of yolk, which "seems to interfere but slightly if at all with either the activities of the cells of the developing larvæ or with other processes of development and differentiation." Although it will, evidently, be in exceptional cases only that the yolk substance causes a meroblastic development, large and yolk-laden eggs are by no means exceptional in Echinoderms. Such eggs appear to be the rule in all the Dendrochirote Holothurians; then very many Asteroids have large, yolk-laden eggs, and it is evidently also the rule among the deep-sea Echinoderms of all groups. So far as my experience goes, it would appear that among Echinoderms as a whole the forms with large eggs rich in yolk are about as numerous as those with minute, clear eggs, containing only a small amount of yolk. The same must hold good for the typical pelagic larvæ, this being in correlation with the size of the eggs.

2. FORMATION OF ENTEROCŒL AND HYDROCŒL.

The differentiation of the archenteron proceeds in the same way as in *Antedon* and *Tropiometra*. A median constriction separates the archenteron in an upper or anterior part, the entero-hydrocœl, and a lower or posterior part, the cœlomic vesicle. In plate XIV, figure 11, the two parts are seen still in connection. A slightly younger stage is figured in plate XIV, figure 6, representing a sagittal longitudinal section. In the stage represented in plate XIV, figure 7, the separation has been completed, a little downward prolongation from the anterior part indicating the former connection between the two parts. The posterior part has already divided into two lateral

[25] A. Russo, Embriologia dell' *Amphiura squamata* Sars, Att. d. R. Accad. d. Sci. fis. e matem. Napoli. Ser. 2 a, vol. v, 1891.

[26] A. T. Masterman, The early development of *Cribrella oculata* (Forbes), with remarks on Echinoderm development. Trans. Roy. Soc. Edinburgh, XL, 1902, p. 377.

vesicles, the right and left enterocœl vesicle. In the stage represented in plate XIV, figures 8 to 10, the two enterocœl vesicles are still united by a narrow transverse canal. (The sections are obliquely directed, which has necessitated representing three of the sections; combined they correspond to that represented in figure 7.) A sagittal, longitudinal section of a corresponding stage is represented in plate XV, figure 1. It is important to notice that *there is no trace of the downward prolongations from the anterior vesicle*, which in *Antedon* embrace the narrow transverse canal that connects the two enterocœlic vesicles. In this regard *Isometra* is in accordance with *Tropiometra*. The lumen of the entero-hydrocœl is very large.

The formation of the *hydrocœl* could not be made out in all details. Probably the upper lobe in plate XIV, figure 6, is the first indication of the hydrocœl, and the faint constriction shown in plate XIV, figure 7, may possibly mean that the whole anterior part of the entero-hydrocœl is destined to form the hydrocœl. The question is not very important, the main thing being that the hydrocœl is formed from the anterior vesicle, as in *Antedon* and *Tropiometra*.

The formation of the *parietal canal* could not be made out in all details, but from the stage represented in plate XVI, figure 1, it is evident that it proceeds in the usual way, being formed as a constriction from the hydrocœl vesicle.

The *ectoderm* (plate XIV, figures 6 to 11) consists of high epithelial cells, the nuclei lying mainly in the middle, forming a more or less distinct layer. The *entoderm* also consists of cylindrical epithelial cells, with the nucleus mostly at the base and the whole space of the cell filled with yolk spherules (plate XV, figure 2). Also the enterocœlic vesicles show the same epithelial structure (plate XIV, figure 7). The mesenchyme cells have become discernible in the stage when the division of the archenteron begins (plate XIV, figure 6). Whether they originate from the entodermic epithelial cells or from the nuclei originally lying spread in the yolk-mass can not be ascertained, but from the fact that they lie at first mainly at the upper end of the archenteron and do not nearly fill out the blastocœl cavity (which has become very large compared with the preceding stage, plate XIV, figure 4), the evidence is decidedly for their originating, as in *Antedon* and *Tropiometra*, from the entoderm epithelium. Gradually the blastocœl cavity is completely filled out by the mesenchyme cells, as seen very plainly by a comparison of plate XIV, figure 6, with plate XV, figure 1. In figs. 8 to 10, plate XIV, they have filled the blastocœl cavity completely. They are from the first filled with yolk spherules, like all the other cells, both of ectoderm, entoderm, and hydrocœl (plate XIX, figure 11); by and by these become less distinct, and the yolk spherules instead collect into round groups which lie scattered irregularly, mainly in the mesenchyme. The nuclei of ectoderm, entoderm, and mesenchyme are not distinctly different in size.

The flattening of one side in the embryo represented in figure 1, plate xv, may indicate the formation of the vestibulary invagination, but it can not be ascertained beyond doubt; the pressure of the embryos against one another within the marsupium may have caused it, as it has doubtless caused the similar flattening in the much younger stage represented in plate xiv, figure 5, in which one could hardly think of seeing the beginning of the vestibulum.

3. THE DIFFERENTIATION OF THE LARVA.

During this period important structural changes take place, leading to the organization of the fully formed larva. Figures 4 to 11 of plate xv serve to illustrate this period.

In its outer appearance the embryo becomes more elongate. The vestibulary invagination appears as a depression on the ventral side (plate xv, figure 5) and likewise a depression is formed in the anterior end of the embryo representing the suctorial disk (plate xv, figure 11). A distinct ciliation is seen in this depression. The *ciliated bands* are developing, the nuclei being arranged in more or less distinct groups corresponding to the bands (plate xv, figures 9 to 11). *Glandular cells* have developed in the ectoderm, especially at the anterior end (plate xv, figure 10), but they may be numerous also in other places (plate xv, figures 5, 7, 11). The *nervous system* has just begun to differentiate (plate xv, figure 10).

The *entoderm* shows a conspicuous difference from the preceding stage, the lumen being very small or even completely obliterated. The cell limits have mostly disappeared, and especially it is important to notice that the cells are not distinctly limited against the lumen of the entoderm, as they are in the previous stage (plate xv, figures 6 to 11). A sort of dissolution accordingly takes place, the yolk spherules wandering into the lumen, where they are evidently being absorbed. The nuclei, which in the preceding stage were lying fairly regularly at the inner border of the entoderm, are now spread over the whole entoderm mass, without order, evidently after having undergone division. This does not correspond to the inwandering of the phagocytes, as is, evidently, the meaning of K. A. Andersson, who points out (*op. cit.*, p. 6) that this process occurs here at a much earlier stage than in *Antedon*. The phagocytes occur during the metamorphosis, as in *Antedon*. This matter is more fully discussed on page 13.

The *hydrocœl* is assuming the shape of a horseshoe, open downwards; there are thus apparently two vesicles in some sections (plate xv, figures 7, 8); its walls consist of high, cylindrical cells, forming a regular columnar epithelium. The *parietal canal* has developed into a large sac with a lining of flattened, endothelial cells. It has a large forward prolongation, reaching to just below the suctorial disk, where a little widening may occur (plate xv, figure 11). At its lower end it is constricted into a long, narrow pore-canal, which may have an exterior opening, the hydropore, situated between the

third and fourth vibratile bands (plate xv, figure 9). Also in the section represented in plate xv, figure 5, the hydropore is present, while the pore-canal is not narrowed. However, it is not constantly opening outwards; *in some embryos of this stage there was certainly no hydropore* (plate xv, figure 4); it may be emphasized that the lack of a hydropore in a case like that in the figure quoted is a real fact, not a feature due to preservation. In the embryo figured in plate xv, figure 11, there also seems to be no outer opening, but there it may possibly be due to preservation. Of course, it may be that the hydropore would have developed also in the embryos, where it is not found in this stage. This I would be inclined to expect, and that the matter is only one of variability in the time of appearance of this structure, as there is unquestionably some variation in the time of appearance of some of the developmental processes—*e. g.*, the formation of the vestibulary invagination or the formation of entoderm and ectoderm (see p. 32-33; plate xiv, figures 4 and 5).

The *enterocœlic vesicles* have assumed their final places, the left (the future oral cœlom) at the posterior end, the right (the future aboral cœlom) at the dorsal and anterior side of the entoderm, forming a mesentery where they meet one another (plate xv, figure 6). From the right enterocœl vesicle or aboral cœlom prolongations into the anterior part of the embryo are developing (plate xv, figure 10); they are the rudiments of the chambered organ. That there are 5 of them, as in *Antedon*, can hardly be doubted, although I have been unable to determine this in the sections at this stage. The epithelial lining of the enterocœl vesicles has for the most part assumed an endothelial character.

In the mesenchyme are often found globular masses of yolk spherules of different sizes, sometimes very large, as the one lying at the dorsal side in the section figured in plate xv, figure 8. More rarely such yolk globules may be found also in the ectoderm (plate xv, figure 4), while in the entoderm the yolk spherules are generally not united into distinctly limited globules.

4. THE FULLY FORMED LARVA.

The shape of the fully formed larva is markedly different from that of the typical Crinoid larva (plate xxii, figures 1 to 8). It is flattened on the ventral side and has a distinct constriction in the middle of the body (see especially figures 6 and 7), between the two circles of skeletal plates, the oral and the basal plates. The vestibulary invagination has the shape of a very narrow slit (in plate xxii, figure 2, it is broader than usual, on account of the more contracted condition of this specimen). The suctorial disk is very distinct, often with thickened edges, the anterior end being then almost snout-like and prominent (plate xxii, figure 3). The state of contraction accounts for the different shape of the anterior end of the larvæ, as exemplified in figures 2 and 3. The depression of the vestibulary invagi-

nation is not sharply limited from that of the suctorial disk (plate XXII, figure 8). The vibratile bands are very well developed. There are four of them. Traces of an anterior band may be seen, but it is very indistinct and is seen only on the dorsal side. The second band, the prevestibulary band, as it may be termed, may be interrupted in the ventral middle line between the suctorial disk and the vestibulum (plate XXII, figure 3). Of the postvestibulary bands, the upper is bent strongly downwards by the vestibulum, reaching almost the next band, which is also bent slightly downwards in the middle line (plate XXII, figures 1 to 3). The posterior band may have a slight bending upwards in the ventral midline. A very remarkable feature in this larva is found at the anterior end of the vestibulum, from which a band may proceed laterally, like an extra, rudimentary ciliated band (plate XXII, figure 2); it is, however, not constantly developed, and there may be only a simple widening of the thickened epithelium at the upper end of the vestibulum (plate XXII, figure 3).

The size of the fully formed larva is 0.5 to 0.6 mm. in length, being thus twice the size of the larva of *Tropiometra* and *Compsometra*, while the larva of *Antedon* also reaches the size of about 0.5 mm. (Seeliger, p. 231). It is still lying within the egg-membrane, as shown in the figures on plate XXII.

The *ectoderm* (plates XVI to XVII) is only more exceptionally distinctly limited from the mesoderm (as in the series, plate XVII, figures 9 to 12); generally no limit can be made out between ectoderm and mesoderm, and it is evidently in this stage that the dissolution of the ectoderm as a separate layer takes place (see above, p. 11-12, for *Tropiometra*). The nuclei of the vibratile bands are arranged in conspicuous groups, although rarely showing any regular arrangement within these groups (plate XVI, figures 6 and 7; plate XVII, figure 8). The *glandular cells* have become enormously developed, especially on the ventral side and along the vestibulum (plate XVI, figures 2 to 5). In the vestibulum a regular arrangement of the glandular cells is apparent. At the anterior end of the vestibulum the glandular cells occupy the bottom of the furrow, while the sides are occupied by simple cells, seen in the sections as very conspicuous masses of nuclei. Proceeding downwards, the nuclear masses gradually pass down into the furrow, narrowing the glandular space in the bottom, until it disappears completely. Then the nuclear masses occupy the bottom; in the same time new glandular masses appear along the sides of the furrow, these in their turn again going deeper down in the furrow, narrowing the nuclear mass to a narrow space in the middle of the furrow, while again new nuclear masses appear along the sides, these latter, however, remaining less conspicuous. This peculiar arrangement is seen in the series of transverse sections represented in plate XVII, figures 1 to 4, 6, 7, and 9 to 12, as also in the longitudinal sections plate XVII, figure 8; plate XVI, figures 3 and 9; and plate XVIII, figures 3 and 8. In the sections (stained with hematoxylin-eosin) it is seen very beautifully, the gland-

ular masses staining dark blue, while the nuclear masses have a beautiful violet color; also, the shape of these nuclear masses is very peculiar, recalling certain magnificent beard fashions (plate XVII, figures 3 and 7). The epithelium of the vestibulum is distinctly ciliated; the cuticula is seen in sections to be perforated, while a regular layer of fine grains is seen just below the cuticula (plate XVII, figure 5).

The *suctorial disk* is large and deep (plate XVI, figure 2; plate XVII, figure 8; plate XVIII, figures 3 and 8). The cells contain a finely granular substance (plate XVIII, figure 9), which stains red in hematoxylin-eosin, thus appearing remarkably different from the glandular cells of the vestibulum, which stain dark blue, as stated above. A slimy mass fills the cavity of the disk, probably representing cilia, destroyed by the preservation. The cuticular structure observed in the vestibulum (plate XVII, figure 5) could not be distinguished here, even in the same series of sections which showed this structure distinctly in the vestibulum. There is no indication of an apical tuft of cilia. The pigmentation has already begun to develop in the skin of the larva before leaving the egg-membrane, viz, some fine, dark spots which give the larva a faint grayish tint.

The *nervous system* is fairly well developed (plate XVIII, figure 3), but not so distinct in the sections as to allow a detailed description. Neither are its histological relations to the epithelium of the suctorial disk distinct enough to show whether the development of the nervous system takes place in the same way as has been described for *Antedon* by Seeliger (*op. cit.*, p. 238). On the other hand, there is no reason to doubt that there is complete conformity in the development of the larval nervous system of the Crinoids.

The *vestibulary invagination* is remarkably narrow (plate XVI, figure 2), though there is, of course, some variation in this regard, evidently due to contraction on preservation. (See plate XVII, figures 1 to 4, compared with figures 6, 7, and 9 to 12 on the same plate.) K. A. Andersson (*op. cit.*, p. 6) states that "die Vestibulareinstülpung zeigt dem gewöhnlichen Verhältnis gegenüber darin eine Verschiedenheit, dass sie am Vorderende am tiefsten ist und dass sich das Verschliessen von da aus vollzieht." It is true that the invagination is deeper at the anterior end, but the same holds good for the other Crinoids thus far known in this regard, *Antedon* as well as *Tropiometra* and *Compsometra;* so there is herein no difference from the condition which may now with more justification be termed the "usual" mode than it could be at the time K. A. Andersson wrote his paper, when *Antedon* was the only type of which the development had been studied. Regarding the other, much more important, departure from the "usual" type pointed out by K. A. Andersson, that the closure of the vestibulum starts from the anterior end, I can not see how he has come to this conclusion, for there is not the slightest doubt that it starts from the posterior end as in the two other

Crinoids where this process has been observed, *Antedon* and *Tropiometra*. This is evident enough from figure 8, plate XVII, and figure 3, plate XVIII. An apparent exception from this would seem to be the embryo from which figures 9 to 12, plate XVII, have been made. Here the invagination appears to be closed in the middle part (figure 11), while it is open posteriorly and anteriorly. Still, this is only an apparent exception. The closure is not real; it is due only to the sides of the invagination lying in this place so close together that it appears quite closed. But there is still a fine vertical line in the middle, indicating that the two side-lobes are in reality separate. However, it would seem that the posterior part of the invagination is closed in the way indicated by these figures, that the side-walls join and coalesce, and that it is only in the anterior part that a covering wall grows upwards, thus closing the invagination, as is evident from figure 8, plate XVII.

A very conspicuous feature in this process of the closure of the vestibulary invagination in *Isometra* is the nearly complete obliteration of the lumen of the vestibulum. As seen in plate XVII, figure 8, and plate XVIII, figure 3, the walls are joining so closely that merely a line is seen indicating the limit between the epithelium of the covering wall and that of the bottom of the invagination. Later on, the walls must again separate, so that the vestibulum acquires the typical shape (plate XVIII, figures 1 and 2). The last vestige of the invagination is a very narrow opening in the shape of a deep canal at the anterior end, just below the suctorial disk (plate XVII, figure 8). It closes completely while the embryo is still lying within the egg-membrane (plate XVIII, figure 3).

The *hydrocœl* has begun to differentiate, the 5 primary tentacles (or radial canals) having appeared (plate XVI, figures 4 and 8). The *stone canal* is developing, but has not yet opened into the parietal canal (plate XVII, figure 7). The *hydropore* is probably still open in the embryo, from which figures 1 to 4, plate XVII, have been drawn, although it could not be discerned beyond doubt in the sections following that represented in figure 4. But in other series, such as that shown in plate XVII, figures 9 to 12, there is certainly no pore. In plate XVI, figure 3, the pore canal can be discerned, but it is impossible to discern an outer opening of it. The result is, then, evidently that the *hydropore*, which was distinct in the younger stage, *has become obliterated or is about to disappear in this stage.* The anterior prolongation of the parietal canal is still distinct (plate XVII, figure 8; plate XVIII, figure 3), but apparently beginning to be reduced. In the *cœlomic vesicles* there is but little change worthy of note. The left or oral cœlom has developed two upward prolongations at the ventro-lateral side, so that two small spaces appear in the transverse sections laterally to the hydrocœl, the whole dorsal side being occupied by the right or aboral cœlom (plate XVII, figures 3, 6, 11, and 12; see also plate XVI, figure 6). The aboral cœlom has acquired a somewhat complicated shape on account of a deep notch in the

upper side of the stomach (plate XVI, figures 5 and 6). The notch in the outer side of this cœlom seen in plate XVI, figure 9, is part of the chambered organ, its peculiar shape being due to the fact that the section has been obliquely directed. It seems unnecessary to give a detailed description of the shape of this cœlomic cavity, which may be gathered from the figures in plates XVI and XVII. The *axial organ* has begun to develop as a thickening of the cœlomic epithelium in the notch at the vertical mesentery (plate XVII, figure 11).

The *entoderm* still remains in the same histological condition as in the preceding stage, the lumen being indistinctly limited or entirely obliterated on account of the inwandering yolk-cells. In plate XVII, figure 6, the epithelium is in places more distinctly limited against the lumen, while in other places yolk-cells appear to be in the act of wandering into the lumen; opposite the hydrocœl the entodermic epithelium is quite thin, almost endothelial; this is, however, an individual variation. The shape of the stomach is no longer quite simple, on account of the notches from the aboral cœlom, being now somewhat lobed (plate XVI, figure 6); one of the lobes probably is destined to form the intestine, but I can not ascertain this with full certainty. Yolk globules, some being very large, are still seen in the entoderm as well as in the mesoderm (plate XVI, figures 3 to 5; plate XVIII, figure 8).

5. THE PENTACRINOID STAGE.

The fact that the vibratile bands of the larva are well developed proves that the free-swimming stage has not been entirely done away with, as is the opinion of K. A. Andersson. On the other hand, the larva must, on account of the strongly developed skeleton, be rather heavy, so that it must be a poor swimmer and probably sinks almost straight down, where it meets the point of the upturned cirri and attaches itself. The fact that the Pentacrinoids are not found attached to all the upturned cirri, but generally only to two or three of them, would seem to indicate a slight amount of swimming, as one would otherwise expect them to be attached to the cirrus just below the place whence they have come.

Dr. K. A. Andersson (*op. cit.*, p. 7) states as an advantage acquired by this supposed giving-up of the free-swimming stage that the larvæ "laufen nicht Gefahr, in zu tiefes Wasser oder in andere Teile des Meeres hinausgeführt zu werden, wo sie auf einen ungeeigneten Boden niedersinken und zu Grunde gehen könnten." While this may be true, still the larvæ are not free of danger during their short passage from the marsupium to the cirrus-tip; on the contrary, they there incur the danger of being eaten by their elder brothers and sisters. As I have stated in my report on the Crinoids of the Swedish Antarctic Expedition [27] (p. 15), I have found quite a large percentage of the Pentacrinoids to contain in their stomach the half-digested

[27] Wissensch. Ergebnisse d. schwedishen Südpolar-Expedition 1901–1903, Bd. VI, 8, 1917.

but still perfectly recognizable remnants of larvæ (plate XIX, figure 5). I have even found quite young Pentacrinoids with the vestibulum just opened and arms not yet developed, with an embryo almost of their own size in their mouths. On account of the large number of Pentacrinoids found attached in clusters to the tip of the upturned cirri (Andersson has counted no less than 99 Pentacrinoids in one specimen), this danger to the embryos is very real, and probably quite a large number of them must thus perish.

K. A. Andersson has observed (*op. cit.*, p. 6) in two cases a coalescence between the larva and the wall of the marsupium, the coalescence having taken place at the posterior end of the larva. He suggests that this may possibly be an adaptation serving to the better nourishing of the embryo; still he does not lay much stress on this point, as he agrees that it may be quite an accidental case. There can be no doubt that it is an accidental abnormality. The fact that the larvæ remain within the egg-membrane until they are ready to leave the marsupium is proof enough that there can be no question of their coalescing with the marsupial wall with the object of extracting nourishment from the tissues of the mother. If there has really been such a coalescence in the cases observed by Andersson—and the figure he gives (taf. II, figure 10) certainly shows that—it must be due to a casual rupture of the egg-membrane.

Andersson further regards the embryo showing this coalescence as a double monster. Judging from the figure, this is a mistake. Evidently he has been misled by the strong development of the suctorial disk, which in the figure quoted is nearly as large as the vestibulum.

I have observed in one case an embryo within a marsupium having developed into the pipe-shape described above for *Tropiometra*. This must be due to the larva not having succeeded in leaving the marsupium, and having thus been unable to attach itself, it has developed in the same way as the unattached *Tropiometra* larvæ.

The young, newly attached Pentacrinoid offers some interesting structural features. As seen from figure 1 of plate XXI, the vestibulum now has assumed the normal place at the formerly posterior (now anterior) end, and it has a distinct lumen. The tentacles have not yet become free. In this stage the Pentacrinoid is otherwise a poor object for the study of the inner structure; hardly anything except the stomach can be clearly distinguished in decalcified specimens, stained and mounted in balsam. In sections (plate XVIII, figures 1, 2, and 7) a very conspicuous difference from the larva is shown to exist in the histological character of the entoderm. A single, fairly regular layer of nuclei is seen along its outer surface, while the whole inner part of it is filled with a dense mass of small grains that stain very strongly in hematoxylin. There is no doubt that this corresponds to the mass of small cells that fills the lumen of the entoderm in the corresponding stage of the young *Antedon*, while nothing quite corresponding was observed

in *Tropiometra*. Seeliger states that this mass consists of degenerating cells derived from the entoderm cells and having the object of serving as nourishment to the embryo until it is able to take its own food from the surroundings. I doubt very much that this is the correct explanation of the phenomenon. First, on purely logical grounds. The meaning of this multiplying of the entoderm cells, in order that the cells thus orginating may serve as food, is, in fact, this, that the embryo is feeding upon itself. Then, regarding *Isometra vivipara*, it will be remembered that the entoderm in the fully formed larva is filled with a yolk-mass in which some nuclei are scattered.[28] (Plate XVI, figures 6 and 9). It seems hardly possible that these few nuclei should have divided at such an enormous rate as to produce the immense number of grains that fill the entoderm, during the short time which must be supposed to be required for the fixation and the transplacement of the vestibulum, judging from the cases of *Antedon* and *Tropiometra*.

The true explanation may be found by comparing this feature of the Crinoid development with what obtains in the Echinoid larvæ during the metamorphosis, for here also the entoderm is filled with a mass of small cells, as first described by MacBride,[29] who regards this process as a kind of histolysis and, like Seeliger, states that the small cells filling the lumen of the entoderm are produced by the entoderm cells, which are said to multiply with great rapidity. More recently L. v. Ubisch[30] has made a very careful investigation of this process, his result being that a histolysis of the entoderm really takes place, as stated by MacBride; but the small cells filling the lumen of the entoderm are not produced by the entoderm cells; they are wandering cells, originating from the mesoderm, which migrate through the entodermal epithelium into the lumen of the entoderm. It could not be decided, whether these wandering cells replace the original entoderm cells or whether only the nuclei of the entoderm cells are dissolved during the histolysis, to be replaced in some way or other after the metamorphosis.

Although no nuclear structure could be discerned in the grains filling the entoderm of *Isometra*, I have little doubt that we have to do with the same thing as in the Echinoids—the mass occupying the entoderm consisting of wandering cells, derived from the mesoderm, which must be supposed to take an active part in the histolysis of the entoderm. That they are not derived from the entoderm cells is indicated also by the fact that they are

[28] That this cell-mass is, as I think, meant to serve as nourishment to the embryo, is something quite different from what Seeliger maintains. It is here, probably, only a sort of diluting of the rich yolk material contained in the entoderm cells, in order to make it more easily digested, or, perhaps, it is essentially a question of space, the multiplying cells being pressed out into the lumen of the entoderm, and, it should be added, it is doubtless only the yolk material, not the nuclei and the protoplasmatic content of the cells, that is digested.

[29] E. W. MacBride. The development of *Echinus esculentus*, together with some points in the development of *E. miliaris* and *E. acutus*. Philos. Trans., ser. B, vol. 195, 1903, p. 309.

[30] L. v. Ubisch. Die Entwicklung von *Strongylocentrotus lividus* (*Echinus microtuberculatus*, *Arbacia lixula*), Zeitschr. f. wiss. Zoologie, Bd. 106, 1913, p. 433.

found likewise in the other parts of the young Pentacrinoid, although in much smaller numbers. This was also found to be the case in *Tropiometra* (see above, p. 17). Of course, the definite proof that this is the correct interpretation can not be given here, the insufficient preservation making such minute histological researches impossible. But it seems to me that all the facts point in this direction, that a histolysis of the entoderm takes place during the metamorphosis, the wandering cells taking an active part in this process.

With the replacement of the vestibulum from the ventral side of the embryo to its posterior end, the hydrocœl and the cœlomic spaces have also occupied their final position (plate XVIII, figures 1 and 2). The inner wall of the vestibulum is very thick, with many of the grains just mentioned lying irregularly, in places more scattered, in others in close groups between the nuclei. A slight concavity in the middle (plate XVIII, figure 2) is the first indication of the future œsophagus; below this place the ectoderm and entoderm are fusing in the middle of the still open hydrocœl ring.

The stone canal has not yet opened into the parietal canal and the pore canal has no exterior opening. The figures (plate XIX, 1 to 4) show the interrelations of these structures very distinctly. In the mesentery inside the parietal canal a slight accumulation of nuclei is seen; it probably represents Russo's primary gonad.

A somewhat more advanced stage is represented in plate XXI, figure 2, and in the sections, plate XVIII, figures 4 to 6. The tentacles have protruded into the vestibulum, which is about to open, a depression having appeared in the middle of its outer wall and the 5 oral valves being about to separate. The mouth and œsophagus have been formed and in the stomach a lumen is beginning to appear, the granular mass being about to be absorbed (plate XVIII, figure 5). Also the intestine has been differentiated, but the anal opening has not yet been formed. The stone canal has opened into the parietal canal (plate XVIII, figure 4), but no outer opening of the pore canal can be discerned as yet. The chambered organ is beginning to assume its typical form and the axial organ is distinct (plate XVIII, figure 6). It appears that the parietal canal has opened into the oral cœlom; but this could not be fully ascertained.

The next important change is the opening up of the vestibulum. The young Pentacrinoid now begins to feed directly, having till now subsisted on the yolk substance contained in the egg. Diatoms, mainly of the *Coscinodiscus* forms, are found in the stomach, and in some cases also larvæ of its own kind, as mentioned above (plate XIX, figure 5). I have found very young, just opened, Pentacrinoids with such a larva hanging half out of its mouth, it being too large to be swallowed.

In plate XXI, figures 3 and 6, are represented two Pentacrinoids of somewhat more advanced stages, with the arms already branching. They have

been decalcified, stained, and mounted in balsam, so as to show the inner anatomy *in toto*. Longitudinal sections of corresponding stages are represented in plate XXI, figures 4 and 5, and transverse sections in plate XIX, figures 5 to 10, and plate XX, figures 1 and 2 and figures 3 to 8.

The *epithelium of the oral surface* has become thin, in marked distinction from the previous stage, before the opening up of the vestibulum (plate XXI, figure 4, comp. with plate XVIII, figures 1 and 2). The mouth may protrude above the oral surface like a small funnel, so as to appear in transverse sections as a ring (plate XX, figure 2). In one case I have found a thickening of the esophageal wall in the anal interradius, which makes a distinctly limited furrow that ultimately closes into a narrow canal. The thickening begins at the level of the hydrocœl ring (plate XIX, figure 5) and continues some way below the rectum, ending as a small ridge that rises into the lumen of the stomach (plate XIX, figures 5 to 10). I am at a loss to explain this structure, which may be some abnormality, perhaps due to the fact that the stomach in this specimen is strongly dilated by the embryo which has been eaten. In any case I have thought it worth while mentioning and giving the series of figures quoted to illustrate it. In plate XX, figure 4, is also seen a thickening of the esophageal wall in the anal interradius. In this specimen, however, the thickening soon widens in passing downwards, and passes gradually into the normal condition of the entodermal epithelium.

The stomach is provided with folds (plate XX, figure 6; plate XXI, figures 5 and 6); in the strongly dilated stomach of the specimen that has eaten an embryo (plate XIX, figure 5) these folds have disappeared; the anal opening has been formed (plate XX, figure 5; plate XXI, figure 6); that the opening is indistinct in plate XIX, figure 8, is evidently due to pressure on account of the contents of the stomach.

The hydrocœl ring is not yet completely closed. In plate XIX, figure 5, and plate XX, figure 3, is seen the narrow wall that still separates the two ends of it. Numerous trabeculæ have been formed in its lumen. A thickening of the epithelium over the upper side of the hydrocœl ring (plate XXI, figure 5 *r. n.*) is the ring-nerve which has begun to develop. Below the nerve is an indication of circular muscle fibers (comp. Seeliger, *op. cit.*, taf. 21, figure 174). The stone canal has lengthened considerably (plate XXI, figure 3), and the pore canal has again acquired an exterior opening (plate XXI, figure 3; plate XX, figure 3). The parietal canal has opened into the oral cœlom (plate XXI, figure 4). In the aboral cœlom some irregularly arranged trabeculæ are seen (plate XXI, figure 6).

The primary gonad (Russo) is distinct (plate XXI, figures 3 and 6); the axial organ has developed into a conspicuous string and the chambered organ is very distinctly quinquelocular, with fairly large lumen (plate XX, figures 7 and 8; plate XXI, figures 3, 5, and 6). An interesting feature is seen in the

arms of the larger Pentacrinoids (plate XXI, figure 6), viz, the primary, azygous tentacle, situated in the cleft of the arm. It remains here and must ultimately become absorbed. This fact was already observed by Wyville Thomson in *Antedon bifida*.[31] Plate XXI, figure 7, which is drawn from a preparation of a Pentacrinoid of *Antedon bifida*, elucidates this point well. It is seen here how the radial canals of the arm-branches originate as side-branches from the primary radial canal a little below the free azygous tentacle. The figure also shows that the distal tentacle is the first to develop in each triplet of tentacles.

6. DEVELOPMENT OF THE SKELETON; THE PENTACRINOID.

The first stage of the skeletal development is represented in plate XXII, figures 4 and 5. The oral and basal plates have the shape of branched spicules arranged in two circles, the plates of the basal circle lying almost exactly below the corresponding ones of the oral circle. The terminal stem-plate has been formed and some few stalk-joints are indicated by very small spicules, 3 in figure 5, 7 in figure 4. Infrabasalia are not seen, nor is there any trace of them in the later stages, so it is evident that they are entirely lacking in this species. In figures 6 to 8, plate XXII, which represent the fully formed larva, the oral and basal plates have become large, fenestrated plates, arranged in two regular half-circles, leaving a broad, open space on the ventral side (plate XXII, figure 6); they are distinctly separated from one another in the middle, where the constriction of the larva takes place, the oral plates thus occupying the posterior and the basal plates the anterior end of the larva (plate XXII, figure 7). The terminal stem-plate is large and fenestrated, and the stalk-joints have augmented considerably in size and number; their exact number is hard to ascertain, because they lie so close together. The plates of the fully formed larva are, upon the whole, strongly developed, and almost convey the impression that the larva is a mail-clad little organism, the naked median constriction apparently affording the line of motion between the mailed anterior and posterior part. As seen in the three figures quoted, the larva in this stage is still inclosed by the egg-membrane, which does not burst till the moment when the larva leaves the marsupium.

The newly attached Pentacrinoid (plate XXII, figure 9; plate XXIII, figure 1) is a curious little, short-stalked, thick-headed organism, the oral and basal plates inclosing it now very completely. The stalk-joints are still very short and so closely packed that it is impossible to count them. The upper third part of the stalk is still inclosed by the basals. As seen in plate XXIII, figure 4, it happens that the young Pentacrinoids attach themselves to the stalk of their slightly elder sisters and brothers. The first

[31] Wyville Thomson. On the Embryogeny of *Antedon rosaceus* Linck. Phil. Trans., vol. 155, 1865, p. 259.

change of shape is produced by the lengthening of the stalk-joints, and it can now be ascertained that there are 18 of them (plate XXIII, figure 2). They are still quite short and with the median ring strongly projecting, which gives the stalk a distinctly serrate appearance. It is now only the very youngest joints that are inclosed by the basals. Contemporaneously with the lengthening of the stalk, the oral plates begin to acquire prominent side-edges. In the next stage (plate XXIII, figure 3; plate XXII, figure 10) this character of the orals is much more conspicuous, the outturned side-edges being large and thickened; upon the whole the calyx plates are now quite thick, massive, and finely tuberculated. Along the lower edge of the orals a growth-zone is very distinct, indicated by the linear arrangement of the holes, which are very small. The radials have appeared, likewise the anal plate, which is slightly larger than the corresponding radial and thus is formed prior to the latter. The stalk-joints have lengthened considerably, especially the lower ones, and are now more rounded in outline, the median ring being much less prominent; 21 joints are counted. The Pentacrinoid in this stage bears a remarkable likeness to the Cystidean *Lepadocrinus quadrifasciatus*,[32] the likeness being, of course, due only to a superficial analogy.

In the following stage, represented in plate XXII, figure 11, and plate XXIII, figure 4, the radial plates have grown considerably and, like the orals and basals, show a distinct zone of growth. The costals have formed and have assumed the shape of an elongate scale. In the tentacles elongate spicules have developed. The anal plate has already been quite outgrown by the corresponding radial; it covers the corner of the latter and of the adjoining oral. It is of the same dense structure as the other plates. The stalk-joints are about to assume their final shape, but the median ring is still slightly projecting; 24 joints are counted. The terminal stem plate is slightly lobed. The short upper joints are somewhat broader than the rest.

Some later stages are represented in plate XXIII, figure 5; in plate XXII, figure 12, and plate XXIII, figure 6. In the first of these the rudiments of the two arms have appeared, joining the outer sloping sides of the axillary; the costals still remain very slender. In the specimen shown in plate XXII, figure 12, and plate XXIII, figure 6, some 6 to 8 arm-joints have developed. The radials are joining one another, thus separating the orals from the basals. The strongly raised side-edges of the orals give them a peculiar shape, somewhat like a trough. The corner of the oral plate joining the anal plate has undergone some absorption, and the corresponding radial plate has the adjoining corner truncated. The costals are widening and beginning to assume their final shape. The number of the stalk-joints has not increased.

The most advanced stage found is that represented in plate XXIII, figure 7. Here the first pinnule has made its appearance, on the twelfth arm-joint, which proves that here also the oral pinnules are not the first to develop.

[32] See Bather. Echinoderma, in Ray Lankester's "A Treatise on Zoölogy," III, 1900, p. 62.

The first circle of cirri have been formed, situated radially as usual, attached to the broad upper stalk-joint. The radials and costals have become much broader and are about to assume their final shape. The orals are widely separated from the basals, lying in the middle of the disk, which has grown very considerably. The anal plate remains small and is no longer contiguous with the adjoining oral and radial. Along the sides of the arms some branched spicules are seen; they represent the side-plates. The stalk has 24 joints, which is evidently the normal number. They are slightly thickened at the ends, those of the upper half of the stalk being the larger; upon the whole the upper part of the stalk is distinctly stronger and more robust than the lower part. The four upper joints are quite short and broadening towards the top joint with the cirri, which is the broadest. Another specimen is slightly more advanced in having 3 pinnules on each arm and the second whorl of cirri beginning to develop, alternating with the first cirri, which are now fully formed, with 14 joints, ending in a terminal claw. K. A. Andersson (*op. cit.*, p. 7) states that in the largest of the Pentacrinoids the pinnulæ have begun to develop, but the cirri have not yet appeared. Evidently he has failed to see the largest specimens, in which the cirri are very distinct; I would even be inclined to think that the specimen (taf. 2, figure 11) he represents as the most advanced stage has no pinnules developed as yet; at least they are not seen in the figure; apparently he has mistaken the tentacles for pinnules.

The developmental history of this species can not be traced any farther, no very young free specimens being represented in the collection; but as no further developed stages of Pentacrinoids are found, it seems probable that they detach themselves soon after having reached the last-described stage.

IV. NOTOCRINUS VIRILIS Mortensen.

(Plates XXIV to XXVI.)

The viviparous habit of this remarkable Crinoid was described in detail in the author's memoir on the Crinoids of the Swedish South Polar Expedition.[33]

The *eggs* are 0.2 to 0.3 mm. in diameter. Quite a number of ripe eggs are found at the same time in each ovary, while never more than 3 embryos were found together in a marsupium, generally only 1 or 2. These facts would seem to indicate that some of the eggs do not develop. In some cases I have found in marsupia without embryos a yellow, coarsely granulated substance which had decidedly the appearance of being eggs in disintegration. The suggestion that some of the eggs are destined to serve as nourishment for the developing embryos lies at hand. The unusual size of the embryos would be naturally explained by this suggestion, while the size of the eggs, which is by no means unusual, not larger than in *Isometra vivipara*, can not account for this feature.

All the embryos are at nearly the same stage of development; they are found in various sizes, but there is no essential difference in their stage of development; only in one case do I find the vestibulary invagination in a much younger stage of development, being represented only by a slight concavity along the ventral side, in which the ectoderm is considerably thickened. Plate xxv, figure 8, is drawn from a series of sections of this larva; it shows a young stage of the development of the glandular sacs (to be mentioned below) not seen elsewhere. Otherwise this specimen is in the same stage of development of the interior processes as the other larvæ. This circumstance, which is very unfortunate for the study of the successive changes of the developing embryo, would seem to indicate that the eggs are emptied into the marsupia a number at a time, as is the case with the Crinoids with free eggs thus far observed, not one at a time and at any time, as in *Isometra vivipara*. The reason for this exceptional feature in *Isometra* is evidently the fact that the spermatozoa are accumulated in a sort of vesicula seminalis in the ovary (perhaps through a copulatory act) and always ready for fertilizing the ova, while otherwise in Crinoids the eggs are emptied only when a male emits sperm, the sperm seemingly acting as a stimulus.

As stated above, no eggs or very young embryos are found in the marsupia, so that unfortunately no information can be acquired about the cleavage (which I would expect to find of the same type as in *Isometra vivipara*) or the first developmental processes. There is, in fact, only one larval stage to describe, viz, the nearly fully formed larva; but this affords so many novel features that considerable interest attaches to it.

[33] In "Wissensch. Ergebnisse d. Schwed. Südpolar-Expedition 1901–1903," Bd. VI, 8, 1918, pages 6, 7, plates III and IV.

The smallest larvæ are 0.9 mm., the largest 1.8 mm. in length. The egg-membrane evidently has been ruptured a long time before the larvæ reach that size. In embryos sectioned *in situ* within the marsupia, parts of what would appear to be an outer membrane are seen close to the skin; otherwise no trace of an egg-membrane can be observed. This accords well with the fact that the larvæ grow to such large size that they must necessarily be assumed to obtain nourishment from the mother animal. That could hardly pass through an egg-membrane. As there is no mouth, it could take place only by absorption through the skin.

It is worth mentioning that on embedding the larvæ in paraffine the skin would always break in various places, in spite of the most careful treatment; but when they were embedded lying undisturbed within the marsupia their skin never broke.

The shape of the larva (plate XXIV, figures 1 to 3) is generally more or less irregular, on account of the pressure in the marsupium, but upon the whole it is somewhat flattened and slightly concave on the ventral side, while the dorsal side is more arched, the hind end generally more so than the anterior end. On the ventral side there is in the anterior end a more or less distinct arcuate depression, the convexity being directed towards the anterior end. This represents the suctorial disk. There is no apical pit. The vestibulary invagination is narrow. In the apparently most normal-shaped larvæ (plate XXIV, figure 1) there is a shoulder-like prominence on each side at the anterior end; but whether this is a typical feature can not be ascertained.

One larva (plate XXIV, figure 3) exhibits a peculiar feature in having a slender prominence, like a thin stalk, on one side, suggesting that it had coalesced with the wall of the marsupium; but as nothing similar was observed in any other embryo it can not be a normal feature.

A very interesting fact is the *total absence of ciliated bands* in this larva. Neither does a general ciliation appear to exist; only in the suctorial disk and the vestibulary invagination are cilia distinctly seen. The *ectoderm* is much thickened in the whole of the anterior end, gradually thinning out towards the posterior end (compare the longitudinal sections, plate XXIV, figures 4 to 9); the extension of the thickened portion differs to some degree, as seen in the figures quoted; in the specimen represented in figures 4 to 6 it passes below the hydrocœl, in the other specimen (figures 7 to 9) it is confined to the part beyond the stomach and the hydrocœl. The histological details are hard to discern in the thick part of the ectoderm; it is a mass of nuclei, intermingled with glandular cells. In the part where the transition to the thin part takes place, an outer layer of small, closely aggregated nuclei and an inner layer of larger nuclei can be discerned, between which is a mass of irregular thread-like structures (plate XXVI, figure 9). It can hardly be doubted that this corresponds to the glandular cells found in the skin of other Crinoid larvæ and it would appear that the inner, larger nuclei belong to the glandular cells. Full certainty can not be acquired on account of the

preservation in alcohol. In the thin part of the ectoderm only some few small nuclei lie close to the surface and glandular cells are seen only here and there (plate XXVI, figures 4 and 5). The ectoderm of the vestibulary invagination differs from the ectoderm of the outer side only in being much thicker (plate XXV, figures 1 to 6).

The bottom of the furrow is richly provided with glandular cells in the part from a little below its anterior end to about where the hydrocœl begins. But there is no such shifting of the glandular and the nuclear parts as was described for *Isometra vivipara*. In the figures on plate XXV the glandular parts are not shown. The reason for this is that they have been drawn from sections stained with hematoxylin, in which the glandular parts are not clearly defined; but in other sections, stained with picrocarmine, the glandular parts are very distinctly differentiated by being of a clear yellow color, while the nuclei are stained beautifully red.

There is a very distinct ciliation in the furrow (plate XXVI, figure 10). The cilia are seen to perforate the cuticula; inside the cuticula is seen a darker line, not a series of fine grains, as was observed in *Isometra* (plate XVII, figure 5).

From the sections represented in plate XXV, figures 1 to 6, it would appear that the closure of the furrow is about to begin at the anterior end. I do not think this conclusion justified. The narrowness of the outer part of the furrow seen in figure 3 is evidently due to accidental pressure and is not found in other specimens.

The *nervous system* is remarkably developed for a larva apparently not in special need of it, being devoid of both the power and opportunity for movement. The nervous system must here be just a morphological reminiscence. It is forming a conspicuous layer below the epidermis in the anterior end (plate XXVI, figure 6), reaching almost as far downwards as to the posterior end of the vestibulary invagination. Ventrally it is more restricted and is seen only below the suctorial disk (plate XXV, figure 1); from here it branches (plate XXV, figure 2) and may then be followed for some distance downwards as a distinct nerve along each side of the vestibulary invagination.

The *entoderm* forms a wide sac with thin walls, with the nuclei arranged in a layer of somewhat varying thickness, in many places even in a single regular layer (plate XXIV, figures 4 to 9; plate XXV, figures 4 to 6). The lumen of the entoderm sac is entirely empty; there is no trace of yolk or inwandering cells in it.

The *hydrocœl* is a half ring, lying in the normal place a little to the left of the vestibulary invagination (plate XXIV, figures 5 and 9; plate XXV, figures 5 and 6). The primary tentacles are just beginning to appear, as indicated by the thickenings of its epithelium seen in plate XXVI, figure 1. Also a slight prolongation towards the parietal canal—not seen in any of the figures, as no section was favorable for showing it—probably indicates the beginning formation of the stone canal. The pore canal is closed (plate

XXIV, figure 9; plate XXVI, figure 4). The parietal canal has a long, narrow anterior prolongation (plate XXIV, figure 4; plate XXV, figures 1 to 3).

The *cœlomic vesicles* have assumed their normal position, the left at the posterior, the future oral end, the right at the dorsal side. The former prolongs upwards on either side of the hydrocœl (plate XXV, figure 6). The chambered organ has been formed and may be followed to near the anterior end (plate XXV, figures 1 to 3).

While there is nothing unusual in the relations of the entoderm, the hydrocœl, and the parietal canal, a very unusual feature is apparently connected with the oral cœlom. In the posterior end of the embryo *a number of fairly conspicuous sacs are seen, looking like large glands, apparently opening outwards* (plate XXIV, figure 2). As seen in transverse sections (plate XXVI, figure 3), they may be fairly regularly arranged, three or four of them on each side; in other cases they are found only on one side, as seen in the frontal section (plate XXIV, figure 7). I think it fairly safe to conclude that these sacs originate as prominences from the posterior wall of the (later) oral cœlom (plate XXV, figure 8). They are afterwards completely separated off from the cœlomic wall and acquire an outward opening through the body-wall (plate XXVI, figure 5). The two figures quoted would seem to leave no doubt that such is their history, but it is impossible to follow the whole process on the single larval stage available. However, it should be recalled that the specimen from which plate XXV, figure 8, was drawn is exceptional, as mentioned above (p. 49) in having the vestibulary invagination in a much younger stage of development than the other larvæ, which seems to accord well with the fact that also the gland ular sacs are in a younger stage of development in this specimen, while none of the other larvæ showed this young stage in the development of the sacs. As regards the outer opening shown in plate XXVI, figure 5, it must be admitted that it is not as distinct as here represented, the opening itself being not quite clear. But I have no doubt that my interpretation is correct.

The histological structure could be made out remarkably well (plate XXV, figure 7; plate XXVI, figure 11). They consist of a single layer of cells, with nuclei somewhat larger than those of the surrounding mesenchyme. On the inner end of each cell is seen a mass of small globules, which stain yellow with picrocarmine and appear conspicuous against the red nuclei and the finely granulated cell-protoplasm. As appears from plate XXVI, figure 5, this structure disappears towards the opening of the sac. It is evident that these sacs must be glandular in nature, the like of which is otherwise unknown in Crinoid larvæ, unicellular glands being the rule—such as are also found in this larva, as stated above. It is quite a novel structure, which one might well suggest may have some relation to the life-conditions of this larva in the marsupium of the mother animal, conditions which are apparently very different from those of the larvæ of *Isometra vivipara*, so far as they must be supposed to derive nourishment in some way from the

mother animal, which does not appear to be the case in *Isometra vivipara*, where the larvæ remain within their egg-membrane all the time till they leave the marsupium, and do not reach any unusual size.

The *mesenchyme* is very extensively developed, as might be expected from the large size of the larva. It has a distinctly fibrillar structure. In the anterior part (plate xxv, figures 1 to 3) one can distinguish an outer layer with very few nuclei and much developed fibrillæ from an inner part, with numerous nuclei and fibrillæ only slightly developed. There may be a fairly distinct limit between the two parts. In the inner part (which surrounds the chambered organ and the stalk-joints) are found, besides the nuclei, a varying number of yolk globules, single or connected into small ball-like masses (plate xxvi, figure 8). Sometimes such yolk globules may be found also in the posterior end of the larva, but they are much less numerous here than in the anterior end.

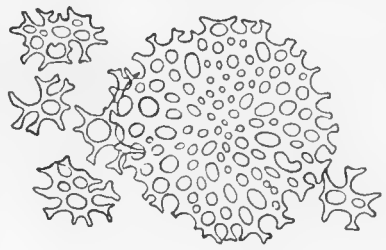

Fig. 7.—Primary and supplementary terminal stalk-plates of *Notocrinus virilis*. ×160.

The *skeleton* is very nearly in the same stage of development in all the larvæ, in spite of the considerable variation in their size. As represented in plate xxiv, figures 2 and 3, the circles of oral and basal plates are typically developed, and there are 4 good-sized infrabasalia. In one case I can distinguish 5 infrabasalia, the two being much smaller than the three others. There are about 25 stalk-joints and a terminal stalk-plate of usual size. But here again we meet with a novel feature: *Beside the large terminal plate there are some smaller supplementary plates*, varying in number from 1 to 5 (text-figure 7). They lie without any definite order around the border of the primary terminal plate. In a few specimens (in which the skeleton is in a slightly younger stage of development than in the specimen represented in plate xxiv, figure 3) there are as yet no supplementary terminal plates; but there is no reason to suppose that they would not have appeared here also in due time.

The meaning of these supplementary terminal plates is hard to guess. It may perhaps be supposed that there is something in the mode of attachment of the Pentacrinoid that has caused their appearance. It is a pity that only this one stage of the development of this unusually interesting Crinoid should be available. Owing to the lack of ciliated bands the larva must be unable to swim and must simply drop to the bottom on leaving the marsupium, or it may attach itself to the walls of the marsupium, the head of the Pentacrinoid protruding through the marsupial opening, as is the case in *Thaumatometra nutrix*. But as the Pentacrinoid of the latter species has no terminal plate, it is hard to see why the Pentacrinoid of *Notocrinus* should have an extra number of terminal plates. Only direct observations can give the answer to these interesting problems.

V. FLOROMETRA SERRATISSIMA (A. H. Clark).[34]

(Plate XXVII.)

During a stay at the Biological Station at Nanaimo, British Columbia (on Vancouver Island), in June and July 1915, I succeeded in finding some specimens of *Florometra serratissima* (A. H. Clark) with Pentacrinoids attached to their cirri. The species was fairly common in a place near Ruxton Passage, in a depth of about 15 to 25 fathoms. It may be worth while mentioning that I observed this species to swim actively in the usual way of Comatulids. Only very few carried Pentacrinoids. In more than 200 specimens only 10 Pentacrinoids were found in all, representing the different stages figured in plate XXVII. The rearing of the embryos was impossible, because the species was not hardy enough to endure the long transport from the place of capture to the station, so that nothing more could be accomplished than collecting the Pentacrinoids. But the study of these alone is of no small interest.

In the youngest stage represented (plate XXVII, figures 1 and 2) the oral valves have opened, the primary tentacles beginning to protrude. The calyx consists as yet only of the basalia and oralia. The basalia are peculiar in having a rather broad unfenestrated lateral edge; the oralia are deeply concave along the middle line, the sides being bent gracefully outwards. *There are no infrabasalia.* Although the first appearance of the calyx plates could not be observed, the absence of infrabasals appears certain. By dissolving the calyx with dilute hypochlorite of sodium directly under the binocular microscope it is easy to isolate each of its components, and in case the infrabasalia are present they are easily made out; but no trace of them was found, and as it can not well be assumed that they could already have disappeared —at least they can not have been absorbed by the centrodorsal, the upper stalk-joints being still quite young, half-moon-shaped—it seems safe to conclude that infrabasals are absent in this species.

While the radialia have not yet been set out, the *axillary has already appeared,* lying as a small, fenestrate plate about midway on the primary tentacle, outside the first sacculus, which is also distinct. In another specimen of the same stage the axillary was only a small spicule, not yet fenestrated. So far as I know, this is the first case recorded where the axillary appears before the radialia. That it is really the axillary which is first formed is shown beyond doubt by the detailed figure (plate XXVII, figure 6), from a slightly older stage where the radial plate has been formed. Here is seen, below the first-formed plate in the tentacle, a small plate which can alone represent the costal. The axillary in this case was found to be slightly abnormal. The anal plate is large and round, encroaching upon the

[34] I am indebted to Dr. A. H. Clark for the name of this species.

adjoining basals (plate XXVII, figure 1). It is the first plate to appear after the basalia and oralia, the order of appearance of the different plates being thus: (1) the basals and orals; (2) the anal plate; (3) the axillary; (4) the radials; (5) the costals.

In the specimen from which figure 6 was drawn the costal had appeared only in one radius, that to the left of the anal radius; the radial plate was also found to diminish in size the same way round, and partly also the axillary, which latter was, however, found to be largest in the anal radius.

The stalk consists of 16 joints, the 4 upper ones being quite short, the middle ones long and cylindrical, with the primary ring slightly prominent, the 3 lower ones quite short; the terminal stem-plate is irregularly lobed.

In the stage represented in plate XXVII, figure 3, the radialia have just been formed, viz, the small star-shaped spicule to the right of the anal plate, while the costal has not yet appeared. Some meshwork is beginning to develop on the oralia and a growth-zone can be observed in the lower part of the oralia and the upper part of the basalia.

On account of the large size of the anal plate, the adjoining radial plate lies to the right of the median line; there is a beginning absorption of the lower part of the oral plate.

A slightly older stage is represented in plate XXVII, figure 4. In this specimen one of the basalia was abnormal, smaller and shorter than the other basals and reaching only half-way down, so as not to join the upper end of the stalk. There are 19 joints in the stalk, the middle ones being very elongate and slender.

The oldest stage represented is that figured in plate XXVII, figure 5. The radials have grown considerably and nearly join one another, separating the orals from the basals. The costals and axillaries have lengthened and now have the appearance of a small arm. The anal plate has apparently not grown and is now pushed out from its original position in the radial midline so as to lie wholly in its own interradius, between the basal and oral plate, while the radial plate has occupied its final position in the mid-radial line; but it is not yet quite symmetrical, the side adjoining the anal plate being somewhat narrower. Some meshwork has developed in the concavity of the orals. The stalk is incomplete in this specimen, but in another specimen only slightly younger there are 23 joints. The terminal plate remains small and unlobed. Plate XXVII, figure 7, represents part of a decalcified specimen (the same as that represented in figure 1) showing the stone canal and pore canal. So far as can be ascertained without sections, the outer pore is closed in this stage. The primary gonad is very small and indistinct.

VI. THAUMATOMETRA NUTRIX Mortensen.

(Plate XXVIII.)

The peculiar viviparous habit of this little Crinoid, carrying the Pentacrinoids on its pinnules, was described in detail in my report on the Crinoidea of the Swedish South Polar Expedition,[35] to which reference must be made.

As the material consisted of only one very poorly preserved specimen, with the arms broken and only a few pinnules left, it could hardly be expected that all the developmental stages should be represented; it is rather more surprising that the Pentacrinoids should present a fairly complete series from the youngest stage to the stage when they are ready to detach themselves. A few eggs were found in the marsupia, but none of them was fertilized, and no information can be given of the cleavage and the larval development. Only the growth changes of the Pentacrinoids can be described.

The youngest Pentacrinoid is represented in plate XXVIII, figure 1. The vestibulum is not yet opened and the oral and basal plates are still in a rather embryonic condition; their middle part retains the original character of a branching spicule; this feature, however, remains distinct, especially in the oral plates, till a much later stage. There is a distinct naked space left between each two adjoining pairs of basals and orals, and it appears that these plates never join completely in the radial midline. Infrabasalia can not be discerned and apparently do not exist in this species. No trace of the radials or the anal plate is seen. The stalk consists of 11 joints; the middle plate of all the joints is still very conspicuous, the joints being still in a very young stage of development. *There is no terminal stem-plate.* It is true the figure gives the impression that there is a small terminal plate, but it is not really so; it is only the lowermost joint that has, on account of pressure in the preparation, assumed such a position that it is seen directly from above. This specimen has attached itself to the upper edge of the marsupial wall, not to a joint of the pinnules, as is the case with the other Pentacrinoids. (See plate v, figure 3, of the Report on the Crinoidea of the Swedish South Polar Expedition.)

The next stage represented is that figured in plate XXVIII, figure 2. The vestibulum has opened and the primary tentacles are protruding. The orals and basals have grown considerably, the growth-zones being indicated by the regular arrangement of the holes. The orals have begun to assume the usual form, concave in the upper part, with the edges outturned. The radial plates have been formed; they are peculiar in having an unfenestrated central part. The stalk-joints have grown somewhat and are now very hard to distinguish from one another, so that their exact number can not be stated.

[35] Wissensch. Ergebn. d. Schwedischen Südpolar-Expedition, 1901–3, Bd. VI, 1918, p. 17.

In the next stage represented (plate XXVIII, figure 3) the radials have grown somewhat and assumed a triangular shape; the costal has appeared as a branching spicule. The anal plate lies wholly outside the radial midline; it has hardly any influence upon the shape of the adjoining radial plate in this stage. The stalk-joints can not be discerned in the upper part of the stalk; the lower ones are assuming their final shape.

In the following stage (plate XXVIII, figure 4) the arms have begun to form; the radials are joining, thus separating the basals from the orals. The anal plate is still small, but the radial to the right of it is now considerably influenced by it (text-figure 8); a naked space, only partly occupied by the anal plate, separates it from the adjoining radial plate to the left. Also the adjoining oral plate has undergone some absorption. The costals are long and narrow, the original spicule still being discernible in the middle. The axillaries are somewhat shorter; along their outer edges the arm-joints have begun to appear in the typical shape of a spicule lying transversely and sending out prolongations proximally and distally. The upper stalk-joints are still indistinctly separated from one another. A slightly more advanced stage is that figured in plate XXVIII, figure 5. The arms have grown considerably, about 6 joints having developed. The axillary has assumed its typical shape with two oblique outer edges. The primary spicule is still distinct, both in the axillary and the costal. The stalk-joints are now assuming their final shape also in the upper part of the stalk. There are still only 11 joints, the same number that was found in the youngest specimen.

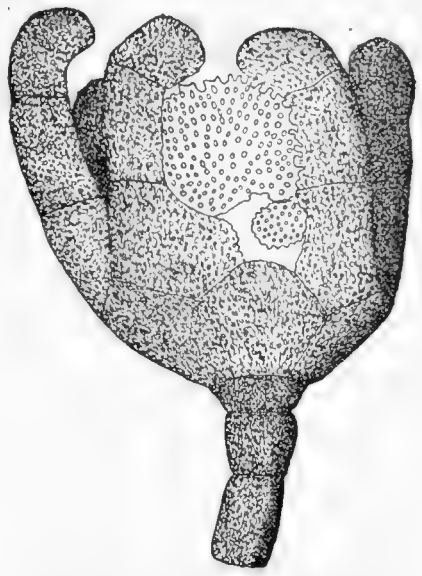

FIG. 8.—Pentacrinoid of *Thaumatometra nutrix*, same stage as that represented in plate XXVIII, figure 4, showing the relations of the anal plate. ×100.

The last stage found is that represented in plate XXVIII, figure 6. Unfortunately not one of these specimens is in good condition, the arms being broken off more or less completely. The first pinnule has appeared; it is on the twelfth arm-joint. The disk has already grown fairly large, the oral plates being now widely separated from the calyx plates. They are of somewhat larger size than usual. The anal cone has been formed and the anal plate remains distinct close to the adjoining oral plate. The cirri are very far advanced in development; those of the first whorl are fully formed, with a conspicuous terminal claw and opposing spine; they consist of 12 joints of about equal length. As usual, the first 5 cirri are radial in position. The second whorl is about to develop, alternating with those of the first whorl. The stalk-joints have now attained their final shape. They are rather short,

not constricted in the middle. The upper 5 joints are gradually widening, the upper one, carrying the cirri, being the widest. A considerable variation, however, occurs in the shape of the stalk, both in the number of stalk-joints and in regard to the shape, especially of the lower joints. Thus, in the stalk figured in plate XXVIII, figure 8, there are only 8 joints besides a ninth (the centrodorsal) which has gone with the detached young Crinoid. Plate XXVIII, figure 7, shows the 3 lower joints of another fully developed Pentacrinoid; here the lower joint is small and wedge-shaped. In the Pentacrinoid figured in plate XXVIII, figure 5, the lower joint is also somewhat wedge-shaped, but evidently would have become considerably larger than the following joints, and in figure 3 the two lower joints would evidently have become larger than the following joints, while in figure 4 the lower joint is much smaller than the second. These differences have something to do with the place to which the Pentacrinoid has attached itself, as a comparison of the figures quoted will show; the wedge-shape of the lower joint (figure 7) is due to the fact that it is attached in the narrow space between two pinnule joints, while the simple shape of the lower joint in figures 6 and 8 is due to the fact that it is attached to a simple surface either on the middle or at the end of the pinnule joint.

The most interesting feature in this Pentacrinoid is, of course, the total absence of the terminal stem-plate, a fact otherwise unknown in Crinoids. The reason for this would seem to be their habit of attaching themselves within the marsupium. In remarkable contrast to this stands *Notocrinus virilis*, with its supplementary terminal stem-plates. Both cases would seem to be in some way abnormal and due only to the special biological conditions of these Pentacrinoids. I should not attach any special importance to the morphology and homologies of the terminal stem-plate of Crinoids in these two cases. But it is, of course, too early to draw definite conclusions regarding this question from the few observations that have as yet been made upon the development of Crinoids. It is a problem for the future.

VII. GENERAL PART.

The researches on the embryonal and postembryonal development of no less than 6 new types of Comatulids put forth above enable us to form a better judgment of the general value of the results obtained from the previous studies in the embryology of Crinoids, these having been based solely upon one type, viz, the genus *Antedon* s. str.; even though three different species of this genus have been the object of these studies (namely, *mediterranea* Lamarck, *adriatica* A. H. Clark, and *bifida* Pennant) they are so closely related that they could hardly be expected to differ essentially in their development. Our previous knowledge accordingly rests only on one single type, and it is then of some value to have the results reached from that one type tested by researches upon other types. As might be expected, some of the results previously regarded as holding for the Crinoids as a whole are now seen to apply only to *Antedon*, but upon the whole the differences are not great, the Comatulids apparently being a very uniform group as regards embryology, in accordance with the fact that, in spite of the great number of genera and families established, this whole group corresponds at most to only a single family of the Crinoids. As A. H. Clark justly says (Monograph of the Existing Crinoids, p. 18), we have here "the curious anomaly of a group which, considered from one point of view is a true class, but considered from another point of view does not even rise to the dignity of a subfamily."[36] Greater deviation from the Comatulid type of development may be expected among the stalked Crinoids, but about this nothing is known as yet.

It is not the intention to enter here on a discussion of the greater questions of Echinoderm morphology and phylogeny. That may be postponed until all the material for the study of Echinoderm development collected by the author has been worked out; and, upon the whole, discussion of these intricate problems may not suffer by waiting for the accumulation of more facts in the ontogeny of the Echinoderms.

1. DEPOSITION OF THE EGGS.

In *Antedon* the eggs are retained in clusters around the genital openings (inclosed in the egg-membrane) until the embryos have developed the ciliated rings and the development has been carried so far that the embryo, almost immediately after the rupture of the egg-membrane, is ready to attach itself

[36] I may also quote from A. H. Clark's "Crinoiden der Antarktis" (Deutsche Südpolar-Exped. XVI, Zoöl., Bd. VIII, 1915, p. 110) the following passage, with which I agree fully: "Daher sind die Comatuliden, rein als integrierendes Element der heutigen marinen Fauna betrachtet, das genaue Äquivalent der Asteroiden, Ophiuriden, Echiniden und Holothurien, während sie phylogenetisch nur eine Abteilung der Pentacrinitiden bilden. Daher wird es notwendig, die anscheinend unlogische Einteilung der Comatuliden in Unterordnungen, Familien Subfamilien u. s. w. anzunehmen, wobei man im Auge behalten muss, dass die ganze ungeheure Reihe von Arten systematisch das Äquivalent der 9 bekannten Genera der Pentacrinitiden ist, . . . und dass zusammen mit diesen 9 Gattungen und *Thiollericrinus* die Comatuliden mit Hinsicht auf die phylogenetische Folge der Crinoidentypen nur eine einzige Familie bilden."

and metamorphose into the Pentacrinoid. That this is a general rule among the Comatulids may be concluded from the fact that in so many cases the Pentacrinoids are found attached to the cirri of the mother specimen, which would not be the case were the eggs free. The only exceptions from this rule, so far as hitherto known, are *Tropiometra* on one side and the 3 viviparous forms on the other side. In *Tropiometra* the eggs are not retained on the pinnules, but either drop to the bottom or, what is more probable, float in the water. The special development of the egg-membrane into a densely spinous structure, recalling what is found in some pelagic fish eggs, as those of *Callionymus*, decidedly points in the direction of the eggs being pelagic.

Whether pelagic or, in any case, free eggs are to be found in other Comatulids is hard to predict.[37] One might be inclined to expect them in forms with small eggs, as are found, according to A. H. Clark, especially in the Thalassometrids; but then the difference in the size of the eggs of Comatulids does not appear to be in any way conspicuous. Thus in *Antedon adriatica* the eggs are (Seeliger, p. 173) about 0.25 mm. or almost exactly the same size as those of *Tropiometra*, the former having them retained on the pinnulæ, the latter having them free. This fact would seem to indicate that the size of the eggs is of no great value in this regard. More importance may be attached to the geographical distribution, free pelagic eggs and larvæ being more likely found in species with a wide distribution than in those having a more restricted occurrence. It was, in fact, the wide distribution of *Tropiometra carinata* that led A. H. Clark to suggest that this species might possibly have a true pelagic larva (see page 3). Although this suggestion did not hold good, the reasoning was correct; the developmental history of this species did give the clue to its exceptional distribution. In the same way, Clark is probably right in concluding, from the markedly solitary habit of the Thalassometrids, combined with the fact that the egg is somewhat smaller than usual in Comatulids, that these forms must have a prolonged pelagic stage,[38] either the eggs being pelagic or only the larvæ having a prolonged free-swimming period.

Of special interest is the discovery of two new cases of care of the brood in the Comatulids *Notocrinus virilis* and *Thaumatometra nutrix*, only one single case, *Isometra vivipara*, being known previously.[39] The latter evidently represents the least specialized case. Here the larvæ still retain their typical

[37] Quite recently, also, *Antedon petasus* (Düben and Koren) has been found to have free eggs like *Tropiometra* (Th. Mortensen: Notes on the development and the larval forms of some Scandinavian Echinoderms. Vid. Medd., vol. 71, 1920, p. 150).

[38] A. H. Clark. On a collection of Crinoids from the Zoölogical Museum of Copenhagen, Vid. Medd., 1909, p. 122.

[39] Possibly *Himerometra pædophora* H. L. Clark (according to A. H. Clark *Ptilometra mülleri* A. H. Clark) also protects its brood. H. L. Clark has found a number of young Pentacrinoids attached to the pinnules of the species. (Scientif. Res. of the trawling expedition of H. M. C. S. *Thetis*, Echinodermata. Mem. Austral., Mus., IV, 1909, p. 525.) But he does not give any more detailed information of the way in which they are attached or whether the eggs are kept in the usual way, in clusters round the genital openings or in a special marsupium. Judging from his figure of the youngest Pentacrinoid (plate XLVII, figure 7) it would appear that they are attached to the dorsal side of the pinnules, so that this case in no way corresponds to what obtains in *Thaumatometra nutrix*.

structure. The ciliated bands are well developed and the larvæ, on leaving the marsupium, must swim a little distance. This step is indeed not so great from the usual case in Comatulids, the embryos being kept on the pinnules until they are nearly ready to attach and, probably, in many cases simply sinking down from the pinnules to the cirri to attach themselves there. *Indeed, it may be said that care of the brood is the normal fact in Comatulids, Tropiometra and Antedon petasus being the only known exceptions.* If it were the usual condition in Comatulids that the eggs were free (or pelagic, as in *Tropiometra*) and then a case was discovered where the eggs and embryos remained attached to the pinnules until the fixation stage is reached, then no doubt anybody would designate that as a case of care of the brood.[40] The three "viviparous" Crinoids named above accordingly represent only further steps in the viviparous habit common to most Comatulids, the formation of a special marsupium being the most essential new feature. In *Isometra* the larvæ are not very much influenced thereby. *Notocrinus* represents a much more specialized case, the larvæ having lost their ciliated bands and probably never leaving the marsupium. At any rate, this is the case in *Thaumatometra nutrix*, where the Pentacrinoids remain attached to the pinnule, just protruding the head through the opening of the marsupium. The same is probably the case in *Notocrinus*. Unfortunately the larva of *Thaumatometra nutrix* is unknown, but it may be expected that it will prove to have lost the ciliated bands, as has the larva of *Notocrinus*.

2. THE CLEAVAGE.

That the total regular cleavage, as found in *Antedon* and *Tropiometra*, will prove to be of general occurrence among the Comatulids there is no reason to doubt. The remarkable meroblastic cleavage of *Isometra vivipara* is evidently an exceptional case, due to the special conditions afforded by the viviparous habit of this species. It may be reasonably expected that a similar meroblastic cleavage will be found to occur also in *Notocrinus* and *Thaumatometra nutrix*, where the conditions for the developing egg are similar. Upon the whole, viviparity in Echinoderms evidently has some connection with the meroblastic type of cleavage. It has been observed only in viviparous Echinoderms, namely, besides *Isometra vivipara*, in the following species: *Cucumaria glacialis* Ljungman, *Amphiura vivipara* H. L. Clark, *Hypsiechinus coronatus* Mortensen, *Abatus cavernosus* (Philippi), and *Amphipneustes kœhleri* Mortensen, and it can hardly be doubted that it will be found in many other viviparous Echinoderms, though not in all of them; in *Amphiura squamata* the cleavage is total, though irregular, and it is also total and quite regular[41] in *Synapta vivipara* [*Synaptula hydriformis* (Lesueur)]. The eggs of the

[40] In fact, Ludwig in his paper "Brutpflege bei Echinodermen" (Zoöl. Jahrbücher. Suppl. VII, p. 699, 1904, counts *Antedon rosacea* among the Echinoderms which protect their brood.

[41] H. L. Clark. *Synapta vivipara:* a contribution to the morphology of Echinoderms, Mem. Boston Soc. V, p. 60, 1898.

latter species are 0.2 mm. in diameter, while those of *Amphiura squamata* are about 0.1 mm.[42]

It is not the size of the egg that is the main reason of the meroblastic cleavage. It is true, the eggs of *Abatus cavernosus* and *Amphipneustes kœhleri* are about 1.2 mm. in diameter and those of *Cucumaria glacialis* 1 mm., and thus of a very considerable size, but the eggs of *Hypsiechinus coronatus* are only 0.5 mm., not larger than those of *Heliocidaris erythrogramma* (Valenciennes), which has a total and regular cleavage.[43] Similarly the eggs of the meroblastic *Amphiura vivipara* are only 0.5 mm., while those of *Ophioderma brevispinum* (Say) with total, regular cleavage are 0.3 mm.[44] and the eggs of *Isometra vivipara* are only 0.3 mm. in diameter, very inconsiderably larger than those of *Antedon adriatica* with total, regular cleavage, while those of *Antedon bifida* are, according to Wyville Thomson,[45] even 0.5 mm. or almost twice the size of the eggs of *Isometra*. It can be said only that the facts hitherto known tend to indicate that *a meroblastic cleavage is probably the rule in such viviparous Echinoderms as have large and yolk-laden eggs*, while in those viviparous forms with small eggs, less rich in yolk, the cleavage remains total and regular, as typical in Echinoderms.

3. THE FORMATION OF THE ENTODERM; THE GASTRULA.

It is rather surprising that there should prove to be considerable difference in the formation of the entoderm in *Antedon* and *Tropiometra*. In both of them a regular invagination takes place, but in *Tropiometra* cells are wandering into the blastocœl, presumably from various areas of the ectoderm, before invagination takes place. These cells lie loosely in the blastocœl cavity, like mesenchyme cells. Then the invagination takes place and all the loose cells unite with the archenteron. The entoderm cells thus appear to be of double origin. In *Antedon* no such inwandering of cells from the ectoderm takes place, the entoderm originating alone from the invagination.

It is, of course, impossible to say which is the general course of entoderm formation in Comatulids, so long as our knowledge is confined to *Antedon* and *Tropiometra* each having its own modus. The third species in which entoderm formation has been studied, *Isometra vivipara*, differs very markedly from the two other forms in this regard, the entoderm being formed by a gradual differentiation, a sort of delamination, no invagination taking place. That this is a consequence of the meroblastic cleavage is evident enough, and

[42] It is a curious fact that there is no direct statement of the size of the egg in any of the rather numerous papers dealing with the embryology of *Amphiura squamata*. Only Fewkes gives the size of the blastula as 0.15 mm. and MacBride states that the earliest larval stage examined by him was 0.2 mm.

[43] Th. Mortensen. Preliminary note on the remarkable shortened development of an Australian sea-urchin, *Toxocidaris erythrogrammus*. Proc. Linn. Soc. N. S. Wales, XL, p. 204, 1915.

[44] Caswell Grave. *Ophiura brevispina*. Memoirs from the Biol. Laboratory of the Johns Hopkins University, IV, 1900. Idem., *Ophiura brevispina*. II. An embryological contribution and a study of the effect of yolk substance upon development and developmental processes. Journ. of Morphology, 27, 1916.

[45] Wyville Thomson. On the embryogeny of *Antedon rosaceus* Linck (*Comatula rosacea* of Lamarck), Phil. Trans., vol. 155, p. 519, 1865.

there is no reason to think that this manner of entoderm formation should occur in any Crinoid with total cleavage.

A characteristic feature of both *Tropiometra* and *Antedon* is found in the shape of the archenteron, which is curved in its upper end. Seeliger has ascertained that in *Antedon* the curvature is directed against the ventral side; in *Tropiometra* the orientation could not be ascertained, but there is, evidently, no reason to doubt that it is in conformity with what occurs in *Antedon*. In *Isometra vivipara* such curvature of the archenteron is not distinct.

It seems very probable that this feature is of some morphological importance. It is a general feature in Echinoderm larvæ that the upper end of the archenteron curves towards the ventral surface in order to meet the invagination, which forms the larval mouth. The suggestion then occurs that the curvature of the archenteron in Comatulids is a morphological reminiscence of a stage in the Crinoid phylogeny when a larval mouth did really develop in that position. The morphological meaning of the vestibulary invagination is, doubtless, that it represents the larval mouth.[46] That it does not open till later, at the metamorphosis, is due to the fact that the egg contains sufficient nutrition for the developing embryo. If true pelagic Crinoid larvæ really exist, comparable to the *Pluteus*, *Bipinnaria*, and *Auricularia* larvæ, of other Echinoderms, self-feeding like these, not subsisting alone on the yolk substance contained in the egg, it will doubtless be found that the larval mouth occurs on the ventral side as in other Echinoderm larvæ, in the place where the vestibulary invagination occurs in the Comatulid larvæ. The fact that the mouth of the Pentacrinoid does open in the bottom of the vestibulum is in itself not a direct proof of the homology with the larval mouth. Also, in the bottom of the amnion cavity of the Echinoid larva the final mouth opens, but the amnion is evidently not at all homologous with the vestibulum of the Crinoid larva.

A noticeable difference between *Antedon* and *Tropiometra* is found in the shape of the blastopore, which is an elongate, transverse slit in *Antedon*, while it is a small, round opening in *Tropiometra*. At the present state of our knowledge of Crinoid embryology, it is of course impossible to say which of these shapes represents the more primitive condition or which is the more general in Comatulids.

4. THE ENTEROCŒL.

In the three forms in which the formation of the enterocœl has been studied, *Antedon*, *Tropiometra*, and *Isometra*, it proceeds exactly in the same way. Immediately after the closure of the blastoporus the archenteron divides into an upper and lower part, the upper forming the entoderm and the hydrocœl, the lower giving rise to the enterocœl. The latter becomes transversely elongated, the middle part narrowing into a thin canal connecting the two widening ends and soon the connecting canal atrophies. The two

[46] Thus far it is not so "sehr unzweckmässig Larvenmund genannt." (Seeliger, p. 195.)

vesicles, the right and left enterocœl vesicles, are thus separated from one another, and gradually occupy their final place, the right at the dorsal side, the left at the posterior, which later becomes the anterior end.

Although the process of the enterocœl formation has not been followed in *Compsometra* and *Notocrinus*, the arrangement of the enterocœl vesicles in the larval stages studied of these, identical with the arrangement found in the corresponding stages of the three other types, leaves no doubt that the whole process is the same in all. There is, then, fair evidence that this will prove to hold good of the Comatulids as a whole.[47]

In one point, however, *Antedon* differs very markedly from both *Tropiometra* and *Isometra*. In *Antedon* there is a pair of posterior prolongations from the anterior part of the archenteron embracing the narrow connecting canal of the two enterocœl vesicles, sometimes even uniting below this canal, which thus goes through a ring (Bury, Seeliger). In *Tropiometra* and *Isometra* I have found no trace of such posterior prolongations from the anterior part of the archenteron. *This complicated structure is, then, not of general occurrence in the embryology of Comatulids.* It is hard to see the reason of its occurrence in *Antedon*, and upon the whole, its morphological value. It may be a morphological ancestral reminiscence; at least it is hardly conceivable that such a complicated structure, apparently without any special importance, should have originated in this genus, while on the other hand it is not so inconceivable that an ancestral reminiscence from it should have been retained in one form and dropped in others. In any case it is highly interesting to note this rather conspicuous difference in the early developmental processes between such nearly related forms as *Antedon* and *Tropiometra*. In *Isometra*, which is still nearer to *Antedon* than *Tropiometra*, belonging to the same family as the former, the absence of the posterior prolongations might perhaps be due to the unusual embryological conditions, and it would certainly be unwise to lay any stress thereon if that were an isolated case; but together with *Tropiometra*, in which the embryological conditions are as normal as possible, this case also counts.

5. THE HYDROCŒL.

Although the development of the hydrocœl could not be followed in detail from its origin in any of the forms studied in the present memoir, such stages as were observed are in perfect accordance with the corresponding ones in *Antedon* as known especially through the researches of Seeliger, and there is no reason to doubt that the hydrocœl in the Comatulids as a whole originates in the same way as a pouch from the upper part of the divided archenteron.[48] From the vesicle thus separated off, lying on the ventral side, proceeds an anterior prolongation, the parietal canal, which in its turn is separated off

[47] In *Antedon petasus* the enterocœl formation appears to be quite different (comp. the author's paper quoted on p. 54).

[48] *Antedon petasus* perhaps makes an exception also in this regard.

from the hydrocœl and then gains an outer opening, the hydropore. Later on, about the time of the metamorphosis of the larva into the Pentacrinoid, the hydrocœl, which has gradually assumed the shape of a horseshoe, the ends of which afterwards join one another so as to form a hydrocœl ring, comes again into connection with the parietal canal by means of the stone canal arising from one end of the hydrocœl. The stone canal arises before the lumen of the hydrocœl fuses into a ring.

The parietal canal has a distinct anterior prolongation towards the apical end of the larva in *Antedon*, as well as in *Compsometra*, *Isometra*, and *Notocrinus*, but not in *Tropiometra*. This is then again a feature of no general value in the embryology of Comatulids.

Russo [49] maintains that the parietal canal does not separate off from the hydrocœl in *Antedon*. As I have said (page 13), this statement of Russo can not be held as a proof against Seeliger's direct statement that it does separate from the hydrocœl. The fact that Russo has *not* observed the parietal canal separate off from the hydrocœl can not weigh against the careful observations of Seeliger, with which my own observations on *Tropiometra*, *Compsometra*, *Isometra*, and *Notocrinus* are in perfect accord. There can therefore hardly be any doubt that *it is a general rule in Comatulids that the parietal canal separates from the hydrocœl*. As previously stated (page 13), figure 12, plate II, of Russo's memoir, to which he refers specially as proving the connection between the hydrocœl and the parietal canal, evidently shows the opening of the stone canal into the parietal canal—that is to say, the secondarily established connection between the two vesicles.

Very interesting facts are connected with the hydropore. Russo maintains that in *Antedon* the original hydropore and pore canal disappear 3 to 4 days after the fixation of the larva. After 3 or 4 days more a definitive hydropore and pore canal ("canale petroso secondario") develop, formed by an ectodermal invagination. This organ of the Crinoid is thus an entirely new formation, and, as Russo emphatically maintains, not homologous with the madreporite and pore canal of other Echinoderms.

Regarding this point, my own observations are as follows: In *Tropiometra* no outer opening of the hydropore was found before the young Pentacrinoid stage; whether it then disappears and is formed again in a later Pentacrinoid stage remains uncertain for want of material of such later stages. In *Compsometra* the hydropore is formed during the larval stage; it is probably closed in the young Pentacrinoid, but it can not be ascertained beyond doubt on the preparations *in toto*, and there is no material of these stages for sectioning. In *Isometra vivipara* the hydropore is formed early in the larval stage *in some specimens, but not in all;* however, the possibility can not be denied that the hydropore would have developed in all of them during the larval stage, there being perhaps only some variation in the time of its appearance

[49] A. Russo. Studii su gli Echinodermi. Atti Accad. Gioenia, XII, 1902, pp. 47, 48.

(see page 37). The main thing is that the hydropore is certainly formed during the early larval stage, at least in some specimens (plate xv, figure 9). In the fully formed larva, ready to leave the marsupium, the hydropore is obliterated, and in the young Pentacrinoid the pore canal has no outer opening (plate xix, figures 1 to 4). At the time when the arms are beginning to branch, *a new hydropore is formed* (plate xx, figure 3; plate xxi, figure 3). In *Notocrinus* the hydropore is closed in the larval stage (plate xxiv, figure 9; plate xxvi, figure 4); in *Florometra* it appears to be closed in the young Pentacrinoid (plate xxvii, figure 7).

While my observations thus (partly, at least) confirm those of Russo regarding the obliteration of the hydropore and the formation of a new pore at a later stage, they do not confirm his statement that the pore canal itself also disappears and that a new pore canal is formed by an ectodermal invagination. The pore canal was always found to be distinct; it is only its outer opening that disappears. Whether the new hydropore is really formed by an ectodermal invagination seems perhaps a little doubtful. The figures given by Russo (plate ii, figures 34 and 36) do not appear to be a sufficient proof of this; they show only that the outer end of the canal has a thickened epithelium. In view of the fact that the original pore canal persists in the other Crinoids examined, and that Seeliger says nothing about its disappearance in *Antedon*,[50] it seems probable that Russo was mistaken in finding it formed anew by an ectodermal invagination, and one feels little inclined to regard his observations and figures as definite proof that the new hydropore itself is formed in this way. My own material is not sufficiently well preserved histologically to give a definite solution to a question so difficult to settle.

The facts hitherto brought to light seem to support the conclusion that it is a rule in Comatulids that *the original hydropore disappears soon after the fixation of the larva*, sometimes even before the fixation, and that *then a new hydropore is formed*, perhaps by an ectodermal invagination. It does not appear that this temporary obliteration of the pore is so important a fact as to necessitate the conclusion that the madreporic pores (together with the later developing additional pores and pore canals) of Crinoids are not homologous with those of the madreporic system of other Echinoderms. Also in some Euryalids new madreporic systems develop, so that there is one in each interradius; but there is certainly no reason to hold the morphological value of these secondarily developed madreporites as quite different from that of the primary one.

Tropiometra appears to be exceptional in having no hydropore in the larval stage; the material available is insufficient to ascertain whether this holds good also for *Notocrinus*.

[50] It should, however, be mentioned that Bury (p. 278) states that "during the transition to the 'Cystid' stage the walls of the parietal canal share in the general histolysis."

The development of the tentacles was found in conformity with what is known for *Antedon*. The primary tentacle remains distinct for some time in the first bifurcation of the arm (plate XXI, figure 7) until it becomes absorbed. Of the triplets of tentacles the distal tentacle is the first to develop.[51] There is no reason to doubt that this will prove the general rule in Comatulids.

A. H. Clark, in his "Monograph of the existing Crinoids" (pages 313, 314), asserts as an established fact that the infrabasals of Crinoids correspond to the oculars of the Echinoids, and makes the following startling statement respecting the radial water tubes of the Crinoids:

> "In the Crinoids the infrabasals lie at the distal end of the radial water tube, in exactly the same position as the oculars are found in the Echinoids. The water tube of the arms is in reality merely a side branch from the true water tube, which runs around the side of the body from the circumoral ring to the infrabasals, and has no further morphological significance. Though in the later crinoids the water tube leading from the edge of the disk to the infrabasals is insignificant when compared with that of the arms, in the earlier forms, in which the calyx was very large and the arms very short, the latter must have been very insignificant when compared with the former. . . . . It should be emphasized that the water tube grows not only outward into the arm (an offshoot of purely secondary morphological importance) but downward into the centrodorsal; in other words, it eventually comes into its true relations with the infrabasals by growing beyond the radials."

I must protest against this representation of the development of the radial water tubes and the relations between infrabasals and hydrocœl. There is not the slightest indication in the developmental history of the Crinoids that the radial water tubes grow downwards into the calyx to meet the infrabasals, and that the radial water tube of the arms is only a side branch from such a downwardly directed main tube. This is only an imaginary construction arising from the desire to find support for the homology that is maintained to exist between the oculars of Echinoids and the infrabasals of Crinoids—an homology for which there is no real support.

6. THE ENTODERM; HISTOLYSIS.

The formation of the stomach and intestine in the forms here studied is in perfect accordance with the results obtained in *Antedon* by Seeliger and his predecessors, so that *Antedon* probably represents the type of formation of these organs common to all Comatulids (unless there exist Comatulids with a typical pelagic, self-feeding larva). There is only reason to repeat here that Seeliger's view, that the mass of small cells filling the lumen of the entoderm during the metamorphosis from the larva to the Pentacrinoid serves as nourishment for the embryo, is evidently erroneous.[52] As maintained by Bury, and as becomes especially apparent from a comparison with what

[51] The same observations were made by Perrier in his "Mémoire sur l'organisation et le développement de la Comatule de la Méditerranée" (Nouv. Arch. Mus. d'hist. nat. Paris, x, 1889, p. 221, plate 2, fig. 18.)

[52] Seeliger's view is also accepted by MacBride in his "Text-book of Embryology," I, p. 552, 1914.

occurs during the metamorphosis of Echinoid larvæ, *the entoderm and the other larval tissues undergo a process of histolysis during the metamorphosis,* and the small cells filling the lumen of the entoderm are the phagocytes which produce the histolysis. The fact that they occur also in the mesoderm and upon the whole in all the tissues of the larva is in good accordance with this interpretation, while it is unintelligible from the explanation given by Seeliger. Also, on purely logical grounds, such a multiplication of cells in order to serve as food is quite unreasonable.

It is noticeable that the phagocytes were found to occur in much smaller numbers in *Tropiometra* than in *Antedon* and *Isometra,* but it is hardly possible to give an explanation of this difference at the present stage of our knowledge of Crinoid development.

7. THE PRIMARY GONAD.

While there is no reason to enter on a discussion of the development of the cœlom and its derivatives, the chambered organ and the axial gland, the present researches being entirely in accordance with the observations of Seeliger in this regard, there is something to say concerning the formation which has been designated as the "primary gonad."

It is the merit of Russo to have called attention to this organ. In his "Studii su gli Echinodermi" (pages 10 to 14) he shows that in the anal interradius there appears a small, distinctly limited group of cells, developing in the mesentery. It corresponds exactly to the developing gonad of the Holothurians, and Russo therefore concludes that it is really a gonad. But while in the Holothurians it develops into the definitive genital organ, it disappears completely in the Crinoid before the detaching of the young Crinoid from the stalk, and a new, secondary gonad is formed, viz, the axial organ, from which the definitive genital organs in the pinnules develop.[53] The primary gonad is an organ of the greatest morphological value, from the presence of which it may be concluded that in the ancestors of the Crinoids there was a single genital organ in the anal interradius. Evidently this was the case in at least some of the Cystids, as may be concluded from the presence of a pore besides the madreporite between the mouth and anal opening, especially in the most primitive of all Cystids, *Aristocystis.* We have herein an additional proof that the Crinoids are derived from the Cystids. The existence of this primary gonad in the Crinoids also indicates a closer relationship between the Holothurians and the Crinoids, while the Asteroids, Ophiuroids, and Echinoids stand more apart.

My own observations regarding this primary gonad are in accord with those of Russo. The less satisfactory histological preservation of my material

[53] Russo (p. 12) further states that a new group of sexual elements develop from the peritoneal cells at the esophagus, which forms a series of hollow genital tubes ("cordoni genitali") round the esophagus, that connect with the axial organ. From this compound structure the genital tubes of the arms and pinnules proceed. I have not been able to verify these observations on the material available for the present studies.

has made it very difficult to discern this minute structure in the sections; but there can hardly be any doubt that the small group of cells seen in the mesentery in plate VI, figure 9, from a young Pentacrinoid of *Tropiometra*, is this gonad. In the young Pentacrinoid of *Compsometra serrata* the primary gonad is seen rather distinctly (plate XII, figure 5). In *Isometra vivipara* it is very distinctly seen in the specimen figured in plate XXI, figure 6. In *Florometra* it is small and indistinct. Finally, I have found it distinct also in *Antedon bifida*.

The present observations thus seem to show that this *primary gonad develops as a rule in the young Pentacrinoids of Comatulids, to be absorbed very soon, the genital organs arising as a new structure in connection with the axial gland.* The primary gonad appears merely as a rudimentary organ, an ancestral reminiscence, being of no physiological value, but of the highest morphological interest. I am inclined to think that the conclusions drawn by Russo essentially from this fact respecting the relations between Crinoids and Holothurians are correct.

8. THE ECTODERM; LARVAL NERVOUS SYSTEM.

The present observations, although checked to some degree by the unsatisfactory histological preservation of the material, are in accordance with those of Seeliger, giving the curious result that the larval ectoderm dissolves, the cells wandering into the mesodermal tissue. The epithelium of the disk and ambulacral furrows of the adult Comatulid are derived from the epithelium of the vestibulum. The dorsal side of the adult *Antedon*, and doubtless of Comatulids as a whole, entirely lacks an epithelial covering, in accordance with the fact that the larval ectoderm disappears.

The remarkable character of the ectoderm in the larva of *Notocrinus* (see page 50) is, of course, due to the special conditions of the developing embryo, which must be supposed to absorb nourishment through the skin, whether this nourishment consists of unfertilized, disintegrated eggs, or of some other nourishing substance secreted by the mother specimen. In connection herewith stands, doubtless, the existence in this species of special glandular structures which originate as outgrowths from the cœlom and open outwards in the posterior end of the larva (see page 52). It is especially noticeable that in *Isometra vivipara* there is nothing corresponding to this. The ectoderm is there of the same structure as in *Antedon* and *Tropiometra* in spite of the fact that the embryo develops within a marsupium. But in *Isometra* the embryo remains within the egg membrane till ready to swim out, and thus, evidently, is unable to absorb any nourishment through the skin, while in *Notocrinus* the egg membrane ruptures at an early stage of the development, so that the ectoderm is directly in contact with the nourishing fluid.

The larval nervous system was found to be well developed in both *Tropiometra*, *Compsometra*, and *Isometra*, and of the same general character as in

Antedon. This may then be regarded as holding good for the Comatulid larvæ as a whole. The fact is very noticeable that the larva of *Notocrinus* has the nervous system exceptionally well developed, in spite of its having no vibratile bands and that it remains inclosed in a marsupium, giving it no space to move. It is hard to see why this larva should have the nervous system so well developed.

9. THE SHAPE OF THE LARVA; VIBRATILE BANDS; VESTIBULUM.

All the Crinoid larvæ thus far known have the same shape as the *Antedon* larva, being simple and barrel-shaped, and provided with a number of ciliated bands. Thus this larva corresponds closely to the *Dipleurula*, the hypothetic bilateral ancestor of Echinoderms. The great question, then, is whether this larval shape is a primary feature, the larva thus representing the original type of Echinoderm larvæ, or whether it is a secondarily acquired form. The interesting observations of Caswell Grave,[54] that a similar arrangement of the ciliated band in rings may occur in both Ophiurids and Echinoids in the metamorphosis stage, a sort of pupa-stage, comparable with that known in the Holothurians already from Joh. Müller's researches, have an important bearing on this question. Such barrel-shaped larvæ, provided with ciliated rings only, occur likewise in *Cucumaria* (and very probably in Dendrochirote Holothurians upon the whole) and in some Ophiurids (besides *Ophioderma brevispinum* in *Ophionereis*[55] *squamulosa* Koehler, and evidently also in the "wurmförmige Asterien Larve" of Joh. Müller).[56] These facts, combined, would seem to point in the direction of this simple larval type being the primary, and that the other types of Echinoderm larvæ (*Auricularia*, *Bipinnaria*, *Ophiopluteus*, and *Echinopluteus*) are secondary adaptations to the pelagic life, as Caswell Grave maintains. This will not mean, of course, that we can not expect to find true pelagic larvæ among Crinoids, corresponding to the other types of pelagic Echinoderm larvæ. As I have said above (page 3), I expect that such will be found, especially among the stalked Crinoids.[57]

The number of ciliated bands is either 4 or 5. In the development of the anterior one of these bands there is some variation. In *Antedon adriatica* and *A. mediterranea* there are 5 distinct bands (Bury, Seeliger), while in *Antedon bifida* there are only 4, according to Wyville Thomson. Whether the latter statement is correct remains to be ascertained, but it is certain that in *Tropiometra* there are only 4 bands, the anterior one lacking completely. In *Compsometra* the anterior band is fairly distinct on the dorsal

[54] Caswell Grave. On the occurrence among Echinoderms of larvæ with cilia arranged in transverse rings, with a suggestion as to their significance. Biol. Bulletin, 1903, p. 169.

[55] Th. Mortensen. On the development of some West Indian Echinoderms. Year Book No. 15 of the Carnegie Institution of Washington, p. 193. 1916.

[56] Joh. Müller. Abhandlungen über die Larven und die Metamorphose der Echinodermen. III, p. 26; IV, p. 40; VI, taf. 1, fig. 15–16 (Abh. d. Akad. d. Wiss. Berlin a. d. Jahren 1848–1853).

[57] MacBride (Text-book of Embryology, I, 1914, p. 560) also expects that true pelagic larvæ will be found in such Crinoids as have small yolkless eggs.

side (plate XII, figure 2); in *Isometra* a faint trace of the anterior band is seen on the dorsal side. In no case have I seen the anterior band so distinct as in the Mediterranean species of *Antedon*, as represented in Seeliger's and Bury's figures. Whether the typical (or original) number is 4 or 5, is hardly to be ascertained at the present stage of our knowledge of the Crinoid larvæ.

Very interesting is the indication of an extra band off the anterior end of the vestibulary invagination seen in the larva of *Isometra* (plate XXII, figure 2), but, this is probably not a character of any greater value to the morphology of the Crinoid larvæ, and the same evidently applies to the fact that vibratile bands are entirely absent in the larva of *Notocrinus*. Both these cases apparently are adaptations to the special life-conditions of these larvæ.

The vestibulum is always situated between the second and third band. In the course of development it may either press the third band downwards, as is the case in *Isometra*, or it may pass across the third band, which thus becomes interrupted in the ventral midline, as in *Compsometra* and *Tropiometra;* also in *Antedon*, according to Bury and Wyville Thomson. The figures given by Seeliger (taf. 16, figures 65 to 67) are rather too diagrammatic to show clearly the relations to the vestibulary invagination of said band, and his text (page 233) is not very clear on this point, but it seems to be his meaning that the band appears interrupted but can be discerned inside the invagination. This may also be the case in *Tropiometra* (see page 11).

Whether the relation of this third band to the vestibulary invagination is of specific or generic value can not be ascertained at the present state of our knowledge. At least it appears to be constant within the species.

The shape of the vestibulum is somewhat unusual in *Isometra* and *Notocrinus*, being a quite narrow slit, while in the other larvæ thus far known it is a broad, oval depression. This difference is evidently due to the special life-conditions of these two larvæ, which probably also have some bearing on the peculiar fact that the lumen of the vestibulum of the *Isometra* larva obliterates completely at the closure, to reappear again when it has assumed its final place at the posterior, or future anterior, end of the metamorphosing larva.

The suctorial disk is very indistinct in *Tropiometra*, a feature hard to understand, as it needs means of fixation just as well as do the other Crinoid larvæ. On the other hand, this feeble development of the suctorial disk would appear to explain the failure of so many of the larvæ in attaching themselves (page 14). The shape of a half-circle assumed by the suctorial disk of the *Notocrinus* larva must evidently be a special adaptation to suit the way of fixation (probably within the marsupium) adopted by this larva, while the *Isometra* larva, which attaches itself in the usual way, has the suctorial disk normally developed.

10. THE SKELETON.

The order of appearance of the primary skeletal plates in the Crinoids studied here is in accordance with what is known from *Antedon*, the oral and basal plates, together with the terminal stem-plates, being the first to appear, the two sets of calycinal plates lying originally in two half-circles open ventrally, not exactly opposite one another, and assuming their final position only about the time of the metamorphosis. The plates of each set do not develop quite contemporaneously, as is seen in figures 1 and 2 of plate IX and figure 3 of plate XII, but it was not found possible to ascertain their exact order of appearance. After the orals and basals follow the radialia, the costals, and axillaries; a remarkable exception to this general rule is afforded by *Florometra serratissima*, in which the axillaries appear before the radials, the costals being the last to develop (plate XXVII, figure 6).

According to Perrier (*op. cit.*, pages 219, 220), the arms do not develop contemporaneously, but successively, in a definite order, as illustrated by his figure 18 of plate 2. The observations recorded in the present memoir on *Compsometra*, *Isometra*, and *Thaumatometra*, do not lend the slightest support to this statement and the same holds good for the observations previously recorded on the Pentacrinoids of *Hathrometra prolixa*,[58] as well as the observations of M. Sars on *Antedon* (*Hathrometra*) *sarsi*[59] and of Wyville Thomson and W. B. Carpenter on *Antedon bifida*. Also the figure of a Pentacrinoid of *Comactinia meridionalis*, figured by A. H. Clark, in his "Monograph of the Existing Crinoids" (page 317), shows the young arms equally developed; and the same is the case in the Pentacrinoids figured by P. H. Carpenter in his *Challenger* Comatulids, plate XIV. There can then be no doubt that *it is a general rule in Comatulids that the arms develop contemporaneously*. Even in *Florometra*, where the radials, costals, and axillaries are developed successively, not at the same time in all the radii, the arms are all of the same size in the young Pentacrinoids (plate XXVII, figure 5). The Pentacrinoid represented by Perrier in the figure quoted is evidently abnormal.

Regarding the *oralia*, it should be mentioned that the observations recorded in the present memoir are in accordance with the statement of A. H. Clark (Monograph of the Existing Crinoids, page 340), that in the macrophreate forms they are concave with out-turned edges, while in the oligophreate they are flat or convex, the edges not out-turned. This latter form they have in the oligophreate *Tropiometra*, while in *Compsometra*, *Isometra*, *Florometra*, and *Thaumatometra*, all macrophreate (of the family *Antedonidæ*), they have the markedly out-turned edges. This difference between the Pentacrinoids of the two main groups of Comatulids thus really

[58] Th. Mortensen. Report on the Echinoderms collected by the Danmark-Expedition at Northeast Greenland, Medd. om Grønland, XLV, 1910.

[59] M. Sars. Mémoires pour servir à la connaissance des Crinoides vivants, pl. v, 1868.

appears to be valid enough, a fact of no small interest and affording proof that this division of the great Comatulid group is in conformity with their natural relationship.

The *anal plate* of Comatulids has of late been maintained by Dr. A. H. Clark to represent the radianal (Monograph of the Existing Crinoids, page 331), while it was hitherto supposed to be homologous with the anal X of Crinoidea Inadunata and Flexibilia. Quite recently Dr. F. A. Bather has published a paper on "The homologies of the anal plate in *Antedon*," [60] in which he reaches the result that there is no real support of a homology between this plate and the radianal. Dr. Bather then maintains his old view, that it is the anal X. The observations recorded in the present memoir have some bearing on this question.

The anal plate was found to appear before the right posterior radial in *Compsometra, Isometra,* and *Florometra,* and apparently also in *Tropiometra;* in the latter the radials have not yet appeared in the most advanced of the Pentacrinoids available. In *Thaumatometra* the first appearance of the anal plate could not be made out with full certainty. In the three first-named the *anal plate lies exactly in the radial midline, the right posterior radial forming to the right of it,* more or less distant from the radial midline, which place it gradually occupies, pushing the anal over to the left side, against the adjoining oral. The mode of formation of these two plates is well seen in plate XIII, figure 2 (*Compsometra*), and plate XXVII, figure 3 (*Florometra*). The named radial appears to be always the last of the 5 radials to develop; the order of appearance of the other 4 radials could not be established; in fact, there seems to be no such definite order of their appearance.

In *Antedon bifida* the anal plate is stated by Wyville Thomson (*op. cit.*, p. 540) to develop "upon the appearance of the second and third radial joints." [61] Finding this statement rather remarkable in view of the observations recorded here, I have examined some Pentacrinoids of this species also, the result being that it appears, as in the species named above, before the radials, lying in the radial midline, the right posterior radial forming to the right of it.

It is seen that this is exactly the same way in which the anal and right posterior radial develop in *Promachocrinus kerguelensis*, according to the description given by A. H. Clark in his "Monograph of the Existing Crinoids," page 332.

Having found this, I re-examined the Pentacrinoids of *Hathrometra prolixa,* naturally expecting that the same facts would obtain here, the more so as also in another, unidentified, Pentacrinoid (from the Philippines) the anal and right posterior radial were found to develop in exactly the same way.

[60] Annals & Magaz. Nat. History, ser. 9, vol. I, pp. 294-302, 1918.

[61] W. B. Carpenter (*op. cit.*, p. 727) says only that "between two of the radials, and on the same level with them, an unsymmetrical plate early shows itself, the subsequent relation of which to the vent proves it to be an anal plate."

It proved that (in the specimen figured in plate IX, figure 2, Report on the Echinoderms of Northeast Greenland) the said radial and the anal had both been formed, being of the same size, the radial lying in the radial midline and the anal lying to the left of it, between the oral and basal plates, a partial resorption of the border of these plates having already taken place. Apparently, a most remarkable difference from what obtains in the other Comatulids, so far as hitherto known, was thus found to occur in this form. Fortunately, however, there was another slightly younger specimen, which proves that there is no such difference. In this specimen the anal plate was found reaching from the midradial line somewhat in between the oral and basal to the left of it—the resorption of the edges having already begun; the radial lies to the right of the radial midline, as in the other Comatulids, and is slightly smaller than the anal. There can accordingly be no doubt that the development of these two plates in *Hathrometra prolixa* takes place in the same way as in the other Comatulids thus far known, and it appears to be a general rule among Comatulids that *the anal plate develops in the radial midline, like the true radials, and before any of those, the right posterior radial developing last of all, to the right of the anal plate, outside the radial midline, between the oral and basal, and only later on in the course of growth assuming the radial position, pushing the anal plate out from this place towards the left, against the right lower corner of the posterior oral.*

It is evident that these observations do not give the slightest support to Dr. Clark's view that the anal of the Comatulids represents the radianal; combined with the objections to this assumption raised by Dr. Bather,[62] they may well be said to prove definitely that *the anal plate of Comatulids is not the radianal*, which always originates *below* the right posterior radial, representing, in fact, the lower half of this plate. Do the observations on the development of the anal plate then support the view that it is homologous with the anal X?

As has been sufficiently proved by Dr. Bather "the anal X is intimately connected with the right posterior radius and is, in fact, a radial element of the Crinoid skeleton. Accordingly we should not be surprised in finding it in a radial position in the embryos, and no objection to its homology with the anal X can then be raised from the fact that it does develop in a radial position.

Dr. Bather has suggested that the anal X originated as a plate homologous with a brachial, and moved downwards and sideways into the interradius as the anal structures widened. The fact that this plate is the first to appear and from the first has perfectly the appearance of being one of the radials, does not seem to me to point towards this supposed homology with a brachial, which further necessitates the supposition of a downward

[62] F. A. Bather. Wachsmuth and Springer's Monograph on Crinoids. Fifth Notice (The Anal Plates). Geol. Magaz., Dec. IV, vol. VI, 1899.

movement, of which there is no trace in the embryological development of this plate. The facts here shown regarding the development of the anal plate and the right posterior radial would seem to lead to the conclusion that *the anal plate of Comatulids, which is evidently homologous with the anal X of Crinoidea inadunata and flexibilia, is really a right posterior radial, which is pushed out of its place and replaced by a new, secondarily formed plate, which latter ultimately assumes the shape, place, and functions of a true right posterior radial.* This would mean, simply, that *the original right posterior radial has,* on account of the widening of the anal structures, *been split up into three parts, after a horizontal and a vertical line, the former cutting off a lower part, the radianal (which has disappeared in Comatulids), the upper part being divided by a vertical line into a left part, the anal X, and a right part, the definite right posterior radial.*

I do not venture to maintain this rather unexpected result as definitely proved, but it seems to me that the facts hitherto obtained from the ontogeny of the Comatulids naturally lead to this suggestion as the true morphological value of these plates.

The plates seen in the skin of the ventral surface and between the base of the arms in the young *Tropiometra* are probably simple perisomatic plates without any special morphological value. Such plates, or other plates that could possibly be interpreted as interradials or pararadials, were not observed in any of the other forms studied in the present memoir.

Infrabasalia were observed in *Tropiometra;* there are only 3 of them, of nearly the same size. In *Compsometra serrata* 4 were generally found, rarely 3 or even 2, never 5. In *Isometra vivipara* infrabasalia do not occur, and the same appears to be the case with *Florometra serratissima* and *Thaumatometra nutrix.* In *Notocrinus* there are 4, sometimes 5 infrabasalia.

These observations, together with those previously recorded, prove that *there is no general rule for the presence or absence* of infrabasalia in *Comatulids* since they may be well developed or entirely absent in nearly related genera. Whether also species of the same genus may differ in this regard, I doubt very much; at least evidence is against such supposition. Dr. A. H. Clark is not of this opinion. I may quote the following passage from his paper "A new European Crinoid":[63]

"A review of the facts presented by the study of Comatulid ontogeny shows that *Antedon bifida,* and especially *A. petasus,* represent a phylogenetically more advanced condition than the comparatively primitive Mediterranean forms, and that of these latter the Adriatic species is less developed than the one found from Italy westward. Now the Adriatic form usually has 4 or 5 underbasals, and the one occurring at Naples, Toulon, and Villafranca 3. No underbasals have ever been found in *Antedon bifida,* but this is not at all remarkable, nor does it reflect upon the powers of observation of the able naturalists who have studied it; for if the comparatively slight specialization of *Antedon mediterranea* over the Adriatic

[63] Proc. U. S. Nat. Mus., vol. 38, p. 330, 1910.

species is sufficient to result in the reduction of the number of underbasals from 4 or 5 to 3, we may readily infer that the much greater degree of specialization of *A. bifida* over *A. mediterranea* would result in the elimination of underbasals entirely from the ontogeny of the former. I can see no reason whatever for doubting the accuracy of the work of Wyville Thomson, Perrier, and the two Carpenters, who, none of them, found underbasals in *Antedon bifida*, and I should be greatly surprised if anyone in the future should find them in that species or in *A. petasus*, except perhaps in sporadic instances."

The same view is pronounced a little more cautiously in A. H. Clark's monograph (page 316).

This whole reasoning looks very interesting and ingenious, but it is, nevertheless, quite untenable. *Antedon bifida has indeed very well developed infrabasalia*, in spite of the fact that Allman, Wyville Thomson, Carpenter, and A. H. Clark himself have failed to see them. On dissolving the young Pentacrinoids under the microscope by means of dilute hypochlorite of sodium, it is very easy to see the infrabasals, generally two larger and one smaller plate, lying in the usual place, around the upper stalk-joint. Even in Pentacrinoids so far developed that the arms have begun to branch, they are still distinct. And it is decidedly not in sporadic instances that they occur; I have found them quite constantly developed.

In the light of this fact it is easily seen that the plate which Allman [64] regards as the centrodorsal, in reality represents the infrabasalia; in the stage figured by Allman (the radials have just appeared) the upper stalk-joints are still in new formation, so there is no centrodrosal as yet. Also in Wyville Thomson's figure 1 of plate XXVII, the plate termed *a* represents the infrabasalia, not the centrodorsal, as stated by Wyville Thomson.[65] This has already been correctly interpreted by MacBride, who, in the reproduction given of the said figure in his "Text-book of Embryology," I, page 555, designates it as under basal plates (*SB*), without otherwise saying anything about it.[66]

After this I have no doubt that also *Antedon petasus* will prove to have infrabasalia. The fact that there was no trace of infrabasalia in the Pentacrinoid of this species figured in my "Report on the Echinoderms of Northeast Greenland (page 251, plate X, figure 3), does not prove anything about it, as it would hardly be possible to see these plates at so late a stage without dissolving the calyx, which was, of course, not done, this being the only specimen known till then.[67]

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[64] Allman. On a pre-brachial stage in the development of *Comatula*. Trans. R. Soc. Edinburgh, XXIII, p. 244, 1863.

[65] This figure, as also the other figures in Wyville Thomson's memoir, gives upon the whole a very rough and inaccurate representation of the calcareous plates.

[66] Evidently by a lapsus calami, MacBride states this figure (as also figure 408) to be "after Carpenter" instead of Wyville Thomson.

[67] Recent researches have given the result that *Antedon petasus* has really infrabasalia (comp. the author's paper, "Notes on the development and the larval forms of some Scandinavian Echinoderms." Vid. Medd., vol. 71, 1920, p. 153).

The suggestion would seem to lie at hand that there might perhaps be some relation between the presence of infrabasalia and the position of the first whorl of *cirri*—that the latter would be interradial in position when infrabasalia were present, and *vice versa*. This is, however, not the case. *The first cirri were found to be radial in position in all cases* where their first appearance could be observed, in *Compsometra*, with infrabasalia, as well as in *Isometra* and *Thaumatometra*, without infrabasalia.

The statement of W. B. Carpenter, that the first cirri of *Antedon bifida* are interradial in position, is in disagreement with these observations; but Carpenter was in error here (comp. page 29); the first cirri are really radial in position in *Antedon bifida*, as they are in all Comatulids where their first appearance has been observed. This is evidently a general rule in Comatulids. A. H. Clark (Monograph of the Existing Crinoids, page 269) sees the reason for the fact that the infrabasals have no influence on the position of the cirri in Comatulids (and Pentacrinites), while they have such influence in the fossil monocyclic forms, therein, that in the former group "the infrabasals have entirely lost their primitive character as important parts of the body-wall and have become entirely negligible constituents of the calcareous structure of the organism." I think Clark is right in this explanation.

While the arms develop contemporaneously, this is not the case with the cirri. Any definite rule in the succession of their development, however, does not appear to exist. My observations regarding this point are in accordance with those of W. B. Carpenter (*op. cit.*, page 733), who found the cirrus "opposite to" the anal plate—that is to say, to the right of it—to be generally, but not always, the latest to appear.

Regarding the formation of the cirrus joints, W. B. Carpenter (*op. cit.*, page 733) has come to the conclusion that the new joints are interpolated at the base of the cirrus. A. H. Clark (Monograph of the Existing Crinoids, page 272) states that "the individual ossicles of the cirri are formed as a result of the segmentation and solidification, and simultaneous division of a primitive spicular calcareous investment of the cirri." Both these statements are without foundation in reality. It is very easy to see that in the young, developing cirri at the upper edge of the centrodorsal of a Comatulid, the lowermost joints are the largest; on dissolving such developing cirrus, by means of hypochlorite of sodium under the microscope, it is seen that *the new joints are added at the end of the cirrus;* the same can easily be ascertained on the cirri developing in the Pentacrinoid. *The terminal joint is the last to form; no intercalation of joints takes place, and no "primitive spicular calcareous investment of the cirri" exists.*

It is worth mentioning that the cirrus joints are formed after another type than that of the columnars or arm-joints. They appear at first as simple, round, fenestrated plates, *with no central* perforation; this is formed later on by *absorption* of the central part of the plate (text-figure 9). The

columnars, as is known from Bury's researches, at first have the shape of a half-moon and gradually assume the shape of a ring; the brachials and also the pinnule joints originate as a simple transverse rod, which never assumes the shape of a ring (see page 29).

The order of appearance of the *pinnules* is this: the first to form is that on about the twelfth arm-joint; then follow some more pinnules along the growing-point of the arm, and it is only after some 5 or 6 arm-pinnules have been formed that the oral pinnules begin to appear, that on the second arm-joint being the first of them. Whether the order of appearance of the oral pinnules observed in *Compsometra* (see page 28) has a more general application remains uncertain, but it is evidently a general rule among Comatulids that the oral pinnules do not appear till after some of the arm-pinnules have been formed. This was previously observed by both W. B. Carpenter and Sars.

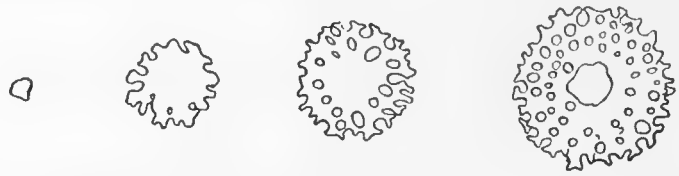

FIG. 9.—Four successive stages in the development of the cirrus joints of *Antedon bifida*. ×180.

Regarding the development of the pinnules, W. B. Carpenter states (*op. cit.*, page 734) that they appear at the growing extremity of the arm "which now presents a bifurcation, the two rami being in the first instance almost equal . . . . One of these rami, however, grows faster than the other, and soon takes a line continuous with that of the axis of the arm, from which the other diverges at an acute angle; so that the former comes to be the proper extension of the arm, whilst the latter soon takes on the characters of a pinnule"—and so on, the point of the arm constantly bifurcating, the branch to the right and left alternately developing into a pinnule, the other branch taking on the character of the arm. This is very clearly expressed thus by MacBride, in his "Text-book of embryology," (page 557): "The apparently single arm of the Crinoid is really a sympodium formed of a succession of the stronger members of successive dichotomies."

There is, however, one serious objection to this representation of the pinnule and arm formation: that it has no foundation in reality. Beyond the axillary there is (in 10-armed Comatulids) no real bifurcation of the arms; *the pinnules appear from the beginning as side branches of the arm*, not as equivalents of the end of the arm. On a closer examination of the growing arm-point it is easily seen that the young pinnule-joints are much smaller than the arm-joints, and they are from their first appearance lying at an angle to the growing arm-point, which latter continues to grow in a straight line, new joints constantly forming at its tip. (Text-figure 10.) It is true,

as Carpenter says, that one of the rami grows faster than the other, but it is the pinnule which grows faster than the arm-joint and soon reaches beyond it, but it never "takes a line continuous with that of the axis of the arm," as Carpenter thought it did. *The Crinoid arm is thus no sympodium, but in reality what it has the appearance of being—a single arm with small alternating side-branches, the pinnules.*

The place of formation of new joints in the growing pinnules was not made out with certainty by Carpenter; he came to the conclusion that "it may be safely assumed that they are not developed at the terminations of the pinnules, since their peculiar terminal hook is formed when as yet the segments are few in number." The new joints must then be intercalated "either between the basal and the second segment, or between the penultimate segment and the terminal claw-bearing segment. Since no such traces of incompleteness present themselves in the segments which follow the basal as would justify the former supposition, we seem compelled to adopt the latter; and it is not a little curious that the increase in the number of segments in the Stem, the Dorsal Cirrhi, the Arms, and the Pinnules should thus take place in different modes—the new segments making their appearance in the Stem immediately beneath its highest segment, in each Dorsal Cirrhus at its base, in each Arm at its termination, and in each Pinnule at the base of its terminal segment." (W. B. Carpenter, *op. cit.*, pages 747–748.)

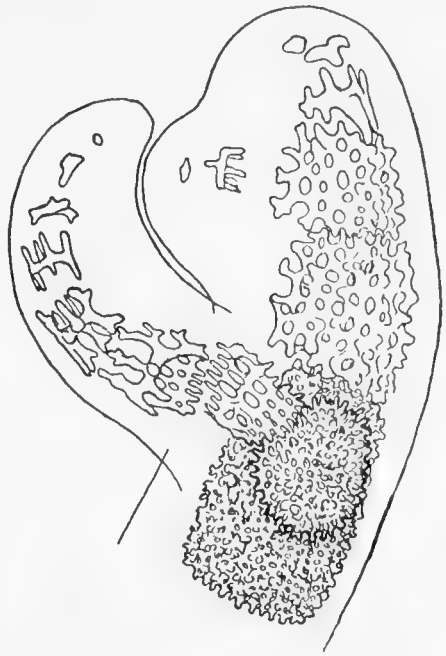

FIG. 10.—Point of an arm of *Antedon bifida*, showing the first rudiment of the outer pinnule and second pinnule with 9 joints, the lowermost of which is almost fully formed. ×180.

That Carpenter is mistaken in this point is easily ascertained by a closer examination of the newly formed pinnules at the point of the arm. *The new joints are formed at the tip of the pinnule,* and the terminal hook is the last to form. All the joints are formed in the course of a very short time, while the pinnule is still very short; already in the third pinnule from the point they are all formed, further growth of the pinnule depending on the lengthening of the joints. (Text-figure 10.)

Thus of the statements quoted above from Carpenter regarding the mode of formation of new joints in the arms, the pinnules, the stem, and the cirri, only the first is correct; in the arms the new joints appear at the termination, as he says; but in the pinnules they do not develop between the two last segments, but at the termination; in the cirri, not at the base, but likewise

at the termination, and finally in the stem they do not develop beneath the highest segment, but at the upper end, the centrodorsal being the last to develop.[68]

Joh. Walther [69] regards the oral tentacles as embryonal pinnules, homologous with the true arm-pinnules, and then arrives at the conclusion that "die Arme entshehen unter die Pinnulæ, nicht die Pinnulæ auf den Armen." There is no reason to enter on a critical discussion of this and the other surprising statements of this author (interradial position of the radials, horizontal rotation of 36° of the main axis of *Antedon*, etc.), deductions from entirely false premises. The indisputable fact that the oral tentacles have nothing to do with the pinnules, but are homologous with the tentacles of arms and pinnules, the primary radial tentacle especially being the homologon of the terminal tentacle of other Echinoderms, alone makes away with these results of the said author's reflections.

Some very curious ideas as to the true nature of pinnules have been set forth. A. H. Clark, in his Monograph of the Existing Crinoids (p. 272) states:

"Morphologically the first two segments of the pinnules are merely atrophied brachials, while the remaining portion of the pinnules, including the third and succeeding segments, is merely a tentacular process exactly comparable to the cirri, but carrying ambulacral structures on its ventral side. . . . Each brachial originates as, and is fundamentally, an axillary; one of the two derivatives from this axillary, after the formation of two ossicles, which are united to each other just as are the paired ossicles of the division series, abruptly ceases its development, while the other continues to increase in size, its basal segments attaining the same diameter as the brachial upon which it rests. The atrophied branch from the original axillary stage of the growing brachial serves as the base from which there extends outward a long tentacular structure with no phylogenetic history, which forms within itself a series of skeletal braces as necessity requires, and which is in every way exactly comparable to a cirrus, which also is a long tentacular structure with no phylogenetic history, forming within itself a series of skeletal braces as necessity requires, excepting only that it bears ambulacral structures along its ventral surface."

The quoted statement, apparently, rests on the assertion of Carpenter that the pinnules arise by a bifurcation of the arm, which has been shown to be erroneous (see page 78-79). Further, the pinnule does not at all "abruptly cease its development" after the formation of the two first ossicles. There is a continued augmentation of the number of pinnule joints till they are all formed (comp. text-figure 10), and not the slightest difference is observable between the two proximal and the following joints in regard to shape and development in the growing pinnule; there is no foundation at all for holding the two proximal pinnule points entirely different from the rest of the pinnule joints in morphological value.

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[68] This statement regarding the place of formation of the young stem-joints is also in contradiction with Carpenter's own observations: "New segments are being developed in the interval between the highest of these (the stem-joints) and the base of the calyx," he says correctly (page 730).

[69] Joh. Walther. Untersuchungen über den Bau der Crinoiden. Paleontographica, XXXII. 1886.

The "long tentacular structure, with no phylogenetic history, which forms within itself a series of skeletal braces as necessity requires" does not agree with embryological facts; this applies to the pinnules as well as to the cirri, which are structures of quite different morphological value, by no means "exactly comparable." This is an imaginary construction grown out of the necessity of finding a support for the astonishing idea held by A. H. Clark that Crinoids (and Echinoderms upon the whole) are derived from the barnacles. In the way quoted the pinnules and cirri are made to represent the original type of Crinoidal appendage, the required homologon of Arthropod legs, originally arranged in five pairs, "the two components of each pair being, so to speak, back to back," and only later on, in the course of development, "enormously reduplicated."

A most remarkable and quite decisive corroboration of the view regarding the morphological value of pinnules held by the present author (and, doubtless, by the great majority of specialists in Echinoderms) is afforded by the curious specimens of *Antedon petasus* described in the author's paper, "Notes on Some Scandinavian Echinoderms." [70] In these specimens some of the pinnules (in some cases the first oral, in others the third pinnule) have developed into true arms of exactly the same structure as normal arms and carrying pinnules in the usual arrangement. These facts necessarily lead to the conclusion that *the pinnules morphologically have the value of arms, but are on physiological grounds reduced to organs especially adapted for generative, nutritive, and respiratory functions* (more rarely for attachment, as in the case of *Comatulella brachiolata*,[71] on which Clark lays so much stress), *but always retaining a latent, potential power of developing in the same way as the normal arms.* For the cirri such development is out of the question, alone for the reason that they have no relation whatever to the water vascular system, as they are upon the whole of quite another anatomical structure than the pinnules.

This result, as regards the morphological value of the pinnules, evidently lends support to the assertion of Clark that each brachial is fundamentally an axillary, although ontogenetically it does not originate as such. Also, the pinnule joints, not the two basal ones alone, have fundamentally the same morphological value, and—as appears from the specimens of *Antedon petasus* referred to—any of them may, in fact, assume the shape and function of an axillary. The instance of a pinnule bifurcating at the fourth joint observed in *Isometra vivipara* [72] likewise bears testimony of the capacity of any pinnule joint of transforming into an axillary, which could, of course,

[70] Vid. Medd. Dansk Naturhist. Foren. vol. 72, 1920.

[71] No information is given by Clark about the anatomical structure of the remarkably transformed pinnules of *Comatulella brachiolata;* but there can hardly be any doubt but that they will prove to agree essentially with the normal pinnules, and not with the cirri, both in regard to anatomical structure and development.

[72] Th. Mortensen. The Crinoida of the Swedish Antarctic Expedition. Wiss.-Ergebn. d. Schwed. Südpolar Expedition, 1901-1903, vol. VI, 1918, p. 13.

not be the case were the joints beyond the second of a totally different morphological value. Also in *Tropiometra carinata* I have observed a pinnule branching, not at the second joint, as should be required according to Clark's view, but much farther out, at what joint can not be ascertained definitely, as the pinnule was found broken off, the basal joints lacking; still, 3 joints are left below the axillary, so that the branching occurs here not lower than the sixth or seventh joint.

The formation of the *stalk-joints* was found to be in accordance with the previous observations by W. B. Carpenter, Bury, and Seeliger, the joints appearing at first as a half-moon-shaped spicule, the concave side being directed ventrally; new joints are formed only at the proximal end of the stalk, the last of them developing into the centrodorsal, either in connection with the infrabasals or, in cases where the infrabasals are lacking, by itself alone.

Seeliger (*op. cit.*, pages 229, 324) finds that new joints may be intercalated between the previously formed ones, concluding from the smaller size of such joints. Similar observations were made on *Tropiometra* (plate IX, figure 1). However, this hardly means a true intercalation, but only a small delay in the appearance of such joints, the place being left open for them (see pages 20–21). The small grains seen between the stalk-joints in plate IX, figure 3, might look more like true intercalated young joints; still their very varying position suggests that they are not destined to form separate joints, but to be soldered with the adjoining columnals. Otherwise this is evidently only an abnormal case.

The absence of the terminal stem-plate in *Thaumatometra nutrix* and the presence of supplementary terminal plates in *Notocrinus* can hardly have any bearing on the morphological meaning of this plate, both these interesting facts being evidently due to the special life conditions of the Pentacrinoids in these two species.

The homology between the stalk and the centrodorsal plate of the Crinoids, or especially the central plate of *Marsupites* and *Uintacrinus*, and the suranal plate of Echinoids maintained by A. H. Clark, I can not accept, even as a "potential" homology. Upon the whole, I think the homologies supposed to exist between the apical plates of Echinoids and the calycinal plates of Crinoids rest on mistaken conceptions. But a discussion of these problems may be left for a future occasion.

EXPLANATIONS OF PLATES.

LIST OF ABBREVIATIONS USED.

a. anal plate.
a. c. aboral cœlom.
an. anal opening.
an. c. anal cone.
arm. c. arm cœlom.
arch. archenteron.
a. t. anal tube.
ax. axial organ.
axill. axillary.
b. basal plate.
c. cirrus.
c. b. ciliated band.
c. gr. ciliated groove.
ch. o. chambered organ.
co. costal.
c. v. cœlomic vesicle.
d. dorsal.
e. h. entero-hydrocœl.
ent. entoderm.
gl. c. glandular cells.
gl. s. glandular sac.
h. hydrocœl.
h. r. hydrocœl ring.
i. intestine.
i. b. infrabasal.
i. t. interradial tentacle.
l. c. left cœlomic vesicle.
m. mouth.
m. s. mesenchyme cells.
n. nervous system.
o. oral plate.
o. c. oral cœlom.
oe. esophagus.
o. v. oral valve.
p. pinnule.
p. c. parietal canal.
po. hydropore.
po. c. pore canal.
pr. g. primary gonad.
pr. t. primary tentacle.
pt. apical pit.
r. rectum.
rad. radial plate.
r. c. right cœlomic vesicle.
r. n. ring nerve.
r. v. radial vessel.
s. sacculus.
s. d. suctorial disk.
st. stomach.
st. c. stone canal.
st. j. stalk-joint.
s. t. pl. supplementary terminal plate.
t. tentacle.
t. pl. terminal stem-plate.
t. v. tentacle vessel.
v. ventral.
v. m. vertical mesentery.
vst. vestibulum.
y. g. yolk globule.

The sections are all 5 μ thick.

PLATE I.

(All figures of *Tropiometra carinata*.)

FIG. 1. An egg immediately after liberation from the follicular membrane. ×200.

FIG. 2. An egg just fertilized. The formation of the egg-membrane has started at one pole, whence it spreads all over the egg. ×200.

FIG. 3. First cleavage stage. The fully formed egg-membrane is represented in this figure and in figures 4 and 5. ×200.

FIG. 4. The 4-cell stage. The different size and shape of the cells in this figure is due to the fact that they are not seen directly from above; in reality they are exactly alike. ×200.

FIG. 5. The 32-cell stage. ×200.

FIG. 6. Optical section through a young blastula, showing the different size of the cells. ×200.

FIG. 7. Section through an embryo 2½ hours old, showing cells lying loosely in the blastocœl. At the lower side of the figure is seen one cell in the act of wandering in. ×290.

FIG. 8. Another section from the same series, showing a considerable number of cells which have wandered in. At the right side of the figure is seen 1, at upper side 2 cells, probably in the act of wandering in. That on the right side has its nucleus in division. ×290.

FIG. 9. Section of another embryo 2½ hours old. ×290.

FIG. 10. Transverse section of an embryo in the gastrula stage. 5 hours old. ×290.

In figures 7 to 10 the egg-membrane is represented as seen in the sections, only in a slightly diagrammatic way.

PLATE II.

(All figures of *Tropiometra carinata*. All ×290.)

FIG. 1. Optical section through an embryo 5 hours old in the beginning of the gastrula stage. No cells have wandered into the blastocœl before the invagination in this specimen.

FIG. 2. Longitudinal section through an embryo in the gastrula stage, 5 hours old. The figure is partially composed from different sections, none of them being sufficiently well preserved to show all the details. At the aboral end of the archenteron the cells are not regularly arranged, these cells probably representing the beginning formation of the mesenchyme cells.

FIG. 3. Optical longitudinal section through an embryo in the gastrula stage, 5 hours old. Only two mesenchyme cells at the aboral end of the archenteron. The curvature of the cavity of the archenteron is seen in this figure, as also, less distinctly, in figure 2.

FIG. 4. Longitudinal section through an embryo 6 hours old, immediately after liberation from the egg-membrane. The archenteron is completely separated from the ectoderm and the blastopore has disappeared. The formation of the mesenchyme cells from the anterior end of the archenteron is in rapid progress. The nuclei of the entoderm and mesoderm are distinctly larger than those of the ectoderm. (In some few places on the right of the section figured the cell-limits were not quite distinct, the figure being thus far slightly reconstructed.)

FIG. 5. Longitudinal section through an embryo 8 hours old. The archenteron is nearly divided into an upper (anterior) and a lower (posterior) part through a median constriction. The blastocœl cavity has been completely filled up by mesenchyme cells. Also the space below the archenteron has been filled up by mesenchyme cells, which are evidently derived from the posterior end of the archenteron. The cell-limits of the mesenchyme cells are not represented exactly in every detail. As regards the entoderm, it has been combined from 2 to 3 sections following directly after one another, both sides of the median constriction not being distinct in one section.

FIG. 6. Longitudinal section through an embryo 10 hours old. The division of the archenteron into an anterior and a posterior vesicle has been completed. This embryo has been rather strongly contracted.

FIG. 7. Longitudinal section through another embryo 10 hours old, in which the division of the archenteron is still incomplete. The widening of the upper vesicle may possibly represent the first beginning of the hydrocœl. The preservation of this specimen was not very good; this accounts for the condition of the mesenchyme.

FIG. 8. Section through an "embryo" 6 hours old. The two large, cell-like bodies possibly represent a parasitic organism. The small spots filling the rest of the space within the membrane have the appearance of very small nuclei. Possibly these represent minute organisms which have devoured the cells of the embryo.

FIG. 9. Transverse section through an embryo 12 hours old, showing the constriction of the cœlomic vesicle, about to divide.

PLATE III.

(All figures of *Tropiometra carinata*. All ×290).

FIG. 1. Longitudinal section through an embryo 10 hours old, probably abnormal. The constriction of the archenteron appears to proceed from only one side.

FIG. 2. Longitudinal, frontal section through an embryo 12 hours old. The division of the archenteron is complete, but the former connection is still partially visible. The posterior or cœlomic vesicle has begun to form the right and left enterocœl.

FIG. 3. Longitudinal, somewhat oblique section through an exceptionally large embryo 12 hours old. The anterior vesicle has a very distinct widening, representing the beginning of the hydrocœl. There is an indication of an apical pit. Not well preserved, so that the mesenchyme could not be represented in a more detailed way.

FIG. 4. Longitudinal, frontal, but somewhat oblique section of an embryo 12 hours old. The cœlomic vesicle has nearly completed its division into a right and a left vesicle, the right and the left enterocœl; they have begun to occupy their later position, the left at the posterior end, the right at the dorsal side of the embryo. The arrangement of the nuclei of the ectoderm begins to show the ciliated bands and the outline of the posterior end shows the characteristic depression occupied by the posterior ciliated band.

FIGS. 5, 6. Two longitudinal, sagittal sections of an embryo 16 hours old; two sections lie between those two figured.

In figure 5 is seen the vestibulary invagination indicated by the numerous nuclei along the slightly flattened ventral (in the figure left) side. The ciliated bands are distinctly seen by the grouping of the nuclei. The cœlomic vesicle is completely divided and the two enterocœls have occupied their normal position, the left at the posterior end, the right along the dorsal side of the embryo covering the entoderm. The hydrocœl has been separated from the rest of the anterior vesicle, which now represents the future entoderm alone. The hydrocœl has occupied a position on the ventral side, just under the vestibulary invagination.

In figure 6 the hydrocœl is seen to divide off a small vesicle at its anterior end, the parietal canal. It is hardly so distinct in the section as shown in the figure, but is combined from this and the preceding section. The lumen of the entoderm is not seen in this figure, which represents a slightly lateral section. The ectoderm is seen to be thickened in the anterior end of the embryo.

FIGS. 7, 8, 9, 10, 11. From a series of transverse sections through an embryo 20 hours old; figure 7 is the foremost, figure 11 the hindmost; figure 7 is from the anterior end, in the region of the vestibulary invagination. The parietal canal is seen in this section and in 4 more sections; it is completely separated from the hydrocœl. The vestibulary invagination gradually disappears towards the posterior end, but is still visible in figure 10. The hydrocœl, as shown in figures 8 to 10, has the shape of a curved tube; it is not yet a closed ring. The relative position and shape of the enterocœls appear from figures 8 to 11. There are 5 sections between figures 7 and 8; figure 9 follows directly after 8; between 9 and 10 there is 1 section, and 3 sections between 10 and 11.

PLATE IV.

(All figures of *Tropiometra carinata*. All ×290.)

FIG. 1. Longitudinal, oblique-frontal section through an embryo 25 hours old, showing the first rudiment of the chambered organ in the shape of a process from the anterior end of the right enterocœl. (The ectoderm of the anterior end of the section figured was destroyed; that has been restored from another series of sections through an embryo of exactly the same age and stage of development.)

FIG. 2. Sagittal section of an embryo 25 hours old. The large cavity of the left (posterior) enterocœl is probably a feature due to the preservation. The hydrocœl is now nearly ring-shaped, which accounts for its appearing as two separate spaces in the section. The character of the ectoderm is to be noted—the secernment of intercellular substance is in full progress, and a distinct limit between the ectoderm and the mesenchyme is no longer to be seen. The epithelium of the cœlomic vesicles has begun to assume an endothelial character.

FIGS. 3, 4, 5, 6, 7, 8, 9, 10, 11, 12. From a series of transverse sections through an embryo 25 hours old. Between figures 3 and 4 there are 5 sections, between figures 4 and 5 only one, while figure 6 follows directly after 5, and 7 directly after 6; there is one section between 7 and 8, while 9 follows directly after 8; between 9 and 10 there is one section and the same between 10 and 11, and finally there are 2 sections between 11 and 12. The series gives the relation between the cœlomic vesicles, the entoderm and hydrocœl, while the parietal canal could not be made out in this series. All the figures are drawn in the same orientation, the ventral side down, the dorsal side upwards.

FIGS. 13, 14. Longitudinal, sagittal sections through an embryo 40 hours old. The sections are somewhat oblique. The two sections figured are separated from one another by 5 sections. ×290.

Figure 13 shows the vestibulary invagination; the suctorial disk is fairly distinct.

In figure 14 is seen the prolongation from the chambered organ through the stalk-joints. The parietal canal is distinct in this and the two following sections, continuing backwards as far as the upper end of the left cœlomic cavity. No pore canal opening exteriorly can be observed. Part of the vestibulary wall is seen on the right side of the figure. The ciliated bands are very distinct.

PLATE V.

(All figures of *Tropiometra carinata*. All ×290.)

FIGS. 1, 2, 3, 4, 5. From a series of longitudinal, frontal sections through an embryo 40 hours old. Figure 3 belongs to another series, but from a specimen of the same age and stage of development as that of the other figures. The section has been turned the other way, so that the internal cavities apparently show the inverse arrangement from the following figures. Figure 3 corresponds to the section of the first series, which follows immediately after figure 2. The following figure is separated from it by one section, and similarly there is one section between figures 4 and 5. Figure 1 gives a transverse section of the vestibulary invagination; the following two sections go through the inner end of it, showing just a round mass of nuclei; there is still a little trace of it in figure 4. Figure 2 shows the five primary processes from the hydrocœl. In figure 3 the hydrocœl is seen to be still in the shape of a curve, not a closed ring, and it is without connection with the parietal canal (*p.c.*). Figures 4 and 5 show the parietal canal about to develop the pore canal (*po. c.*) which does not, however, reach through the ectoderm. The apical tuft of cilia is distinct in the section figure 5 and the two adjoining sections. In the ectoderm numerous glandular cells are seen.

FIGS. 6–10. From a series of transverse sections through an embryo 40 hours old. There is one section between figures 7 and 8, and likewise one section between figures 9 and 10, while two sections separate figure 8 from figure 9. Fig. 6 is from the anterior end, separated from figure 7 by six sections.

PLATE VI.

(All figures of *Tropiometra carinata*.)

FIGS. 1–4. From a longitudinal, sagittal series of sections through an embryo 3 days old, nearly ready to attach itself. There are two sections between figures 1 and 2, and between 2 and 3, only one section between 3 and 4. The closure of the vestibulary invagination has begun. In figure 1 one of the primary tentacles is cut longitudinally. ×290.

FIGS. 5, 6. From a series of transverse sections of an embryo 4 days old. Figure 5 is from the anterior end, with the vestibulary invagination, the chambered organ, and the parietal canal, the latter continuing only in one more section forwards.

Figure 6, which is separated from figure 5 by five sections, shows the pore canal (*po. c.*), which continues through two more sections downwards. It has no opening to the exterior. ×290.

FIGS. 7, 8, 9. From a longitudinal section through an embryo 4 days old, pipe-shaped, with incompletely closed vestibulum.

Figure 7 shows the axial organ and the outer end of the rectum. In the vestibulum are seen the sections of 3 of the primary tentacles.

Figure 8, which is separated from 7 by 3 sections, shows the stone canal (*st. c.*), which is in connection with the hydrocœl ring two sections from this.

In figure 9, which follows immediately upon 8 in the series, the stone canal is seen to open into the parietal canal. The latter continues through 3 more sections and then the pore canal appears. In the left mesentery is seen an accumulation of cells, representing the primary gonad (*pr. g.*).

Figures 7 and 8, ×290; figure 9, ×375. The small spaces seen in a row in the epidermis are from the oral plates; in figure 9 also from one of the basal plates.

PLATE VII.

(All figures of *Tropiometra carinata*. All ×290.)

Fig. 1. From a transverse section of an embryo in the Pentacrinoid stage, showing the separate origin from the hydrocœl ring of the oral tentacles. The figure is part of the section following directly after that represented in plate VIII, figure 5, viz, the radius marked with an asterisk (*).

Fig. 2. Section through the stalk of a pentacrinoid (the same as plate VIII, figures 4 to 8), shows the chambered organ.

Fig. 3. Longitudinal section through an embryo 8 days old, just attached. The vestibulum is closed normally and the mouth opening is about to form. The cœlomic spaces are not very clear in this series.

Fig. 4. Longitudinal lateral section through an embryo 4 days old. The vestibulum is not normally closed and the embryo is pipe-shaped. The lumen of the entoderm is very spacious in this specimen, and no cells have wandered into it.

Fig. 5. Longitudinal median section through another embryo 4 days old, pipe-shaped, with the vestibulum not normally closed. The relations of the cœlomic spaces not quite clear in this series; the oral cœlom apparently in open connection with the aboral cœlom.

Figs. 6, 7. Longitudinal sections through an embryo 8 days old, normally attached and with the vestibulum normally closed. In figure 6 the stalk is omitted. The left side of the figures is the anal side. Figure 6 shows the chambered organ and the rudiment of the axial organ in the vertical mesentery. Figure 7, which is slightly lateral, shows that the esophagus and mouth have opened into the vestibulum. On the left side of the figure one of the primary tentacles has been cut longitudinally.

Fig. 8. Longitudinal section of an abnormal, pipe-shaped embryo, 8 days old, with the vestibulum incompletely closed. The axial organ more developed than in the specimen represented in figure 6. In the incomplete vestibulum is seen a primary tentacle cut; the mouth-opening is about to develop.

PLATE VIII.

(All figures of *Tropiometra carinata*. All ×290).

Fig. 1. Median, longitudinal section through a normal Pentacrinoid (attached to the surface film), the vestibulum still closed. The pore canal is seen close to the surface at the left side; it is present in two sections more, but has no opening to the exterior; the skin forms a little elevation over it. A thick membrane is formed over the basal surface of the stalk. The chambered organ is seen to continue almost to the basal surface of the stalk. (The part of the figure representing the stalk combined from two to three sections.)

Figs. 2, 3. From the same series as figure 1. In figure 2, which is separated from 1 by two sections, the pore canal is seen joining the parietal canal; in figure 3 the parietal canal opens into the oral cœlom; the stone canal is seen just above the parietal canal.

Figs. 4, 5, 6, 7, 8. From a series of horizontal sections through a normal Pentacrinoid in the same stage as that figured in figures 1 to 3.

Figure 4 shows the tentacles, 3 in each radius, in the vestibulary cavity. They are separated from one another by fine but distinct lines, which seem to indicate the presence of a slimy substance in the vestibulary cavity.

Figure 5, which is separated by four sections from figure 4, is in the level of the origin of the tentacles from the hydrocœl ring. Here the hydropore is seen to open to the exterior. Besides the 3 radial tentacles, 2 interradial tentacles are also developed (cf. plate VII, figure 1, which is taken from this series).

Figure 6, which is separated from figure 5 by two sections, is in the level of the hydrocœl ring, which is seen nearly complete in the section. Numerous fine trabeculæ are seen within the ring. The narrowing in the anal (upper) interradius is the point of closure of the ring.

Figure 7, separated from figure 6 by four sections, shows the stone canal opening into the parietal canal; this section goes through the esophagus.

Figure 8, separated from figure 7 by two sections, passes through the rectum, which is seen to have not yet opened to the exterior.

PLATE IX.

(All figures of *Tropiometra carinata.*)

FIG. 1. Embryo 24 hours old, with the first rudiments of the skeleton. ×250.
FIG. 2. Embryo 24 hours old; the skeleton slightly advanced beyond figure 1; the first rudiments of the infrabasalia are seen. ×250.
FIG. 3. Embryo 30 hours old. The body of this larva not very well preserved, so the position of the vestibulary invagination could not be seen. Only two infrabasalia are represented, the third probably hidden by the basal plate. ×250.
FIG 4. Embryo 40 hours old, seen from the ventral side. ×250.
FIG. 5. Abnormal embryo 6 days old; the vestibulum incompletely closed. ×300.
FIG. 6. Abnormal embryo 6 days old, pipe-shaped. The vestibulum incompletely closed. ×300. In figures 5 and 6 the details of the calcareous plates not quite exact; on account of the dark color of the object the details could not be drawn with the camera.
FIG. 7. Embryo 8 days old, the skeleton dissolved. ×180.
FIG. 8. Embryo of same age as the one represented in figure 7. Normally closed vestibulum, into which the primary tentacles are seen to protrude. ×180.
FIG. 9. Upper part of a young Pentacrinoid (5 days old), decalcified; in the vestibulum, which is about to open, are seen the tentacles (only some few of them drawn). On the left side are seen the pore canal (*po. c.*) and the stone canal (*st. c.*). The axial organ (*ax.*) is seen passing from the chambered organ (*ch. o.*) up between the stomach and rectum. ×260.

PLATE X.

(All figures of *Tropiometra carinata.*)

FIG. 1. Embryo 20 hours old. ×180.
FIG. 2. Embryo 40 hours old; drawn from a specimen stained with paracarmin and cleared in Canada balsam. In this specimen the continuation of the second ciliated band along the inside of the edge of the vestibulum could not be seen, but it was fairly distinct in another specimen of the same age. ×180.
FIG. 3. Normal young Pentacrinoid 6 days old. The infrabasalia could not be discerned on account of the dark color of the embryo. The details of the plates for the same reason only partially quite correct. ×180.
FIG. 4. Young Pentacrinoid 6 days old. One of the infrabasalia is abnormally situated outside the calyx and therefore distinct. ×200.
FIG. 5. Young Pentacrinoid 6 days old. ×200.
FIG. 6. Pentacrinoid, fully formed, with the vestibulum opened and tentacles protruding. ×200.
FIG. 7. Pentacrinoid with the beginning formation of the anal plate. ×70.
FIG. 8. The calyx of the same specimen as figure 5. The first sacculus is indicated. ×180.
FIG. 9. Calyx of young Pentacrinoid, seen from above. ×200.
FIG. 10. Lower stalk-joints and terminal stem-plate of Pentacrinoid from the surface film. ×200.

PLATE XI.

(All figures of *Compsometra serrata.* All × 290.)

FIG. 1. Sagittal section of a young embryo, showing the beginning formation of the vestibulary invagination and the suctorial disk. The right cœlomic vesicle somewhat swollen at the anterior end.
FIG. 2. From the same series as figure 1, separated from the latter by five sections; shows the arrangement of both cœlomic vesicles, entoderm and hydrocœl.
FIG. 3. Longitudinal, oblique section, showing the formation of the parietal canal from the hydrocœl. The ciliated bands have begun to form.
FIG. 4. Sagittal section of an embryo slightly older than the specimen represented in figures 1 and 2. The formation of the vestibulary invagination, suctorial disk, and ciliated bands somewhat farther progressed. The swelling of the anterior end of the right cœlomic vesicle very distinct (beginning formation of chambered organ).
FIG. 5, 6, 7. From a series of transverse sections of an embryo somewhat older than those represented in figures 1 to 4; the vestibulary invagination considerably deeper; the chambered organ has been formed, the parietal canal has opened to the exterior through the pore canal; the hydrocœl has begun to form the primary lobes; the right cœlomic vesicle covers the whole dorsal side of the entoderm. In figure 5 are seen the nerves in the edges between the vestibulary invagination and the ectoderm.
FIG. 8. Sagittal section through an embryo of the same age; shows the well-developed suctorial disk, the anteriorly prolonged parietal canal, and the chambered organ. The nervous system very well developed; the ciliated bands fully formed. The small spaces along the strands of the chambered organ show the place of the young stalk-joints.

FIG. 9. Longitudinal, frontal section through an embryo of the same age. Shows the large size of the parietal canal and its anterior prolongation.

FIG. 10. Longitudinal frontal section through another embryo of the same age, showing the opening of the pore canal. In figures 8, 9, 10 glandular cells are rather strongly developed in the anterior end. The embryos represented in this plate all lie within the egg-membrane.

PLATE XII.

(All figures of *Compsometra serrata*.)

FIGS. 1, 2. Fully formed embryo, ventral view (1) and side view (2); the latter from a specimen mounted in balsam and stained with paracarmin. The dark line inside the contour-line represents the layer of nuclei. ×150.

FIGS. 3, 4. Two stages of the formation of the skeleton. The small calcareous grain inside the basal circle in figure 3 represents the first infrabasal; in figure 4 the 4 infrabasals are well developed. ×270.

FIG. 5. Young Pentacrinoid, decalcified; vestibulum still closed; shows the primary gonad, pore canal, and chambered organ. The pharynx is distinctly compressed. The intestine and rectum fully formed. The stone canal could not be traced very distinctly, but the form shown in the figure apparently is correct. ×200.

FIG. 6. Pentacrinoid showing the young costal and axillary. ×105.

FIG. 7. Slightly older Pentacrinoid; the anal plate is seen partly overlying the adjoining oral. The long tentacles with their spicules are noticeable, as in the preceding figure. ×90.

PLATE XIII.

(All figures of *Compsometra serrata*.)

FIG. 1. Young Pentacrinoid, the vestibulum just opened. ×105.

FIG. 2. Slightly older stage of Pentacrinoid; the radials and the anal plate have appeared. ×105.

FIG. 3. Pentacrinoid, later stage; the arms have begun to form. The oralia have been separated from the basalia. ×43.

FIG. 4. Pentacrinoid, further stage of development; the cirri have just begun to appear. The radialia are laterally in contact and the oralia are widely separated from both radialia and basalia. The pinnules have not yet begun to form. ×43.

FIG. 5. Nearly fully formed Pentacrinoid. Cirri distinct. The first pinnules have been formed. The large anal plate is seen at the base of the high anal tube, through the walls of which is seen the oral of the anal interradius. The lower end of the stalk has been placed alongside the rest of the stalk in order to have it all included within the space of the plate. ×43.

PLATE XIV.

(All the figures represent *Isometra vivipara*. All ×165.)

FIG. 1. Young cleavage stage. The egg-membrane has been indicated in this figure alone, but has been omitted in all the following figures.

FIG. 2. Later stage of cleavage. The nuclei have augmented considerably and the grouping near the surface and in the middle is beginning to be distinct.

FIG. 3. More advanced cleavage stage, showing more distinctly the arrangement of the nuclei near the surface and in the middle of the yolk-mass.

FIG. 4. The ectoderm and entoderm have become differentiated, cell limits being distinct. At one end, probably the anterior end of the embryo, a space has appeared between ectoderm and entoderm, filled with groups of yolk-spherules. A large cavity is formed in the archenteron. The part of the ectoderm marked * has been represented more magnified in plate XV, figure 3.

FIG. 5. Beginning formation of the cavity of the archenteron. The ectoderm cells not yet distinctly limited, although the nuclei have augmented beyond the stage represented in figure 4. The concavity on the right side is probably due simply to mutual pressure of the embryos lying in the marsupium.

FIG. 6. Sagittal longitudinal section of an embryo, showing beginning differentiation of the archenteron into cœlomic vesicle (*c. v.*), entoderm (*ent.*), and hydrocœl (*h.*); mesenchyme cells are seen lying in the blastocœl cavity. Part of the entoderm (at the mark *) has been represented more magnified in plate XV, figure 2.

FIG. 7. Frontal, longitudinal section of an embryo, with the division of the archenteron completed. The cœlomic vesicle has separated into the two enterocœl vesicles, right and left (*r.c.* and *l.c.*). The downward prolongation of the entoderm marks the former connection between the entoderm and the cœlomic vesicle.

FIGS. 8, 9, 10. Three frontal longitudinal sections of an embryo, with the cœlomic vesicle separated from the entoderm, but the left and right enterocœlic vesicles are still connected by a narrow transverse canal. The sections have been somewhat obliquely directed and the three figures combined correspond to figure 7.

FIG. 11. Frontal, longitudinal section of an embryo, showing the separation of the archenteron in an upper part (entero-hydrocœl) and a lower part (cœlomic vesicle) not yet completed.

PLATE XV.

(All the figures represent *Isometra vivipara*.)

FIG. 1. Sagittal, longitudinal section of an embryo, in which the division of the archenteron into the cœlomic vesicle and the entero-hydrocœl has been completed. The mesenchyme cells have not yet filled the blastocœl cavity completely in the lower part. The concavity on the left (ventral) side represents the beginning formation of the vestibulary invagination. ×165.

FIG. 2. Part of the entoderm from the section represented in plate XIV, figure 6. ×535.

FIG. 3. Part of the ectoderm from the section represented in plate XIV, figure 4. ×535.

FIG. 4. Transverse section of an embryo in which the parietal canal does not open outwards; it is not distinctly apically elongated, being present in only five sections upon the whole, and thus represents a comparatively younger stage of development than figure 5, as is also seen from the fact that the vestibulary invagination is quite indistinct. In the mesoderm a fairly large yolk globule (*y. g.*) is seen. ×165.

FIG. 5. Transverse section of an embryo, showing the parietal canal opening outwards; the vestibulary invagination is a slight but distinct concavity on the ventral side. ×165.

FIGS. 6, 7. Two transverse sections of an embryo. The two sections figured are separated from one another by five sections.

Figure 6 is a section from the posterior end, showing the two enterocœl vesicles surrounding the entoderm separated from one another in the dorsal and ventral midline by a thin wall, the mesentery. The entoderm with a mere indication of a lumen, otherwise filled with a yolk-mass, containing nuclei.

Figure 7. More anterior section, showing the hydrocœl cut in two places. The pore canal is indistinct in this series; it is represented only by a compact mass of cells, no lumen being discernible. The left enterocœl has disappeared in this section. Glandular cells are fairly numerous in the ectoderm. ×165.

FIG. 8. Transverse section, corresponding to that represented in figure 7; shows a very large globule of yolk and some smaller ones in the mesoderm. In this embryo there is a rather large lumen in the entoderm, in which a fine granulated mass is seen, probably dissolved yolk-mass. The extraordinary outline of this figure, which has even been slightly corrected, is due to the fact that the embryo has been irregularly compressed by the mutual pressure of the embryos within the marsupium. ×165.

FIG. 9. Longitudinal, frontal section, showing the parietal canal opening outwards through the hydropore. The hydrocœl is visible in this section only as a small mass of nuclei lying between the left (oral) cœlom and the pore canal. The vibratile bands are distinct. ×165.

FIGS. 10, 11. Two longitudinal, frontal sections of an embryo.

Figure 10. The more dorsal of the two, showing the beginning formation of the chambered organ as prolongations from the right, aboral cœlom. The nervous system is beginning to develop.

Figure 11. A more ventral section, separated from that figured in figure 10 by sixteen sections. It shows the anterior prolongation of the parietal canal; no opening of the pore canal could be discerned in this series. In the aboral cœlom the vertical mesentery has been formed. The concavity of the anterior end of the embryo is the suctorial disk. The vibratile bands are distinct. ×165.

PLATE XVI.

(All the figures represent *Isometra vivipara*. All ×165.)

FIG. 1. Transverse section of an embryo showing the formation of the parietal canal as an outgrowth from the hydrocœl. The outline of the figure slightly corrected.

FIGS. 2 to 5. From a frontal, longitudinal series of sections of a fully formed larva. Figure 2 is the more ventral of the sections; nine sections lie between figures 2 and 3, four sections between figures 3 and 4, twelve sections between figures 4 and 5.

Figure 2 is in the level of the outer opening of the vestibulary invagination.

Figure 3 is at the bottom of the invagination, which is seen to be deeper in its anterior part The different arrangement of the glandular cells and the nuclei around the invagination in figures 2 and 3 is to be noted. The notch in the anterior end in figure 2 is the suctorial disk. In figure 3 the parietal canal and the apparently obliterating pore canal are seen. Parts of the nervous system appear in the anterior end of this figure; in the posterior end some yolk-globules are seen.

Figure 4 shows the hydrocœl, from which the primary radial canals are about to develop. The dark mass above is a group of glandular cells from the bottom of the vestibulary invagination in transverse section. In the posterior end is seen a pair of large yolk-globules. The groups of nuclei in the ectoderm of this and the following figure indicate the vibratile bands. The cilia are indistinct in this series on account of the egg-membrane lying very close to the epidermis.

Figure 5 goes through the middle of the entoderm, showing the indistinctly limited lumen in the middle of the mass of yolk-cells. The series of narrow lumina above the vertical mesentery are due to the decalcified young stalk-joints.

FIG. 6. Frontal, longitudinal section of a fully formed embryo, showing the beginning specialization of the entoderm, which is without a lumen, being completely filled with yolk-cells in which larger groups of yolk-globules are seen. The upward prolongations of the oral cœlom are seen. The ciliated bands are distinct.

FIG. 7. Corresponding section from a slightly younger embryo. The outline has been slightly corrected.

FIG. 8. Part of frontal longitudinal section, showing the primary lobes of the hydrocœl.

FIG. 9. Sagittal longitudinal section, somewhat oblique, which accounts for the suctorial disk not being seen in the section; showing the lobes from the aboral cœlom; the outer one of them represents part of the chambered organ. The arrangement of the glandular cells in the vestibulum is to be noticed.

PLATE XVII.

(All figures represent *Isometra vivipara*. All, except figure 5, ×165.)

FIGS. 1, 2, 3, 4. From a transverse series of a fully formed embryo, figure 1 being the more anterior, figure 4 the more posterior of the sections. There are twelve sections between figures 1 and 2, four sections between figures 2 and 3, and twelve sections between figures 3 and 4. In this series the vestibulum is more than usually wide. The difference in the relative position of the glandular and nuclear parts of the vestibulary epithelium from the anterior to the posterior part of the vestibulum is to be noticed.

Figure 1 shows the chambered organ, the aboral cœlom, divided into two parts by the vertical mesentery and the upper part of the parietal canal.

Figure 2 is below the vertical mesentery, the aboral cœlom being then undivided. The hydrocœl is slightly prolonged towards the pore canal, probably the first indication of the stone canal.

In figure 3 the forward prolongations of the oral cœlom are seen.

In figure 4 the oral cœlom occupies the whole space round the dorsal side of the entoderm. The pore canal is seen close to the surface, but no opening is discernible in the following sections.

FIG. 5. Part of the epithelium within the vestibulary invagination, showing the structure of the cuticula. Only a few of the outer nuclei have been drawn. In the right end of the figure is seen a glandular cell. ×750.

FIGS. 6, 7. From a series of transverse sections; ten sections lie between the two figures, figure 6 being the more posterior. The arrangement of the glandular and nuclear portion of the ectoderm in the vestibulary invagination is to be noticed. In figure 6 the forward prolongations from the oral cœlom are seen. In figure 7 the dorsal or aboral cœlom is divided in two parts by the vertical mesentery. The stone canal is seen in this section, as is also the chambered organ.

FIG. 8. Sagittal, median longitudinal section, showing the vestibulum nearly closed, only a very narrow opening, discernible only in two sections, still remaining. Above the opening is seen the suctorial disk. The large space above the hydrocœl is the parietal canal. The chambered organ has been cut only in the lower part; the horizontal spaces above it indicate the dissolved stalk-joints. The figure has been slightly combined from two sections. It is to be noted that there is no indication of an apical tuft of cilia above the suctorial disk.

FIGS. 9, 10, 11, 12. From a series of transverse sections. There are twenty sections between figures 9 and 10, one section between figures 10 and 11, and seven sections between figures 11 and 12. Figure 9 is the foremost of them. The figures show the considerable difference in the depth of the vestibulary invagination in the anterior and posterior part; the narrowness of the vestibulum is noticeable. In figures 10 and 11 it appears to be closed, but is not really so; the two side-walls have joined very closely, but there is still seen a median line separating them. In figure 10 the beginning of the stone canal is seen; in figure 11 the first indication of the axial organ is seen.

PLATE XVIII.

(All figures of *Isometra vivipara*.)

FIGS. 1, 2. Longitudinal sections of a newly attached Pentacrinoid. The stomach is filled by a granular mass, consisting of phagocytes; the entodermal nuclei lie in a single layer close to the surface. The vestibulum has a wide lumen; in the middle of the thick lower wall a slight depression (figure 2) indicates the place of the future mouth opening. Seventeen sections between figures 1 and 2. ×165.

FIG. 3. Sagittal, longitudinal section of a fully formed larva with the vestibulum closed. ×165.

FIG. 4. Opening of the stone canal into the parietal canal; from a longitudinal section of the same series as figures 5 and 6. ×290.

FIGS. 5, 6. Longitudinal sections from a Pentacrinoid with the vestibulum still closed. The tentacles have protruded into the vestibulum; the mouth and esophagus have been formed. In figure 5 the stone canal is seen in its connection with the hydrocœl ring. There are ten sections between the two figures. ×165.

FIG. 7. Transverse section of a newly attached Pentacrinoid, corresponding to figures 1 and 2, showing the granular mass (phagocytes) filling the stomach. The formation of the rectum and anal opening is indicated. ×165.

FIG. 8. Sagittal, longitudinal section of fully formed larva, with vestibulary invagination still open. ×165.

FIG. 9. Section of the suctorial disk of a fully formed larva. ×535.

PLATE XIX.

(All figures of *Isometra vivipara*.)

FIGS. 1, 2, 3, 4. From a series of longitudinal sections of a newly attached Pentacrinoid, corresponding to plate XVIII, figures 1 and 2, showing the interrelations of stone canal, parietal canal, and pore canal. In figure 1 is seen the origin of the stone canal from the hydrocœl ring; in figure 2 the hydrocœl has almost disappeared, the stone canal originating from the end of the still horse-shoe-shaped hydrocœl. Figure 3 shows the end of the stone canal, which does not yet open into the parietal canal. The space appearing above the stone canal is the oral cœlom. In figure 4 the stone canal has disappeared and only the parietal canal and pore canal are seen; the latter can be traced through four more sections, but there is no outer opening. Between the parietal canal and the entoderm some nuclei are seen which may indicate the primary gonad. There are four sections between figures 1 and 2, three sections between figures 2 and 3, and one section between figures 3 and 4. The entoderm is filled with a granular mass, as in plate XVIII, figures 1 and 2. ×290.

FIG. 5. Transverse section of a Pentacrinoid, containing a half-digested larva in the stomach. The section is somewhat oblique, which accounts for the fact that only part of the hydrocœl is seen, the two ends of which are represented, separated by a narrow wall. The oval space outside the hydrocœl is the pore canal. The thickening of the entoderm in the anal interradius is noticeable. Figures 1 and 2 of plate XX represent two more anterior sections of the same specimen, the latter separated from the section here represented by 25 sections. ×165.

FIGS. 6, 7, 8, 9, 10. Series of figures from the same specimen showing the shape of the entodermal thickening in the anal interradius.

In figures 6 and 7 the stone canal and parietal canal are seen; figure 8 goes through the rectum, the anal opening being indistinct on account of the pressure caused by the devoured larva.

In figure 9 the entodermal thickening has closed into a canal which is seen in the three consecutive sections.

Figure 10 is some distance below the thickening; only a small ridge is seen here.

There are five sections between figures 5 and 6; two sections between figures 6 and 7; seventeen sections between figures 7 and 8; nine sections between figures 8 and 9, and twenty-five sections between figures 9 and 10. ×165.

FIG. 11. Part of a section of a young larva with beginning formation of the vestibulary invagination, showing the distribution of the yolk spherules in all parts of the larval tissues: ectoderm, hydrocœl, entoderm, and cœlom. Stained with hematoxylin and eosin. ×535.

PLATE XX.

(All figures of *Isometra vivipara*.)

FIGS. 1, 2. Transverse sections of a Pentacrinoid; other sections from the same series figured in plate XIX, figures 5 to 10.

Figure 1 is through the upper part, above the mouth. The five concave parts are the oral valves, between which the arms protrude.

Figure 2 is further down, at the base of the arms. The mouth has been protruding like a funnel in this specimen and thus appears as a ring in the section. The direction is somewhat oblique, which accounts for the fact that sections of tentacles are seen in part only of the figure. ×165.

FIGS. 3, 4, 5, 6. Transverse sections of a Pentacrinoid of a stage corresponding to that represented in plate XXI, figure 6.

Figures 3 and 4 show the hydrocœl ring with its trabeculæ. The fact that the hydrocœl is not seen in the interradius turned up in the figure must be due to some accidental contraction and to a slight obliquity of the section, not to a normal sinuosity of the ring. In figure 3 is seen the opening of the pore canal and at * the narrow wall still separating the two ends of the hydrocœl.

Figure 4 shows the parietal canal and the stone canal, partly horizontal and partly in transverse section. The cœlom has sent prolongations into the arms. A thickening is seen in the esophageal wall in the anal interradius.

Figure 5 shows the anal opening.

Figure 6 is from the middle part of the body, showing the intestine in longitudinal section. In both figures the axial organ is seen between the stomach and intestine, as a hollow cord. Noticeable is the concavity corresponding to each arm in which the cœlomic epithelium is much more closely nucleated than in the rest of the cœlom. This concavity continues into the arms, forming the arm-cœlom.

There are eight sections between figures 3 and 4, thirty-five sections between figures 4 and 5, and twenty-eight sections between figures 5 and 6. Figure 3 is to a slight extent combined from two sections, the opening of the pore canal being distinct only in the section following upon the one that has been drawn. All four sections ×75.

FIGS. 7, 8. Part of sections lower down in the same series, showing the chambered organ (figure 8, somewhat oblique) and its continuation into the stalk (figure 7). ×290.

PLATE XXI.

(All figures except figure 7 represent *Isometra vivipara*.)

FIG. 1. Young Pentacrinoid, decalcified. The vestibulum not yet opened; the tentacles not yet protruding into its lumen. ×75.

FIG. 2. Slightly older Pentacrinoid, decalcified. The tentacles have protruded into the vestibulum, which has not yet opened; but there is a depression in the top of the wall and the oral valves are differentiating. The stone canal has lengthened considerably and the intestine has been differentiated, but there is no anal opening formed as yet. ×75.

FIG. 3. Pentacrinoid, with beginning branching of the arms; decalcified. The opening of the pore canal is seen. The little thickening in the mesentery passing below the stone canal is the primary gonad. In the stomach folds are beginning to appear. Trabecules are seen in the cœlomic cavity. The chambered organ has widened considerably; from its middle the axial organ is proceeding towards the stomach. The arms are not drawn in a very detailed way. ×55.

FIG. 4. Longitudinal section of a Pentacrinoid in a stage corresponding to that represented in figure 3. The parietal canal is seen to open into the cœlom. The outer opening of the pore canal may be seen eight sections from the one figured. ×105.

FIG. 5. Longitudinal section through a more advanced Pentacrinoid. The thickening at the upper side of the hydrocœl is the place where the ring nerve (*r. n.*) is developing. ×90.

FIG. 6. Pentacrinoid of an advanced stage, decalcified. The anal opening has been formed. The primary gonad is distinct; the axial gland is a distinct cord, continuing through the whole of the body cavity. In the arm in the middle of the figure the primary tentacle is seen in the cleft. The arms are otherwise not drawn in a more detailed way. At the base of the arms the interradial tentacles are seen. ×70.

FIG. 7. Arm of a Pentacrinoid of *Antedon bifida*, showing the primary tentacle in the arm cleft. ×55.

PLATE XXII.

(All figures of *Isometra vivipara*.)

FIG. 1. The larva in its egg-membrane; seen from the ventral side; not specially treated. ×75.

FIG. 2. A larva, stained in carmine and mounted in balsam, showing the band-like widenings from the anterior end of the vestibulary invagination. ×75.

FIG. 3. Another larva, treated as the one represented in figure 2, but much less contracted, the anterior end with the suctorial disk standing out almost like a short proboscis. The widenings from the anterior end of the vestibulary invagination not so strong and band-like as in figure 2. ×75.

FIGS. 4, 5. Two young larvæ showing the first rudiments of the skeleton, viz, the five orals, the five basals, the terminal stem-plate, and a few stalk-joints. The specimen represented in figure 4 slightly older than that drawn in figure 5. ×105.

FIGS. 6, 7, 8. Full-grown larvæ with their skeleton, in ventral, dorsal, and side view. ×105.

FIG. 9. Newly attached Pentacrinoid. ×200.

FIG. 10. Later stage of Pentacrinoid; the radials have been formed. The orals have got a strong out-turned edge. ×65.

FIG. 11. Further stage of development of the Pentacrinoid. Above the radials the costal and axillary have been formed. Spicules are seen in the tentacles. × 65.

FIG. 12. Later stage of development of the Pentacrinoid. The arms have already about 6 joints. The radials are joining one another, separating the orals from the basals. The anal plate is seen lying between the oral and the radial, both the latter having the corner joining it partially absorbed. ×45.

(Figures 4, 5, 6, 7, and 8 have been drawn in a wrong position, with the anterior end downward.)

PLATE XXIII.

(All figures of *Isometra vivipara*.)

FIG. 1. Newly attached Pentacrinoid. ×45.

FIG. 2. Slightly older stage; the stalk has lengthened and the orals have begun to form the out-turned lateral edge. ×45.

FIG. 3. Further advanced stage. The radial plates have appeared. ×50.

FIG. 4. A slightly older Pentacrinoid, with two very young Pentacrinoids attached to its stalk. ×20.

FIG. 5. Further advanced stage. The costals and axillaries have been formed and the arms are beginning to develop. ×20.

FIG. 6. Later stage of the Pentacrinoid. Several arm-joints have developed, and the stalk-joints are assuming their final shape. ×20.

FIG. 7. The latest Pentacrinoid stage. Pinnulæ are beginning to develop, and the first whorl of cirri has been formed. The little piece represented in figure 7*a* is the lowermost part of the stalk of the same specimen. The terminal stem-plate was wanting. ×20.

PLATE XXIV.

(All figures of *Notocrinus virilis*.)

FIG. 1. Fully formed larva, in ventral aspect. ×28.

FIG. 2. Larva, mounted in balsam so as to show the skeleton. In the posterior end are seen the glandular sacs. One supplementary plate is seen besides the primary terminal stem-plate. Dorsal view. ×55.

FIG. 3. Side view of a larva with a process apparently coalesced with the marsupial wall. Four supplementary terminal plates are seen. The glandular sacs were not distinct in this specimen. ×55.

FIGS. 4, 5, 6. From a series of sagittal, longitudinal sections of the larva.

Figure 4. A nearly median section, showing the anterior prolongation of the parietal canal.

Figure 5. A somewhat more lateral section in which is seen the hydrocœl.

Figure 6. A still more lateral section, showing a downward prolongation from the parietal canal: the closed pore canal.

The indentation in the anterior end of the two first of these figures is the suctorial disk. In figure 6 the anterior part has been slightly restored. There are thirty-five sections between figures 4 and 5, eighteen sections between figures 5 and 6. ×80.

FIGS. 7, 8, 9. From a series of frontal, longitudinal sections of the larva. Figure 7 the more dorsal, figure 9 the more ventral of the sections.

Figure 7 shows four glandular sacs in section.

Figure 8 shows part of the anterior prolongation of the parietal canal.

Figure 9 shows the hydrocœl and the downward prolongation from the parietal canal representing the closed pore canal. The small accumulation of cells, marked ** in the anterior part is part of the anterior prolongation of the parietal canal. The little space between the two parts of the hydrocœl is part of the oral (left) cœlom and is seen to unite with it a few sections farther on.

There are 28 sections between figures 7 and 8, 10 sections between figures 8 and 9. ×80.

PLATE XXV.

(All figures of *Notocrinus virilis*.)

FIGS. 1, 2, 3, 4, 5, 6. From a series of transverse sections of a larva, figure 1 being the anterior of them. (A continuation of the series is given in plates XXVI, figures 1 to 3.) ×70.

Figures 1 and 2 are from the part above the vestibulary invagination, through the region of the suctorial disk, which is indicated by the double indentation. In the middle is seen, below the thick ectoderm, the nervous system, undivided, almost ganglion-like in figure 1, branching in figure 2. A little inside the nervous system is seen the section of the narrow anterior prolongation of the parietal canal, and nearer the middle is seen the chambered organ.

Figure 3 is from the anterior part of the vestibulary invagination; the nerves have disappeared, but in the interior are seen, as in the foregoing sections, the parietal canal and the chambered organ.

Figure 4 shows the origin of the pore canal from the parietal canal. The small space seen between this and the dorsal cœlom is an anterior prolongation from the oral cœlom. The dorsal cœlom is divided in the middle by the vertical mesentery.

Figure 5 is from the region of the hydrocœl. On the left side of the hydrocœl is seen the anterior prolongation of the oral cœlom; the space on the right side of the hydrocœl is the parietal canal; the dorsal cœlom is an undivided space covering the whole dorsal side. In the skin to the left of the hydrocœl are seen two small spaces, the minor of them being the pore canal, the larger a glandular sac.

In figure 6 the oral cœlom has also appeared to the right of the hydrocœl.

There are two sections between figures 1 and 2, about sixty between figures 2 and 3, about thirty between figures 3 and 4, seven between figures 4 and 5, and sixteen between figures 5 and 6.

FIG. 7. Part of a section showing 3 glandular sacs. ×290.

FIG. 8. Part of a transverse section, in a slightly younger stage than that from which the series of transverse sections have been figured, the vestibulary invagination being represented by only a slight concavity. In the figure is seen an evagination from the oral cœlom, which appears to represent a glandular sac in formation. The small ring seen outside the cœlom is the pore canal in section. It is closed also in this specimen. ×105.

PLATE XXVI.

(All figures of *Notocrinus virilis*.)

FIGS. 1, 2, 3. Continuation of the series of sections represented in figures 1 to 6, plate XXV.

Figure 1 shows the beginning formation of the primary tentacles from the hydrocœl. The oral cœlom is still divided in two lobes, one on each side of the hydrocœl.

Figure 2 is from the region below the vestibulary invagination, also below the hydrocœl. The oral cœlom now occupies the whole of the ventral side. Two glandular sacs are seen in either side of the larva.

Figure 3 is below the stomach; the dorsal cœlom has disappeared, the space in the middle representing solely the oral cœlom. Three glandular sacs are seen on either side.

Figure 1 is eighteen sections removed from figure 6 of the foregoing plate, and there are eighteen sections between this and the following figure. Between figures 2 and 3 there are eleven sections. ×70.

FIGS. 4, 5. Posterior part of two sections from a sagittal, longitudinal series.

Figure 4 shows the closed end of the pore canal; on the left side of the figure is seen a glandular sac in oblique section.

Figure 5, which is five sections removed towards the median line, shows the same glandular sac opening to the exterior (though not quite so distinctly as shown in the figure). ×105.

FIGS. 6, 7. From a longitudinal, frontal series of sections. The figures represent only the anterior part, showing the nervous system below the thickened ectoderm. At the lower end of the figures the anterior end of the vestibulary invagination is indicated.

Figure 6 is the more dorsal of the two figures. The thickening of the ectoderm in the anterior end of figure 7 is due to the suctorial disk, the upper part of which is just touched by the section. ×105.

FIG. 8. Part of the mesenchyme surrounding the stalk and the chambered organ; showing the yolk-granules, single or in globular masses. ×290.

FIG. 9. Part of the ectoderm, from the transitional region between the thick anterior and the thin posterior part; showing the outer layer of small nuclei and the inner layer of larger nuclei, probably belonging to the glandular cells. ×290.

FIG. 10. Part of the ectoderm in the vestibulary invagination. ×780.

FIG. 11. Part of the wall of a glandular sac. On the inner end of the cells are seen small masses of globules, evidently resulting from the secretory function of the cells. Picrocarmine. ×750.

PLATE XXVII.

(All the figures represent *Florometra serratissima.*)

FIG. 1. Young Pentacrinoid. The anal plate has appeared; in two or three of the primary tentacles the first rudiment of the axillary was seen, but not in the anal radius. The specimen had sixteen stalk-joints. ×100.

FIG. 2. Another Pentacrinoid in the same stage of development. In the primary tentacle is seen a small calcareous body, the axillary. ×100.

FIG. 3. Somewhat more advanced stage of the Pentacrinoid. The radialia have appeared (the small spicule to the right of the anal plate). The axillary is a rather large, fenestrated plate lying above the first sacculus. The first costal has not yet appeared. ×100.

FIG. 4. The same stage, represented with the stalk in its whole length. ×45.

FIG. 5. Later stage of the Pentacrinoid. The arms are distinct, consisting of a long costal and a large axillary. The radials are nearly joining and have separated the oralia from the basalia. ×90.

FIG. 6. Part of a Pentacrinoid, slightly more advanced than that represented in figure 3. Between the axillary (which is slightly abnormally shaped) and the sacculus is seen a small spicule, the first rudiment of the costal. The radius figured is that to the left of the anal interradius. ×180.

FIG. 7. Part of the Pentacrinoid represented in figure 1, mounted in balsam after the dissolution of the skeleton. Showing the stone canal and pore canal, which has the appearance of being closed. The primary gonad is very indistinct. The anal opening has been formed. ×290.

PLATE XXVIII.

(All the figures represent *Thaumatometra nutrix.*)

FIG. 1. Newly attached Pentacrinoid, with the vestibulum still closed. ×130.

FIG. 2. A more advanced stage; the oral valves are open and the primary tentacles protruding. The radials have appeared. ×130.

FIG. 3. Further stage of development. The radials have grown somewhat, and the costal I is appearing above them (in the figure distinguishable only to the left). The anal plate has appeared. The right side of this specimen has undergone some pressure, so that the oral plate to the right is lying nearly flat instead of in profile, as would be its natural position. ×105.

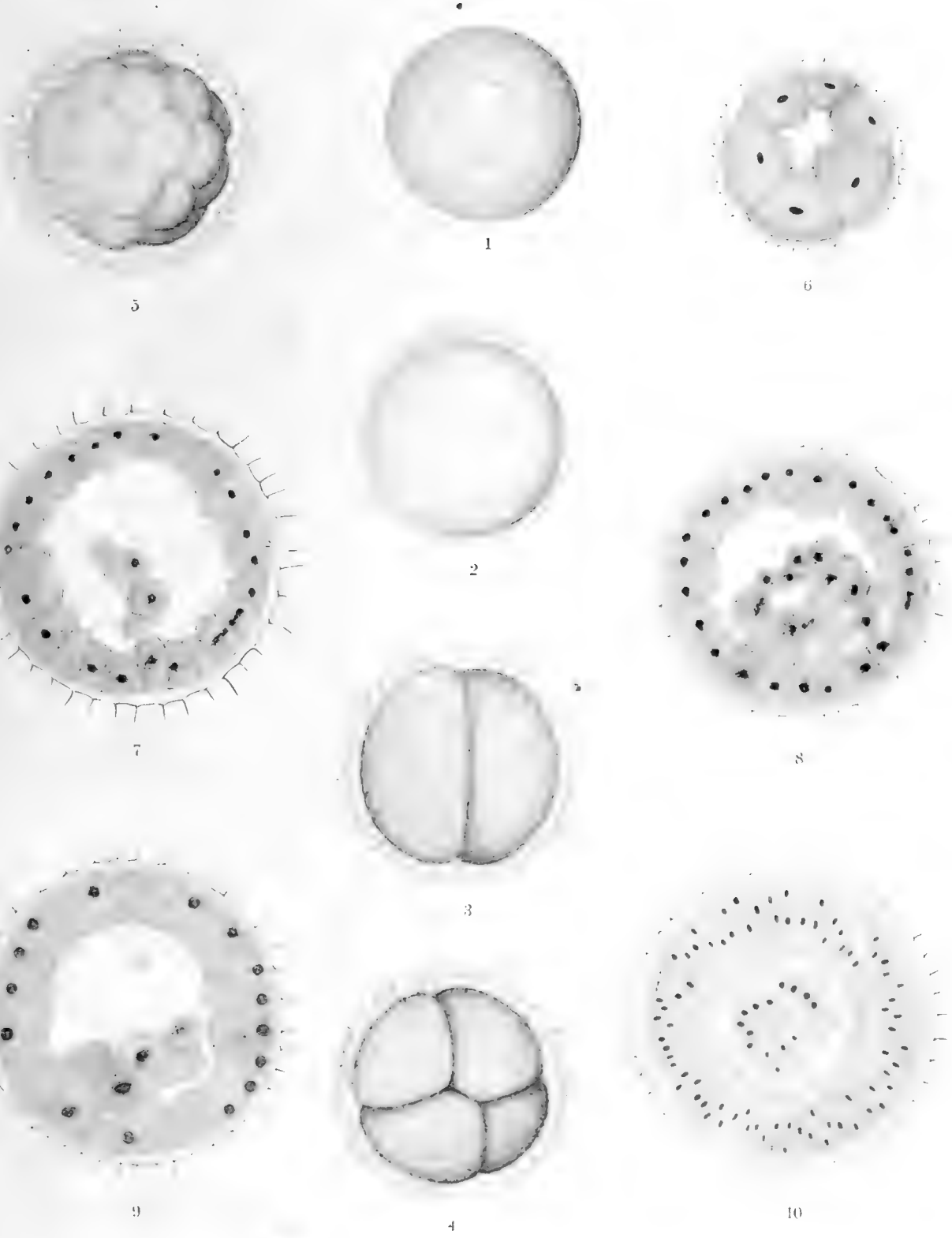
FIG. 4. Further advanced stage. The axillary has been formed and the arm-joints have begun to form. The incision in the oral plate to the right is a casual abnormality. ×100.

FIG. 5. Still further advanced stage; the arms are distinct, with about six joints. ×60.

FIG. 6. Fully formed Pentacrinoid, with the first whorl of cirri in complete shape and the second whorl about to appear. The arms have been broken off. At the upper edge of the disk are seen the orals and the anal plate. The anal cone has been formed. ×40.

FIG. 7. Two lower stalk-joints of a Pentacrinoid, attached between two pinnule joints. ×37.

FIG. 8. The stalk of a Pentacrinoid, which has detached itself. The stalk is attached to the middle of a pinnule joint. ×37.



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Tropiometra carinata.

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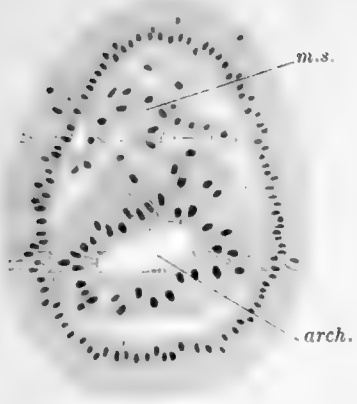

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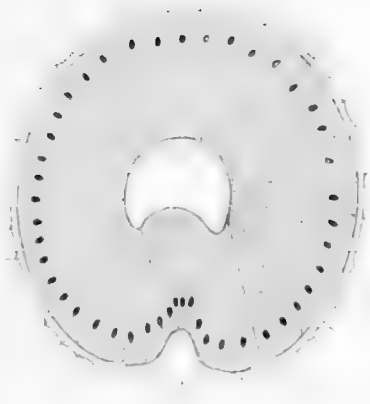

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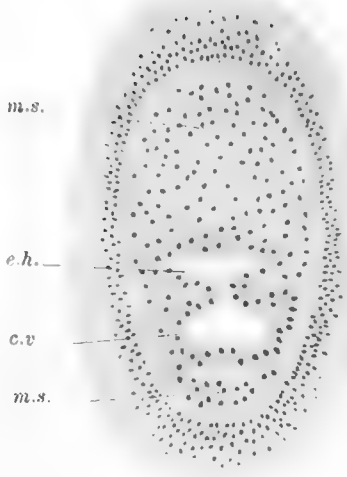

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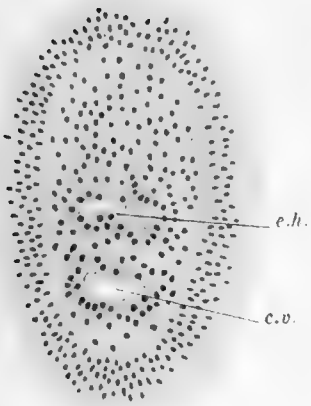

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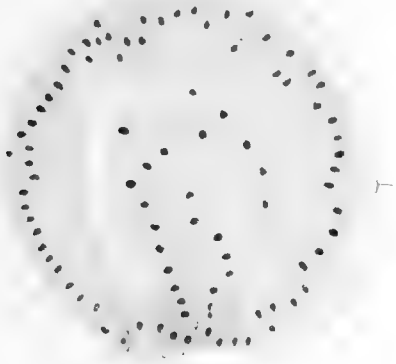

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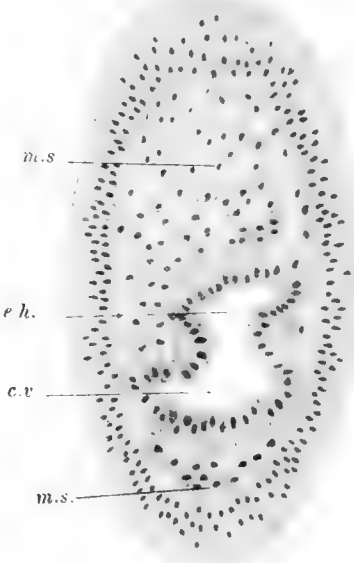

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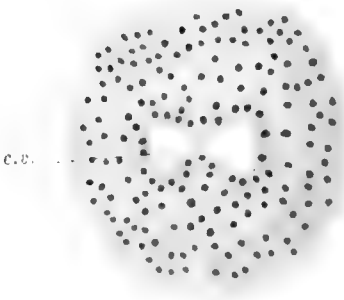

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Tropiometra carinata.

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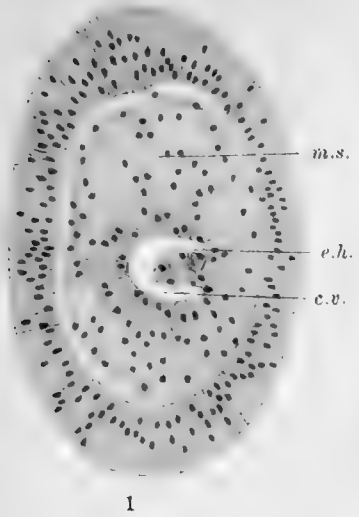

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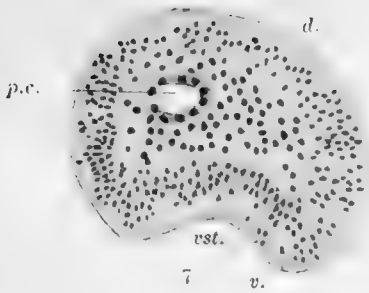

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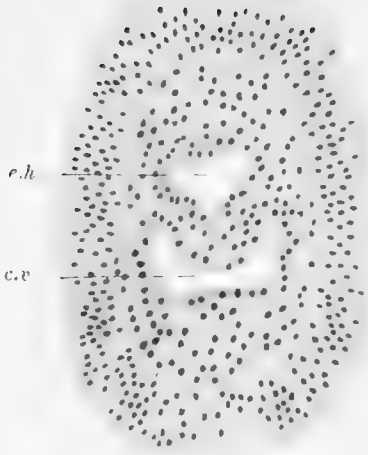

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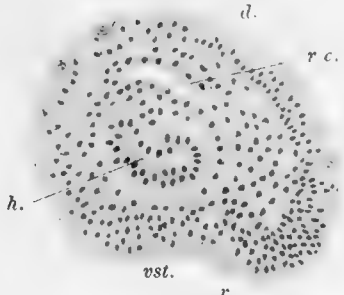

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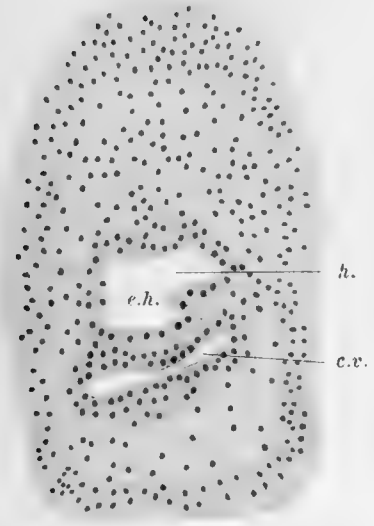

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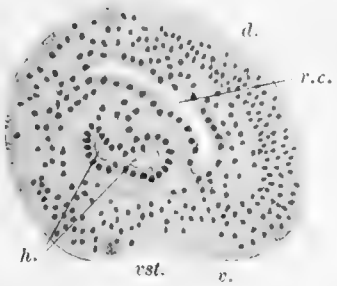

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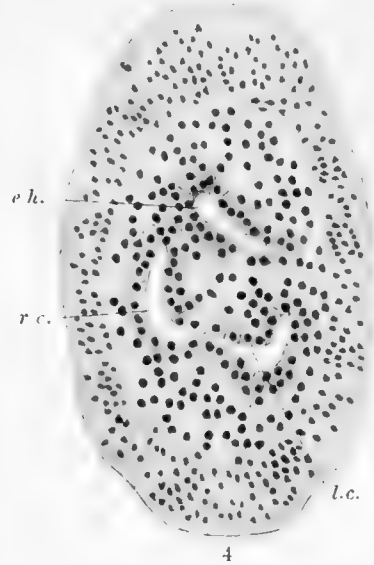

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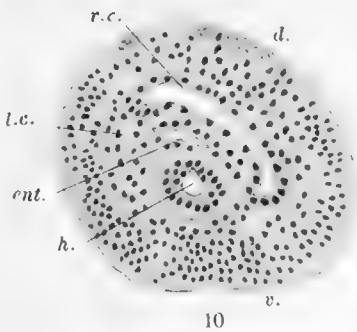

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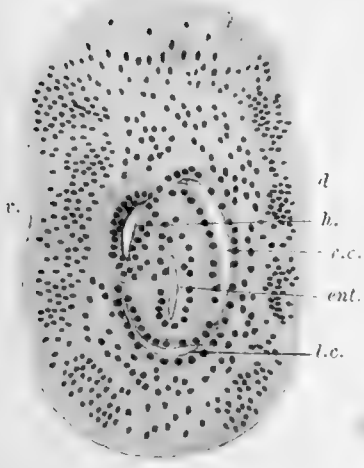

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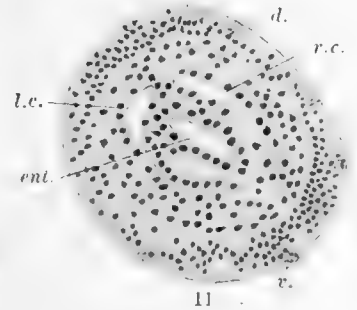

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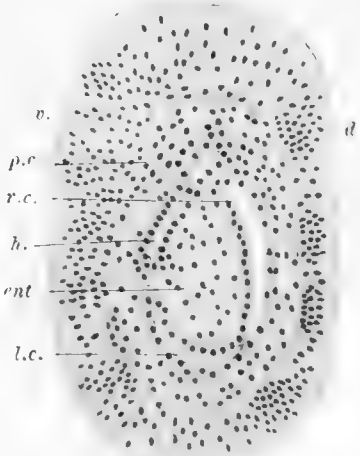

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Tropiometra carinata.

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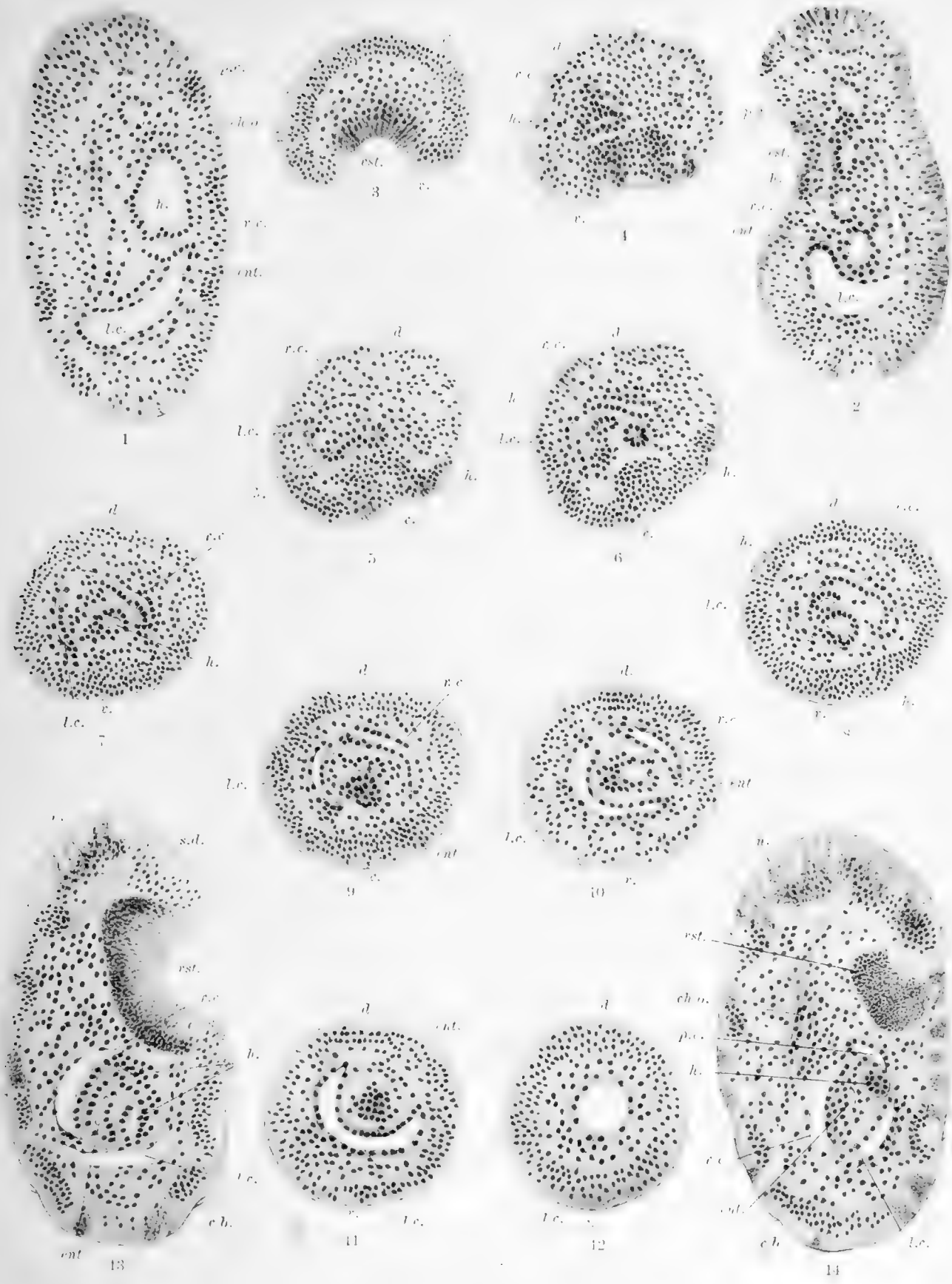

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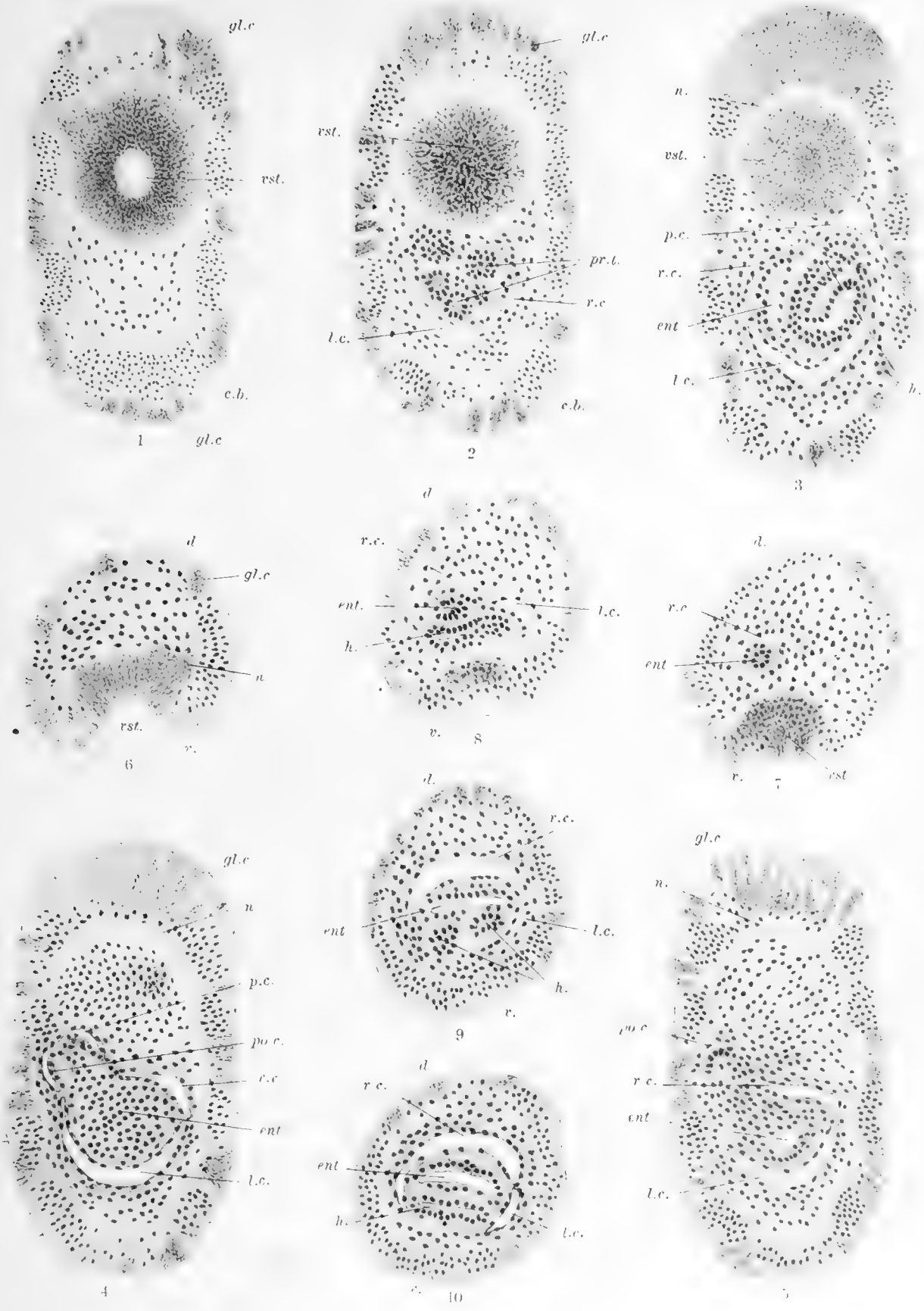

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Tropiometra carinata.

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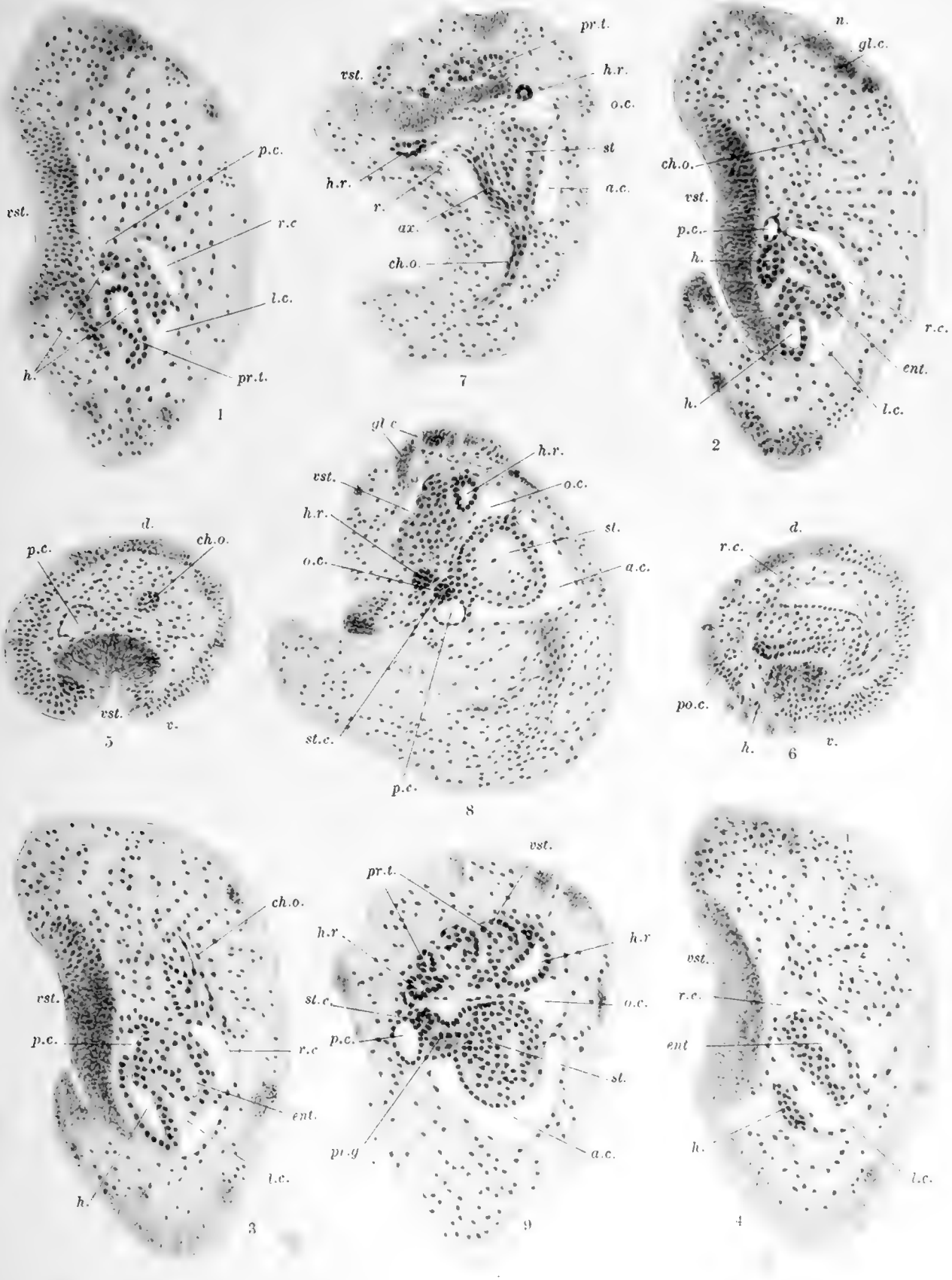

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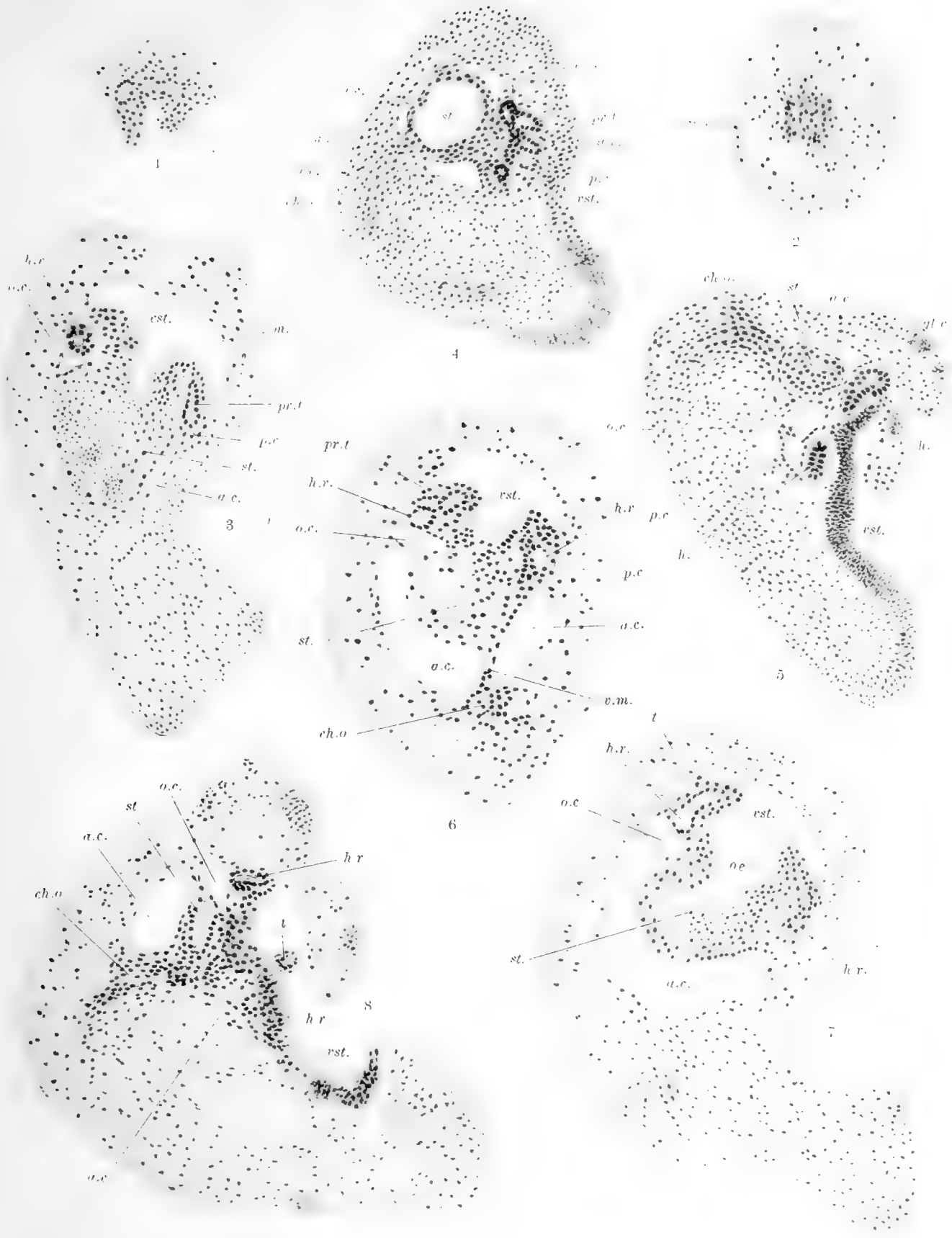
Tropiometra carinata.

HELIOTYPE CO. BOSTON



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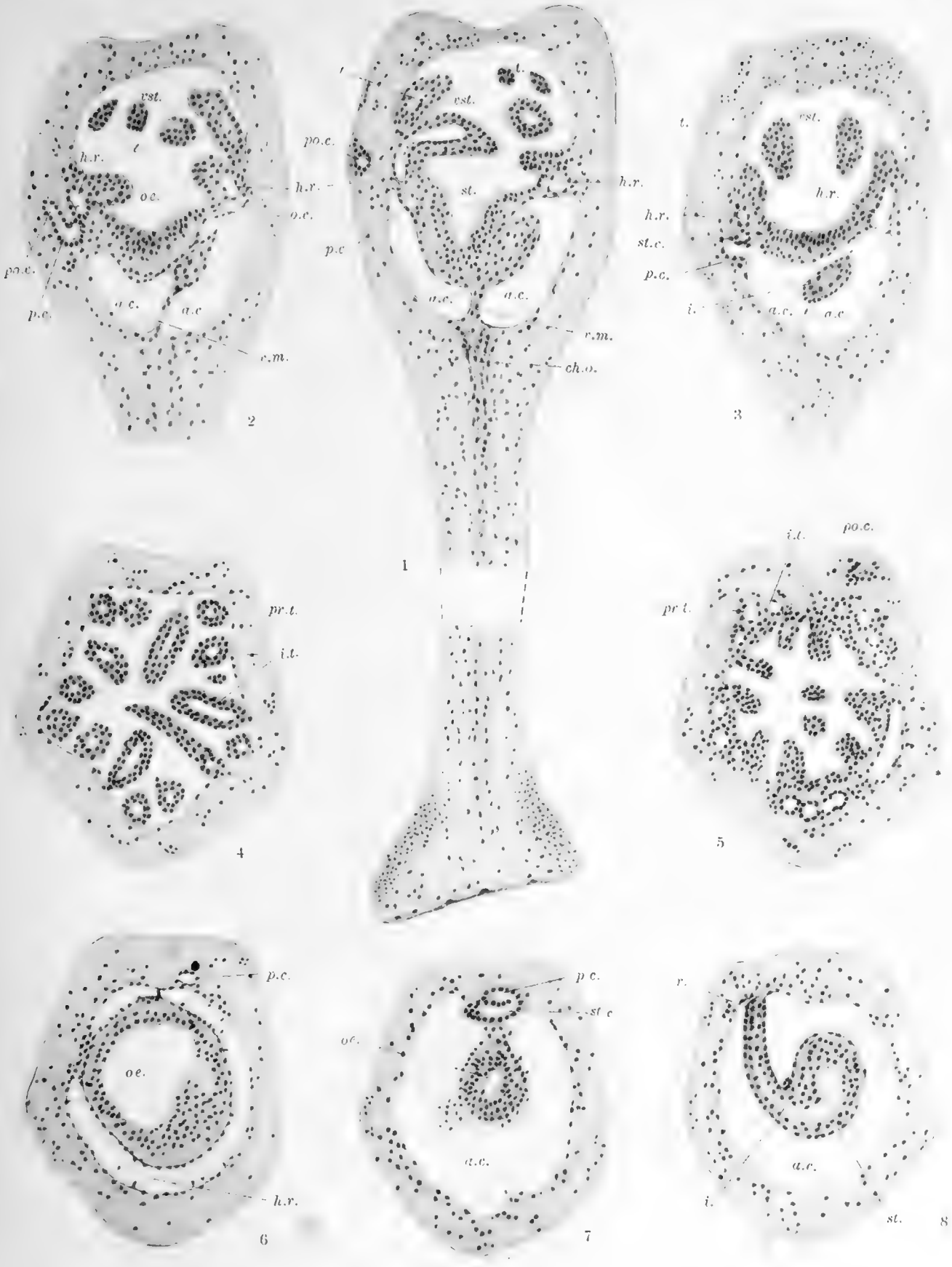
Tropiometra carinata.

HELIOTYPE CO. BOSTON



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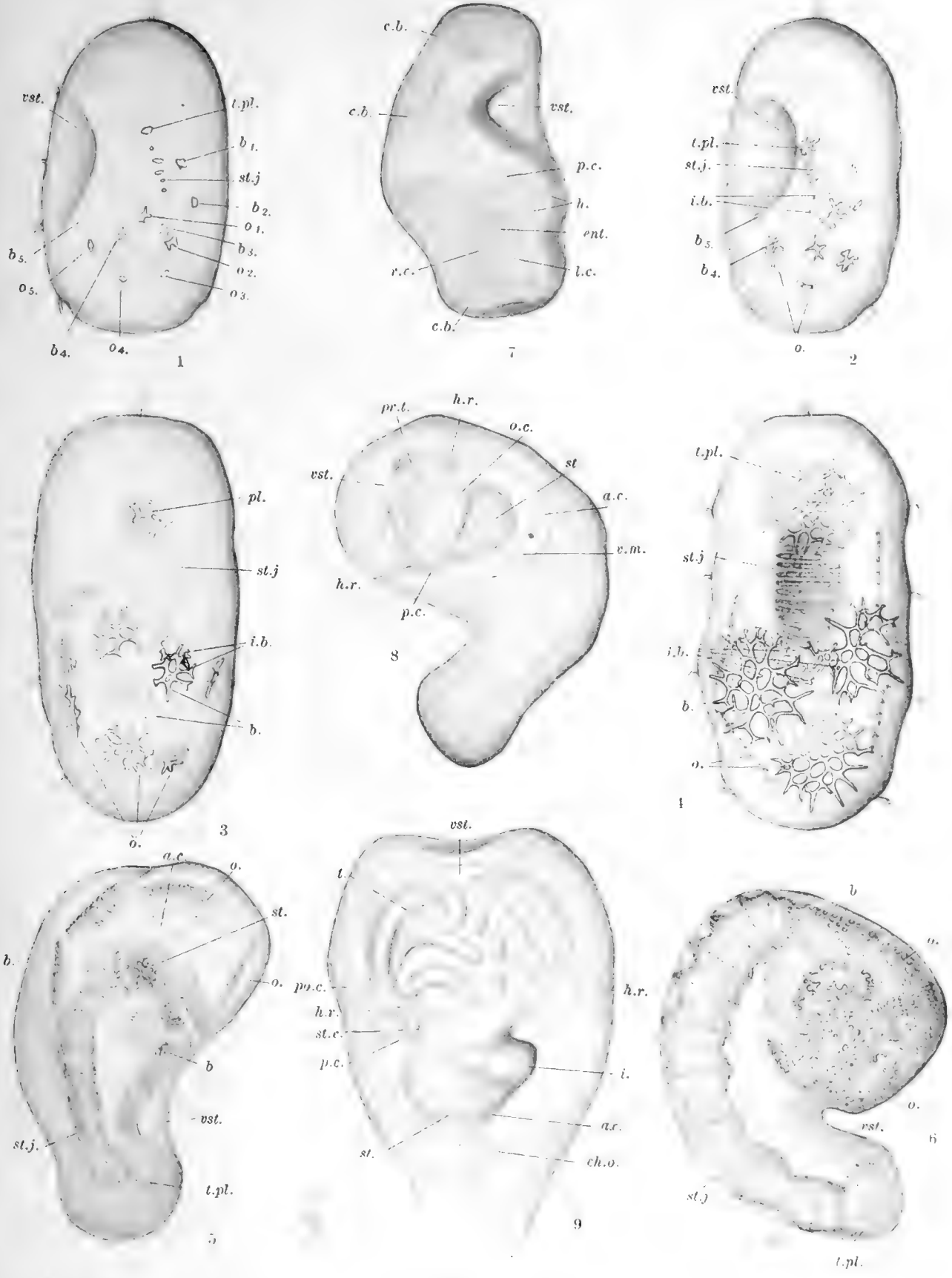
HELIOTYPE CO. BOSTON



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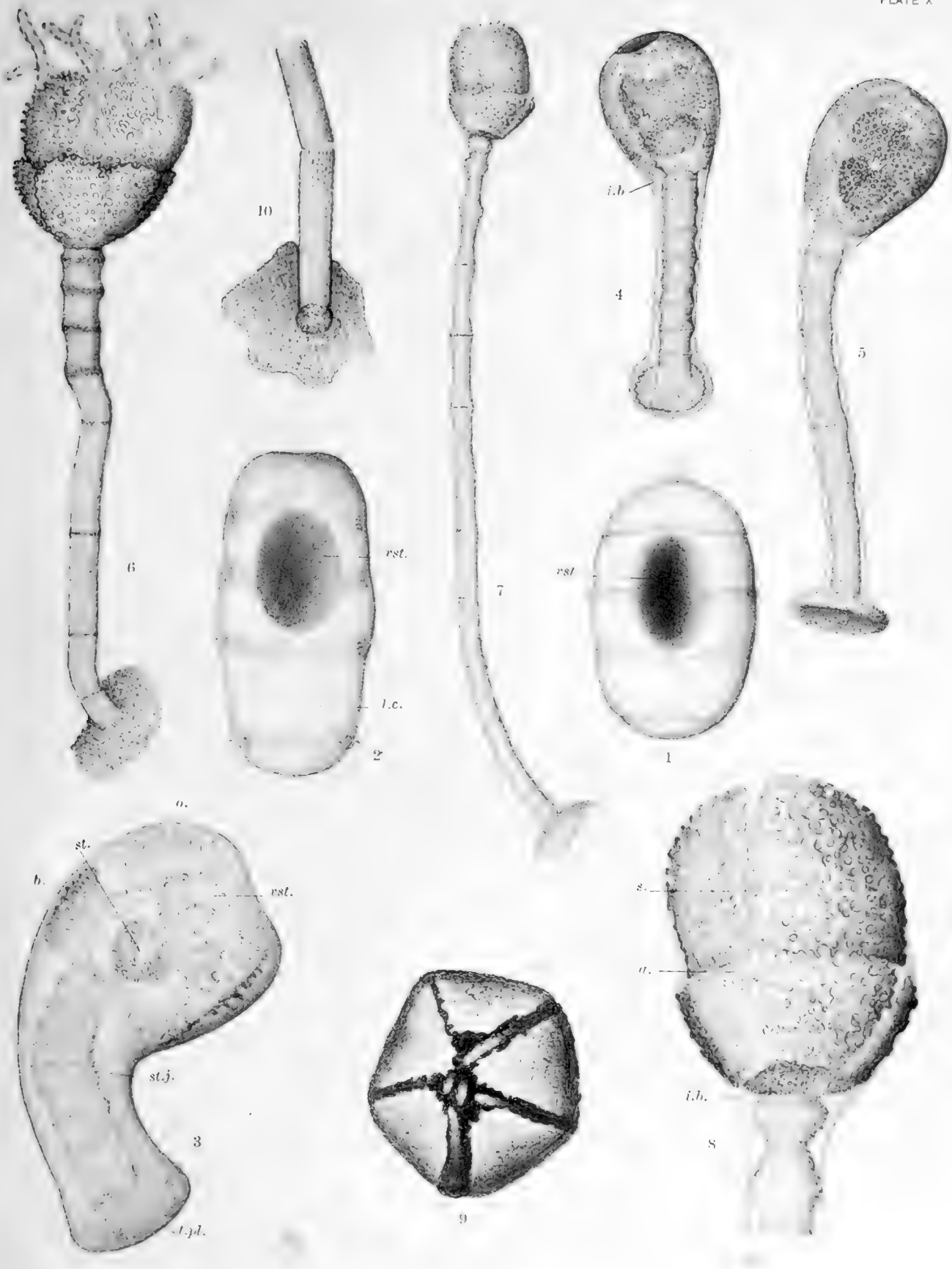

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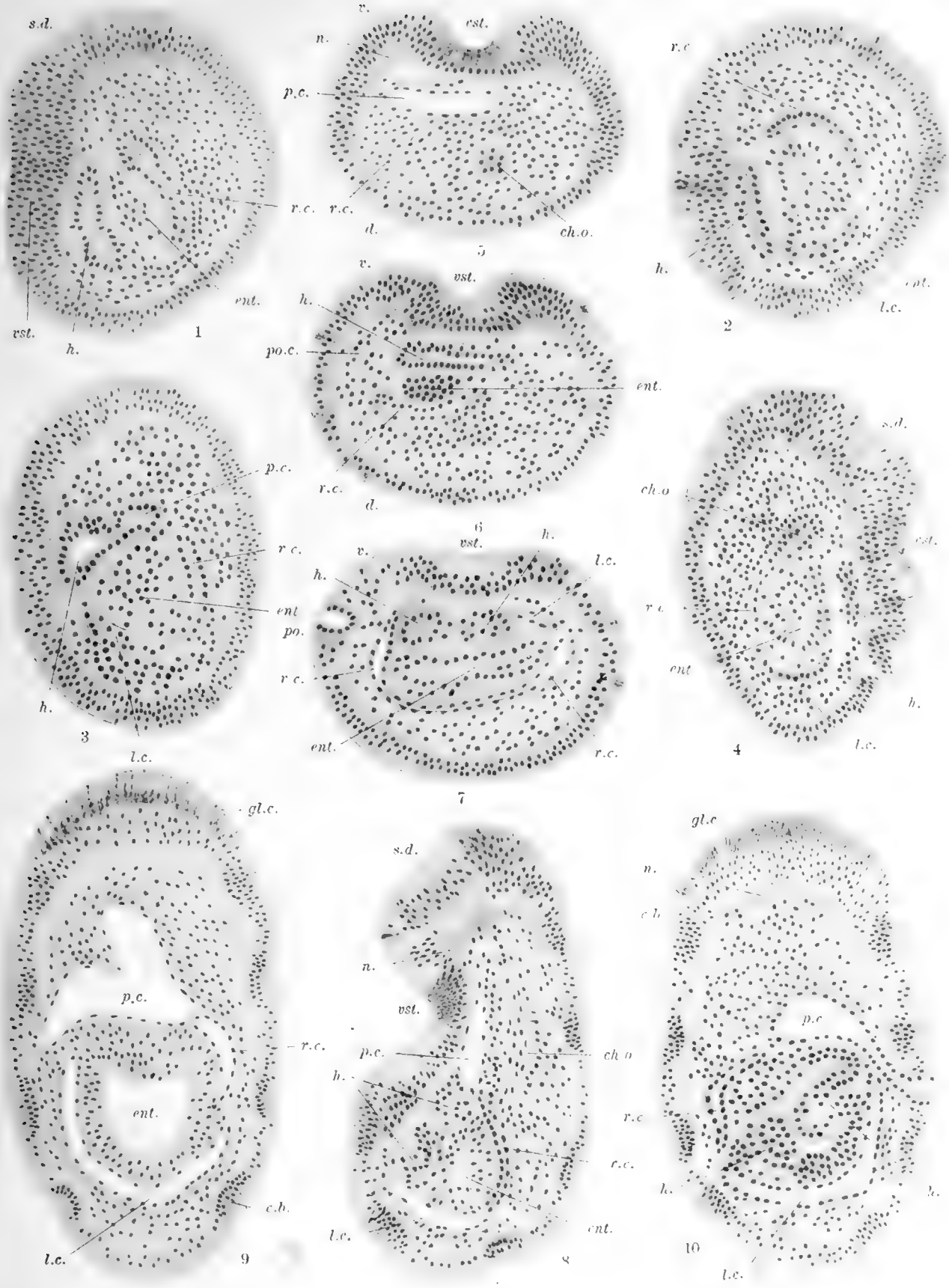

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Compsometra serrata.

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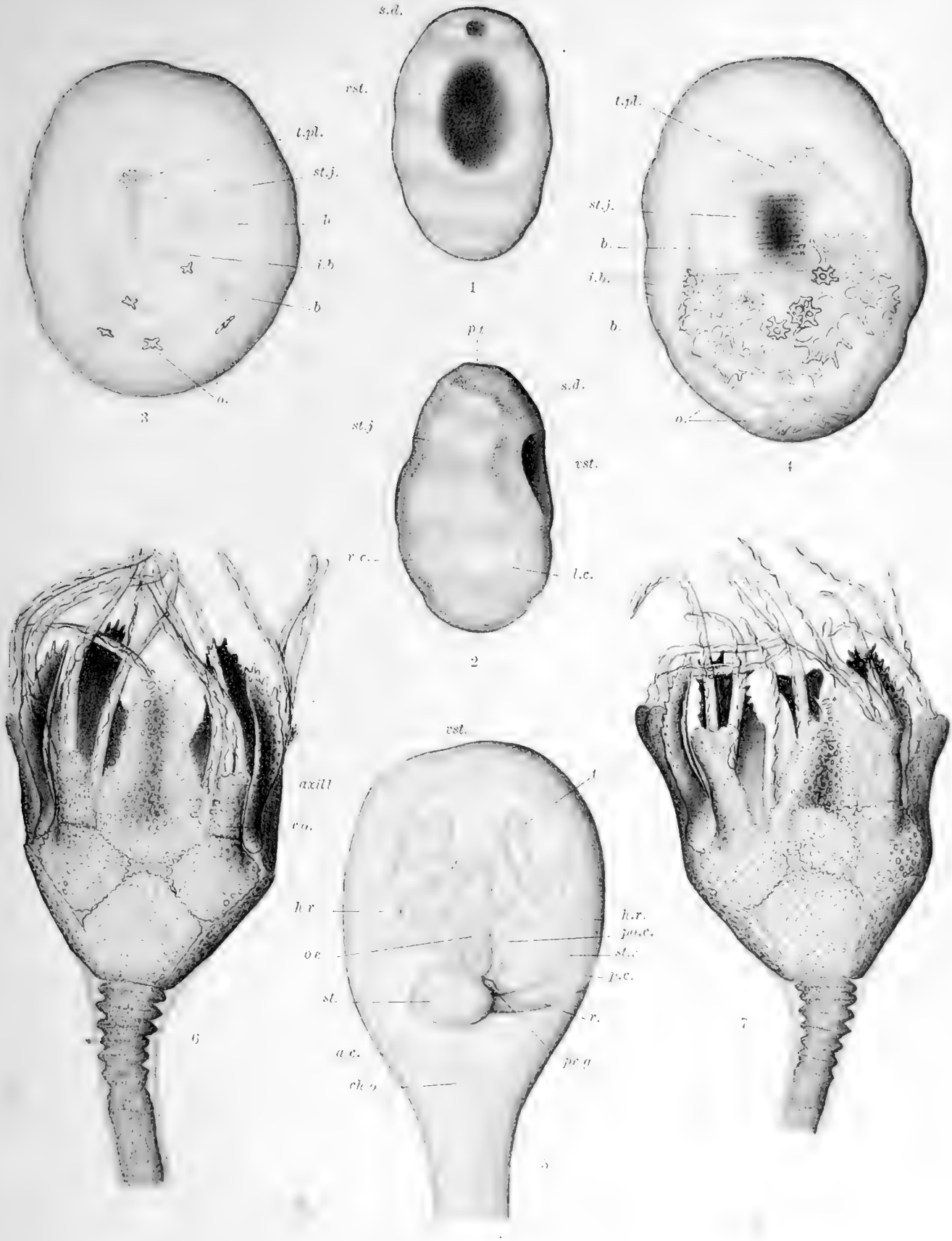

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Compsometra serrata.

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Compsometra serrata.

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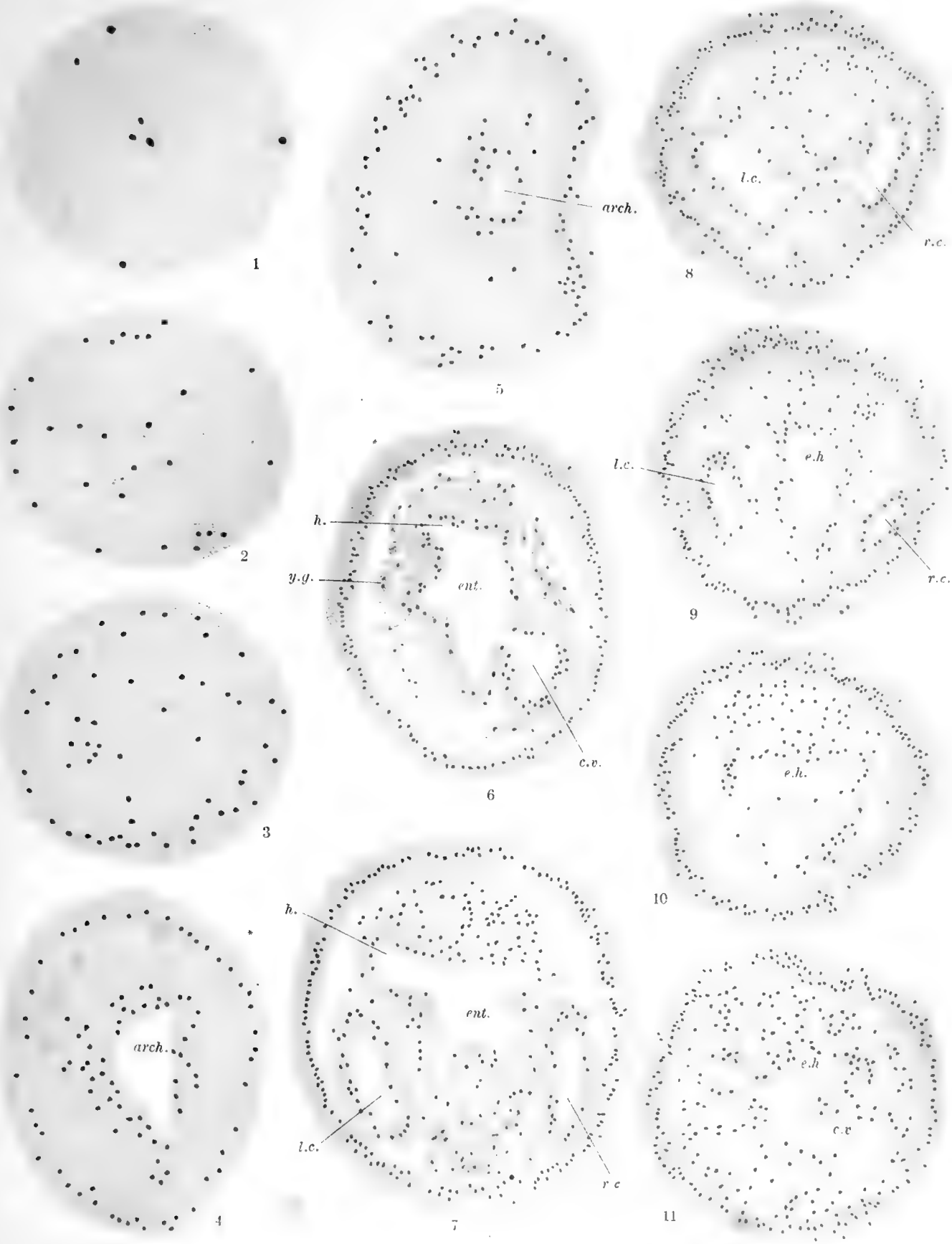

Th. M. del.

Isometra vivipara.

HELIOTYPE CO. BOSTON

Th. M. del.

Isometra vivipara.

HELIOTYPE CO. BOSTON

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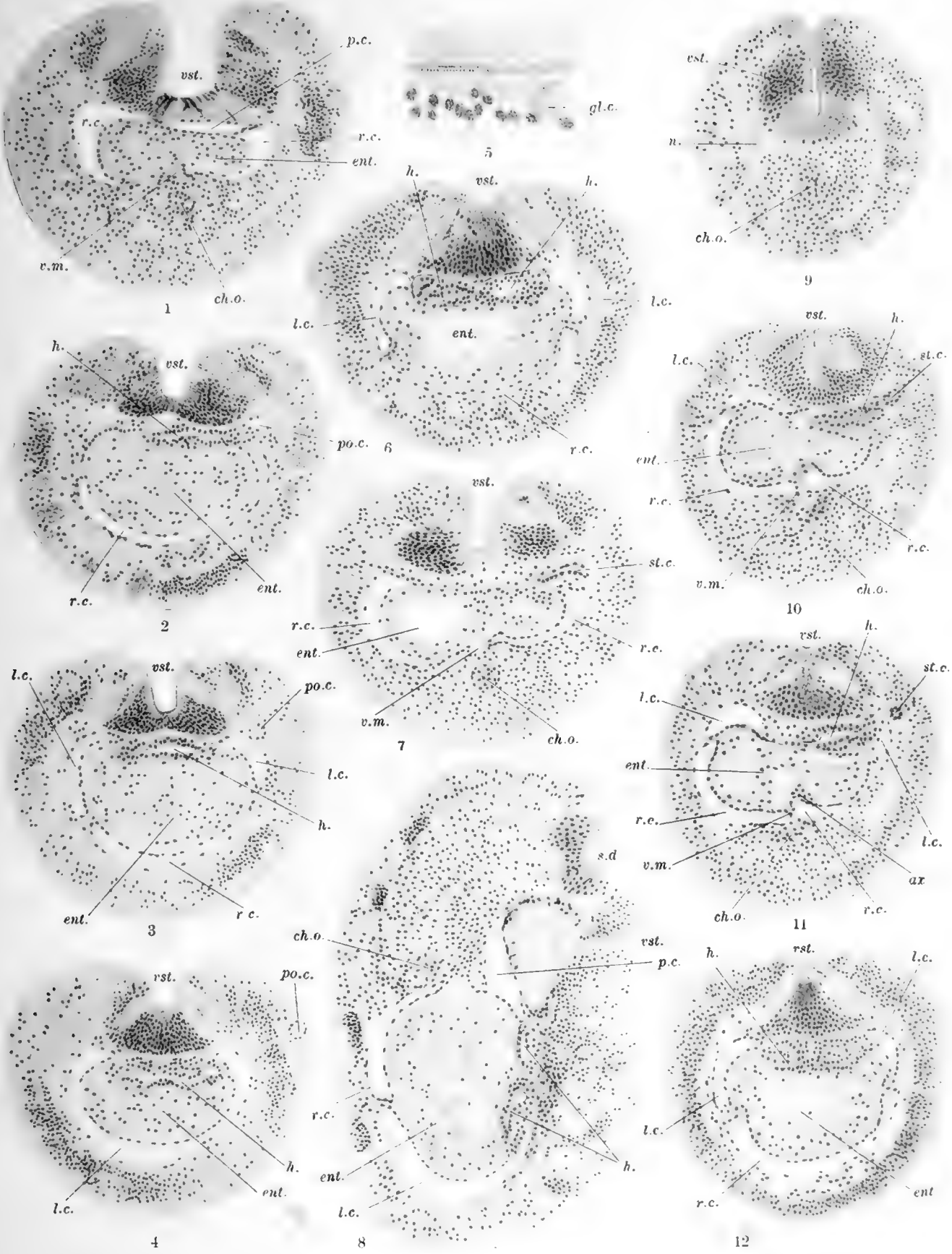
Isometra vivipara.



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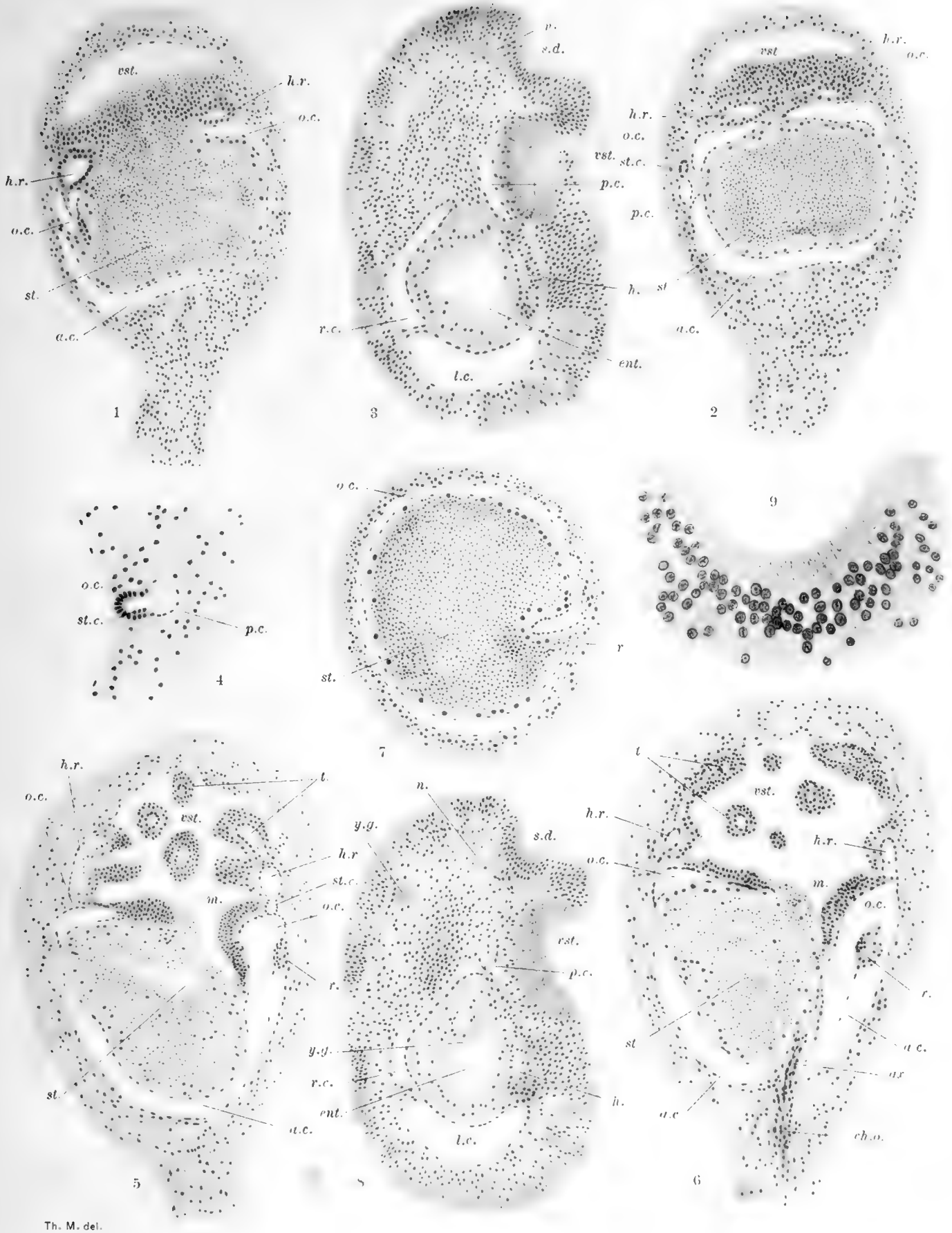

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Isometra vivipara.

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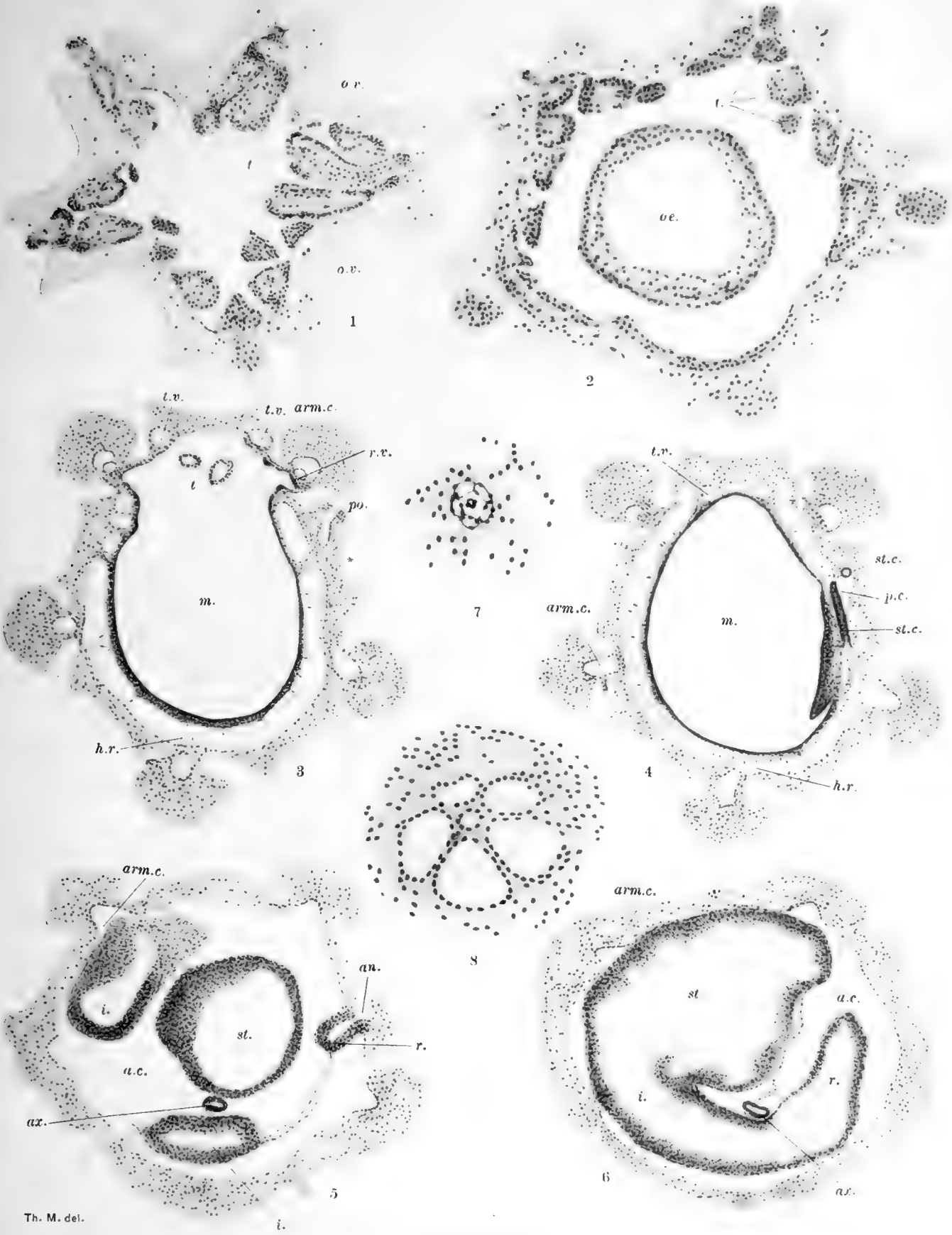
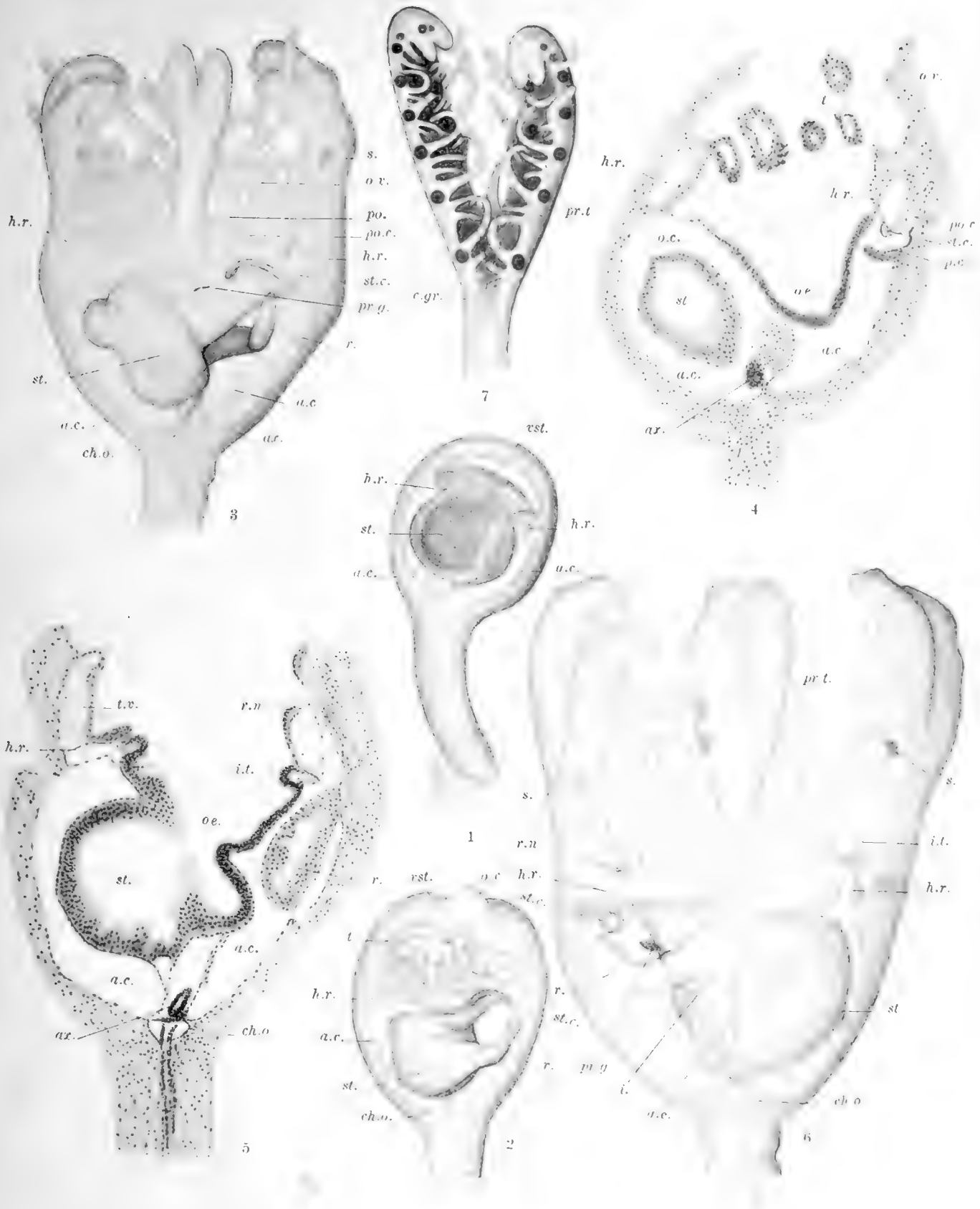


Isometra vivipara.

HELIOTYPE CO., BOSTON



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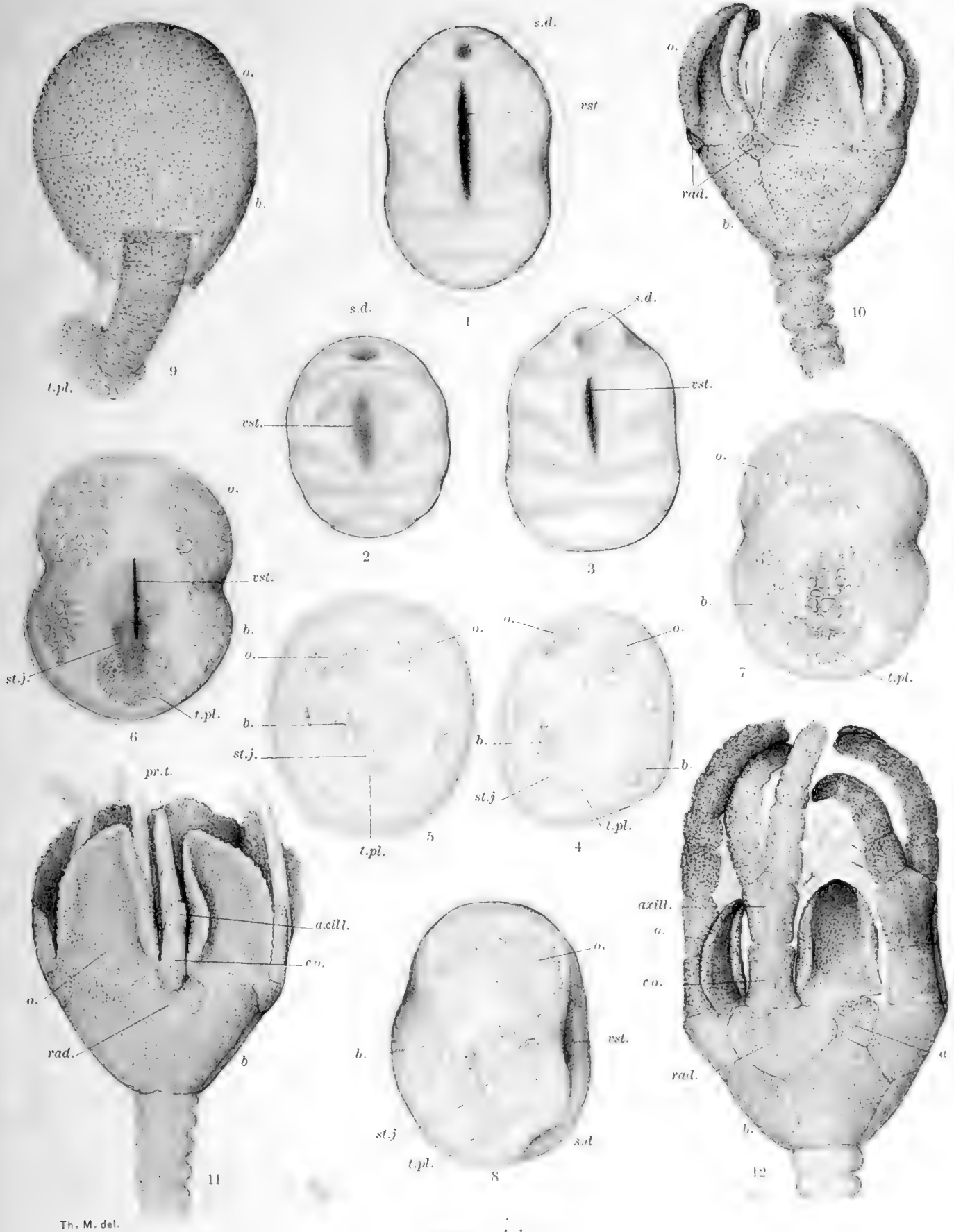

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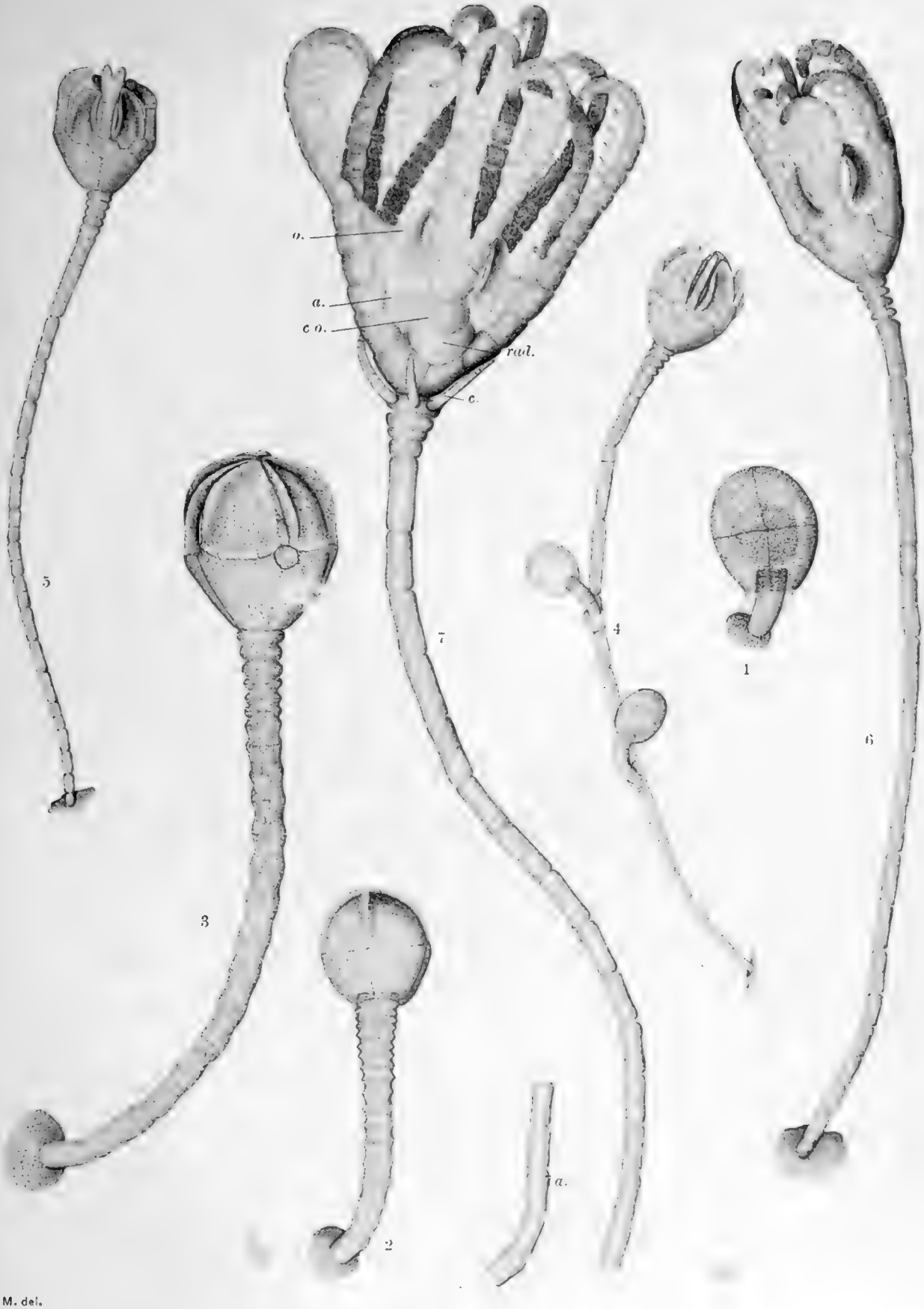


Th. M. del.

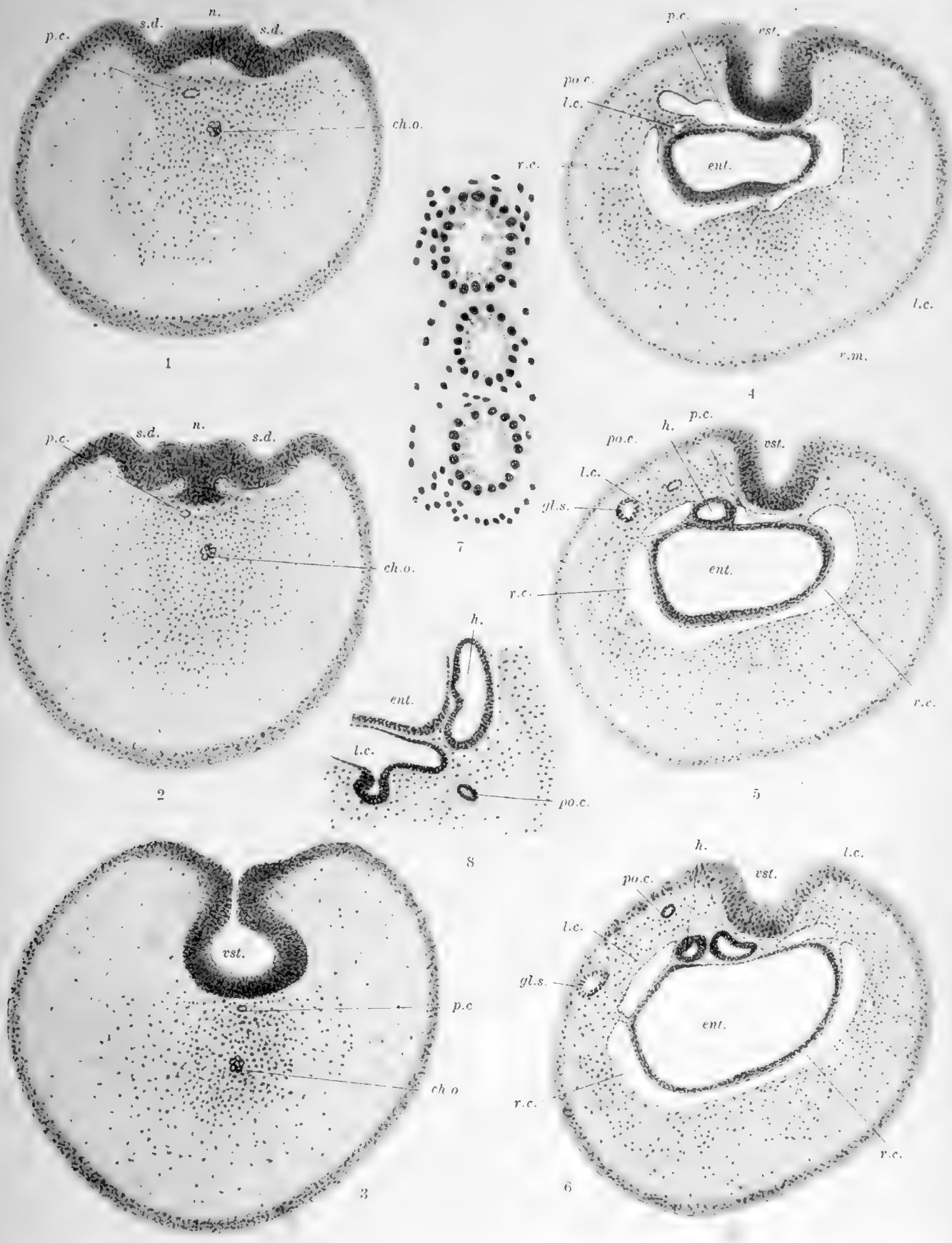
Isometra vivipara.

HELIOTYPE CO. BOSTON

Th. M. del.

Notocrinus virilis.

HELIOTYPE CO. BOSTON



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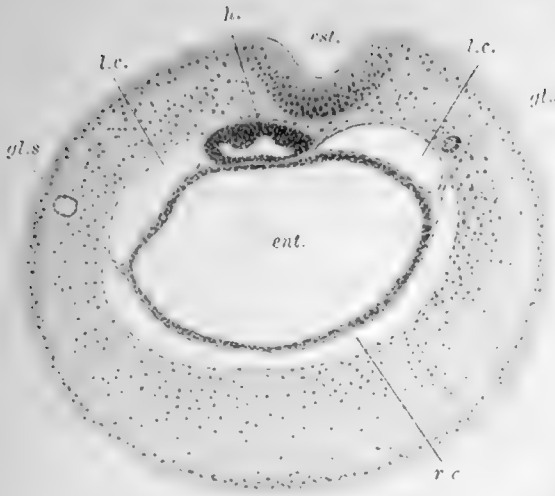
Notocrinus virilis.

HELIOTYPE CO., BOSTON



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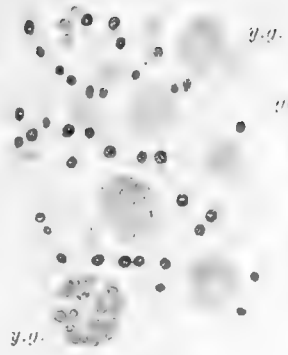

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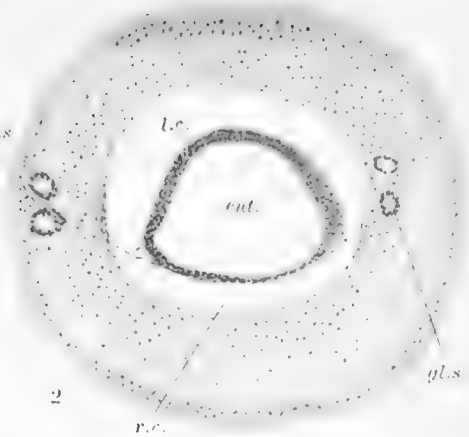

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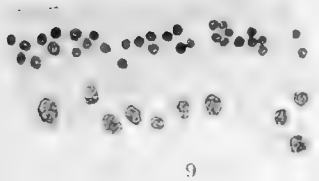

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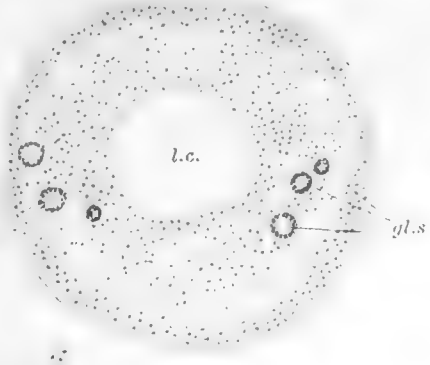

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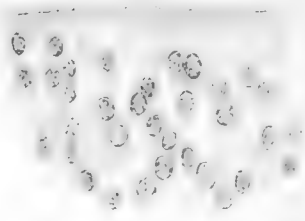

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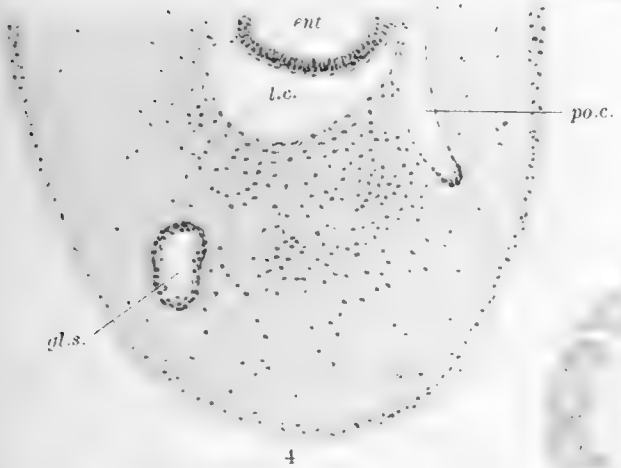

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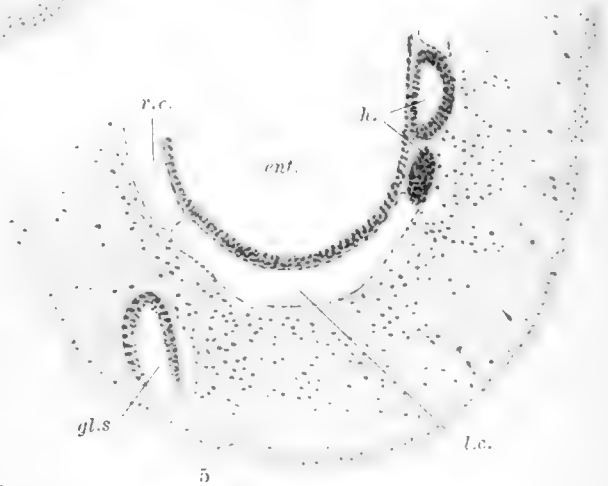

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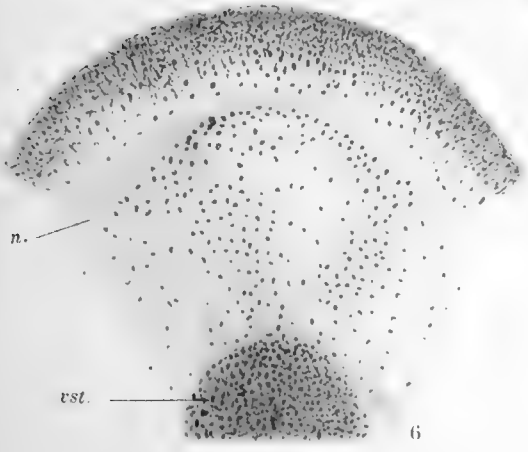

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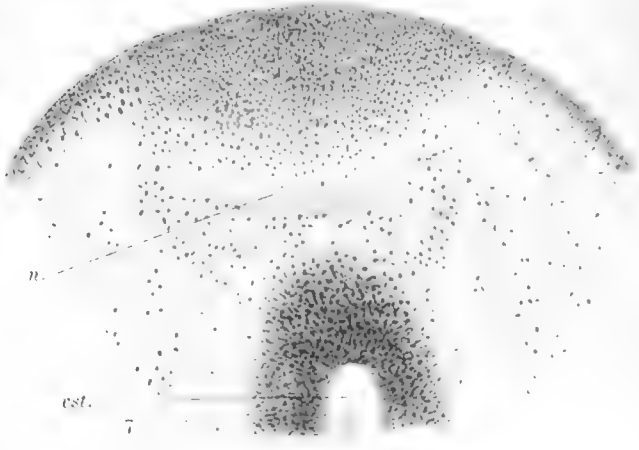
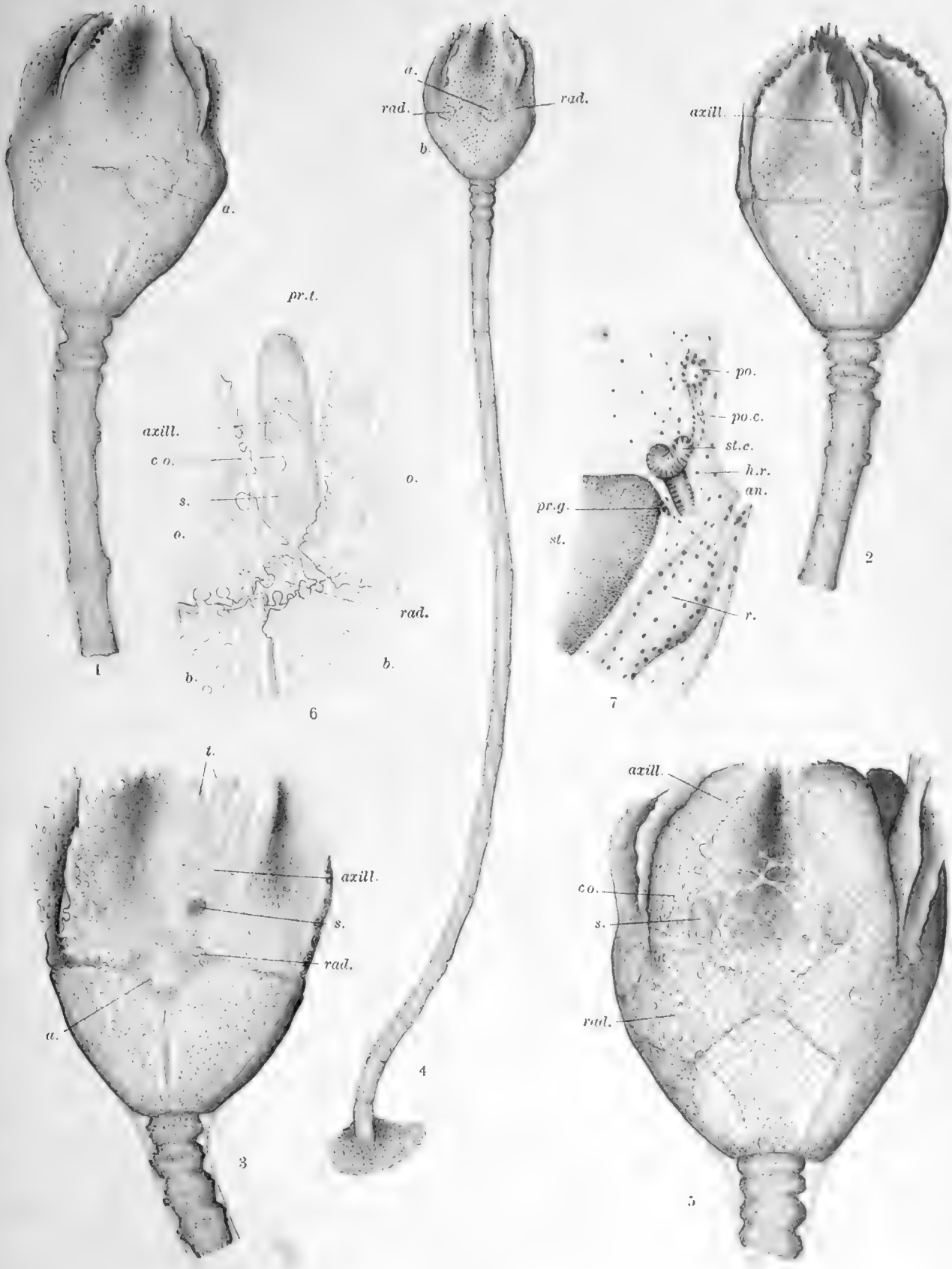


7

Tn. M. del.

Notocrinus virilis.

HELIOTYPE CO. BOSTON



Th. M. del.

Florometra serratissima.

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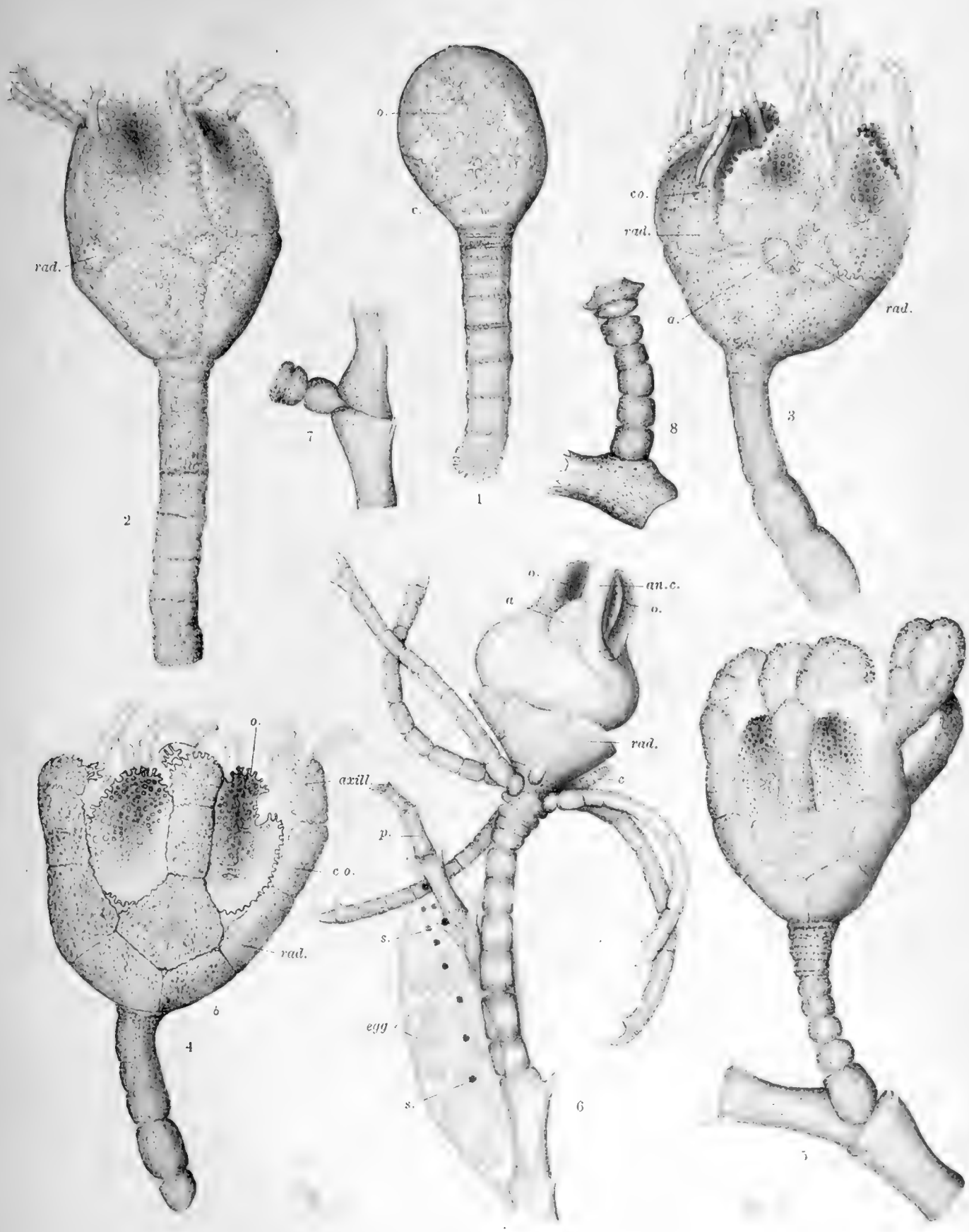

Thaumatometra nutrix.

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