IX. *On the Embryogeny of* Antedon rosaceus, *Linck* (Comatula rosacea *of Lamarck*). *By* Professor WYVILLE THOMSON, *LL.D., F.R.S.E., M.R.I.A., F.G.S., &c.* *Communicated by* THOMAS HENRY HUXLEY, *F.R.S.*

Received December 29, 1862,—Read February 5, 1863*.

IN the year 1827 Mr. J. V. THOMSON, Deputy Inspector-General of Military Hospitals, described and figured what he believed to be a new recent Crinoid, under the name of *Pentacrinus Europæus*; and in June 1835 communicated to this Society a "Memoir on the Star-fish of the genus *Comatula*, demonstrative of the *Pentacrinus Europæus* being the young of our indigenous species." In this memoir the author describes and figures a series of *Pentacrinus Europæus* from its earliest stage, in which it is represented as "an attached ovum in the form of a flattened oval disk, by which it is permanently fixed to the point selected, giving exit to an obscurely jointed stem ending in a club-shaped head"; to its most perfect attached condition, in which the head is compared with, and found closely to resemble the youngest free *Antedon* taken with the dredge.

The period of the disappearance of the pentacrinoid larvæ on the oar-weed exactly corresponds with that of the appearance of the most minute free *Antedons* in the water. Mr. THOMSON'S observations were conclusive. I am not aware that they have hitherto been repeated in detail on the European species, but the "pentacrinoid" stage of *Antedon* has ever since been the frequent and familiar prize of the dredger, the wonderful beauty and gracefulness of its form and movements, and its singular relations to the Echinoderm inhabitants of modern and of primæval seas, rendering it an object of ever recurring admiration and interest.

The remarkable discoveries of Professors SARS and JOHANNES MÜLLER on the metamorphoses of the embryo and its appendages in other Echinoderm orders rendered it probable that the germ of *Antedon* might pass through some earlier transitional stage before assuming the fixed pentacrinoid form.

Dr. W. BUSCH undertook this investigation, and for this purpose he visited Orkney in July 1849, and procured a supply of specimens in Kirkwall Bay. As those of Dr. BUSCH are the only recorded observations on the early stages in the embryology of the Crinoids, I shall briefly abstract his results published in MÜLLER'S 'Archiv,' 1849, and more fully

* Subsequently to the reading of this paper it was arranged that the author should take up a somewhat later stage in the development, which he had at first intended to leave to Dr. CARPENTER. The paper was accordingly returned to him that it might receive the necessary additions; but no alteration of importance has been made in the description of the earlier developmental stages, which formed the subject of the memoir presented to the Royal Society.

in his own 'Beobachtungen über Anatomie und Entwickelung einiger wirbellosen Seethiere' (Berlin, 1851).

The author alludes to the position of the ovary in *Antedon*, and to the peculiar way in which the impregnated ova remain hanging in bunches from the ovarian aperture. He describes the formation from the segmented yelk-mass of a uniformly ciliated club-shaped embryo, which escapes from the vitelline membrane and swims freely in the water (Beobachtungen, &c., pl. 13. fig. 13). During the next four-and-twenty hours a bunch of long cilia appears on the narrower anterior extremity, and near it, on the side of the embryo which is turned downwards in a state of rest, a small round opening which he regards as the provisional larval mouth. Three slightly elevated ridges now gird the body transversely at equal distances (*op. cit.* pl. 13. fig. 14), and gradually become clothed with long cilia, the smaller cilia disappearing from the intervening spaces. The integument between the first and third ciliated ring becomes inverted into a large oval depression, a fourth ciliated band appears near the posterior extremity of the embryo, and a few delicate areolated calcareous plates are developed within the integument. The embryo now becomes slightly curved, the large oval opening which the author regards as the excretory orifice becomes more distinct in the centre of the ventral surface, and the embryo attains its most perfect larval form (pl. 14. figs. 1 & 2). The form of the larva now rapidly alters; on the ninth day (pl. 14. fig. 3) the posterior extremity has become much enlarged and invested with a thick gelatinous integument. This distended extremity becomes slightly lobed, the anterior bunch of cilia and the posterior ciliated bands disappear, the mouth and anus become indistinct (pl. 14. fig. 5), and at length (pl. 14. fig. 6) a row of four delicate tubes bearing pinnules appears along either side of the larva, the rudiments of the arms of the Crinoid. Dr. Busch was unable to pursue his researches further. In many points his observations are inconsistent with those which I have repeated during the last three years with great care, and I believe that he has misconceived the nature and relations of the organs of the larval embryo. Dr. Busch's account of the first appearance of the pentacrinoid form is certainly contrary to my experience; I have been led, however, by inconsistencies in my own observations upon different broods in different seasons, to believe that the mode of development may to a certain extent vary with circumstances. I find, for instance, that when the ova are liberally supplied with fresh sea-water and placed in a warm temperature, the later stages of larval growth are, as it were, hurried over; so that the free larva scarcely attains its perfect form before being distorted by the growing crinoid. In other instances, in colder seasons and in a less favourable medium, the larva reaches a much higher degree of independent development, and retains for a longer period the larval form.

In 1859 I communicated to this Society a short notice (Proc. Royal Society, vol. ix. p. 600) of the earlier stages in the development of *Antedon*. My observations were made upon one or two broods of *Antedon* in a single season. I had an opportunity at that time of tracing carefully the earliest phases in the development of the pseudembryo, but

subsequent observations have led me to believe that in some of the later stages the young of *Antedon* were confounded with those of a Turbellarian, which resembled them closely, and which during that season accompanied them in great numbers. These earlier observations were imperfect and hurried in consequence of the difficulty which I then experienced in rearing the young, of their extreme delicacy, and of the rapidity with which they passed through their developmental steps. These difficulties have since been to a certain extent overcome by the frequent repetition of the observations, and by due regulation of the temperature of the tanks and of the supply of food and water.

M. DUJARDIN has figured* with great accuracy, but without any description, an early stage in the development of the pentacrinoid young of *Antedon Mediterraneus*, Lam., which he observed at Toulon in May 1835. The figure represents the oral valves partially open, with a group of tubular tentacles protruded from the cup. It is highly characteristic.

On the 16th of February, 1863, Professor ALLMAN communicated to the Royal Society of Edinburgh† a paper "On a Prebrachial stage in the development of *Comatula*." The author procured a single specimen of the stage represented by DUJARDIN, and in Plate XXVI. of the present memoir, among the refuse of a dredging boat on the coast of South Devon. Dr. ALLMAN describes this minute Crinoid as consisting of a body and a stem; the body formed of a calyx covered by a pyramidal roof. The calyx is composed of five large separate plates. Between the lower edges of these plates and the summit of the stem, there is a narrow zone, in which "no distinct indications of a composition out of separate plates can be detected." Between the upper angles of every two contiguous plates there may, with some care, be made out a minute intercalated plate. The pyramidal roof which closes the cup is composed of five large triangular plates, each supported by its base upon the upper edge of one of the large plates of the calyx, and with the small intercalated plates encroaching upon its basal angles. Long flexible appendages or cirri rise out of the calyx, and in the expanded state of the animal, are thrown out between the edges of the five diverging plates of the roof. Dr. ALLMAN counted fourteen of these appendages, but could not determine their exact number. "They appear to be cylindrical with a canal occupying their axis; as far as they can be traced backwards they are seen to be furnished with two opposite rows of rigid setæ or fine blunt spines. Between every two opposite setæ a transverse line may be seen stretching across the cirrus, and indicating its division into transverse segments." The author never succeeded in tracing these appendages to their origin. Besides these long extensile cirri, there is also an inner circle of short apparently non-extensile appendages. It was only occasionally that the author succeeded in getting a glimpse of these. "They appear to constitute a circle of slightly curved rods or narrow plates probably five in number, which arch over the centre and are provided along their length with two opposite rows of little tooth-like spines. They seem to be articulated to the upper or

* Suites à Buffon. Zoophytes Echinodermes, par M. F. DUJARDIN et par M. F. HUPÉ. Paris, 1862.

† Transactions of the Royal Society of Edinburgh, vol. xxiii.

ventral side of the calyx by their base, and may be seen in a constant motion, which consists in a sudden inclination upon their base towards the centre, followed immediately by a resumption of their more erect attitude." The interior of the calyx is occupied by a reddish-brown visceral mass, obscurely visible through the walls. The author did not succeed in getting a view of the mouth, and detected no anal aperture. Dr. ALLMAN accurately describes the general structure of the stem (*loc. cit.* p. 243); he conceives, however, that "the multiplication of the segments of the stem seems to take place by the division of the pre-existing ones, and this division seems indicated by the transverse ridges, which in several of the segments may be seen running round the centre."

A detailed description of the developmental stage which forms the subject of Dr. ALLMAN'S communication will be found at pp. 525 & 526 of the present memoir. It is unfortunate that so able an observer had not an opportunity of making himself fully acquainted with this interesting form by the study of a sufficient number of specimens.

In 1856 Professor SARS communicated to the Seventh Meeting of the Scandinavian Association a most interesting paper on the Pentacrinoid stage of *Antedon Sarsii* (DUBEN and KOREN). The only specimen observed was dredged on the 14th of March with *Halichondria ventilabrum*, from a depth of 50 fathoms near Bergen. It was in every respect a fully developed *Antedon*, from the centre of whose centro-dorsal plate proceeded a long thin cylindrical articulated stem attached inferiorly to the sponge. The disk with its central mouth, the long, cylindrical, excentric anal tube, the radial grooves, the ten arms with their characteristic articulations and syzygies, the pinnules with their tentacles, the rows of red-brown spots on the margins of the grooves on the arms and pinnules, and the dorsal cirri, were completely developed as in the adult form. All the arms were unfortunately broken, the portions left bore nine to ten pairs of pinnules. Six of these were of the ordinary form; the three or four proximal pairs, which alternated less regularly, were setaceous, destitute of tentacles and pigment spots, the innermost pair longer than the others, as in the adult; all the pinnules were attenuated, the generative element being as yet undeveloped. The dorsal cirri, twenty to thirty in number, were thickly set round the circumference of the centro-dorsal plate. They were fully formed, and the joints and terminal claws had the form characteristic of *A. Sarsii*. The stem was 20 millimetres in length, and consisted of thirty-one joints; but as it was broken from its place of attachment, some of the inferior joints may have been lost. The two or three lowermost joints preserved became shorter towards the base, and the upper joints towards the attachment of the stem to the centro-dorsal plate decreased likewise in length; the second joint was about half the length of the third, and the first only half that of the second; but the first joint was dilated upwards to its insertion. The middle joints of the stem are three to three and a half times longer than wide, and are all dice-box shaped like the joints of the dorsal cirri of the species.

From this observation it would appear that the development of *A. Sarsii* is continued

to a much later period in the pedunculated condition than that of *A. rosaceus*; the disengagement of the latter species from its stem constantly occurs between the middle of August and the middle of September. The capture of the specimen described by Sars in March would seem to indicate that the development of the Pentacrinoid of *A. Sarsii* extends over nearly a year.

The early portion of the history of the development of *Antedon* described in the following pages divides itself naturally into two stages.

The Echinoderms present in the most marked degree a peculiarity which seems to be only imperfectly indicated in the other invertebrate subkingdoms. This peculiarity consists in the successive development from a single egg, of two organisms, each apparently presenting all the essential characters of a perfect animal. These two beings seem to differ from one another entirely in plan of structure. The first, derived directly from the germ-mass, would appear at first sight to homologate with some of the lower forms of the Annulosa; the second, subsequently produced within or in close organic connexion with the first, is the true Echinoderm. The extreme form of this singular cycle, in which the development of a provisional zooid as a separate, independent, living organism, is carried to its full extent, is by no means constant throughout the whole subkingdom, although its existence has been established for all the recent orders. In each order it appears to be exceptional, and in certain cases it is known to be carried to its most abnormal degree in one species, while in a closely allied species of the same genus the mode of reproduction differs but slightly from the ordinary invertebrate type.

To avoid ambiguity in the discussion of such singular relations, I believe it is necessary to introduce certain new terms. For an organism which possesses all the apparent characters of a distinct animal, which is developed from the germ-mass, and which maintains a separate existence before the appearance of the embryo, I would propose the term *pseudembryo*; and for all the appendages which homologate with the whole or with parts of such a pseudembryo, even although they do not assume fully the characters of a distinct animal form, I would propose the term *pseudembryonic appendages*. The same prefix may distinguish the organs of the temporary zooid, where such exist, *pseudostome*, *pseudocele*, *pseudoproct*, &c. The reason for the retention of this series of terms, and for the rejection as applied to the provisional organism of the ordinary terms "embryo" and "larva," will be fully discussed hereafter.

The first stage includes the development, structure, and life-history of the pseudembryo.

While the special external form of the pseudembryo is still perfectly retained, and while its special functions are still in full activity, the form of the pentacrinoid embryo is gradually mapped out within the provisional zooid, and the permanent organs of the embryo are differentiated within its sarcode-substance. The pseudembryo then becomes gradually distorted by the embryo developing within it, its special assimilative and locomotive organs disappear, and the external layer of its sarcode-substance subsides into the

general integument of the embryo, still retaining sufficiently the histological characters of the pseudembryonic integument to leave no doubt that it is simply produced by its modification and extension.

From the appearance of the first traces of the permanent embryonic structures within the pseudembryo, the development of the pentacrinoid larva advances steadily; and there is no natural separation into stages of its subsequent progress until the young *Antedon* drops from the larval stem. At one period, however, during the development of the pentacrinoid there is a marked change in the external form and in the anatomical relations of the larva, owing to the sudden widening out of the radial portion of the disk, and the breaking through of the anal opening. Division of labour has been found expedient in the present investigation, and my portion of the task ends just before the development of the Pentacrinoid has reached this point. I think it only right, however, to mention that Dr. CARPENTER, who has been at the same time working out the later stages in the development of the Pentacrinoid and the structure of the mature *Antedon*, has most freely communicated to me all his results. My description of the development of the pentacrinoid larva has had therefore all the advantage of the light thrown upon the earlier stages by Dr. CARPENTER'S researches on the later.

The observations whose combined results have been condensed into the present communication have extended over the last four years. I have had an opportunity each season of watching the more or less favourable development of one or two sets of embryos. As stated above, these observations have not in all cases thoroughly tallied; their inconsistencies depending, I believe, in some instances upon error of observation, and in others upon actual discrepancies in the process of development under different circumstances. In Arran, in June 1860, I had a most favourable opportunity of tracing a single brood from the segmentation of the yelk almost to the maturity of the pentacrinoid young. I took the opportunity to revise and check previous special observations; and each stage of the development of this group was described and figured with great care, and with the advantage of previous familiarity with the successive modifications in form. To avoid all possibility of confusion, I have incorporated in the following detailed description those results only which were confirmed by these later observations; and all the figures of the free pseudembryos, and of the origin of the pentacrinoid form, refer to the successive stages in the development of this single brood. On this occasion the pseudembryos remained for perhaps a somewhat shorter time than usual in their free condition, and their growth was early arrested by the development of the permanent calcareous plates. The pseudembryos, however, during their brief independent existence, attained their perfect and usual external form; and the subsequent transitions, though rapid, were normal.

The ovaries of *Antedon* have been frequently described. During the latter part of summer, autumn, and early winter they can only be traced as delicate lines of whitish stroma, beneath the integument of the upper (oral) surface of the pinnules, and immediately beneath the tentacular canals which in the ordinary condition of the pinnules

lie in the groove of the calcareous joints. About the end of February or the beginning of March, the integument of the pinnules becomes slightly turgid; and this turgescence increases till towards the end of May or the beginning of June, when the eggs are fully formed.

The mature ovaries are short, entire, fusiform glands distending widely the integument of the pinnules, and provided with a special aperture which perforates the distended skin on that side of the pinnule which is turned towards the end of the arm. The aperture is bounded by a somewhat thickened ring of apparently elastic tissue, which acts as an imperfect sphincter. Examining the ovary by compression shortly after it has begun to enlarge, the meshes of the stroma (Plate XXIII. fig. 1) are found to contain a clear mucilaginous protoplasm with minute ova in various early stages of development. Tracing the development of the ova, the formative fluid first becomes slightly opalescent, and a minute, highly refractive, lenticular body makes its appearance, which subsequently declares itself as the germinal spot. This body remains some time slowly enlarging without much further change. A delicate film now rises from one side of it, and this film gradually extends till the germinal spot appears to be attached to the inner wall of a spherical cell with perfectly transparent fluid contents, the germinal vesicle (Plate XXIII. fig. 2, *a–c*). The blastema in the neighbourhood of the germinal vesicle becomes slightly granular; and the granules accumulate so as to form a distinct granular layer round the cell. This layer, the nascent yelk, is shortly found to be invested by a delicate vitelline membrane; but this membrane does not appear to originate from the germinal vesicle as a nucleus, as in the case of the latter from the germinal spot. The impression rather is that the surrounding fluid is influenced to a certain distance by the chemical forces acting in the germinal vesicle, and that a membrane is produced at the point of junction between the blastema so influenced and the general fluid contents of the ovary. The egg now increases in size without much further change in structure. The vitelline membrane rapidly expands (Plate XXIII. fig. 2, *d–o*), and its contents become more dense, till at length it has attained a diameter of about ·5 millimetre, and is entirely filled with a yelk-mass composed of oil-cells of the usual form.

The ripe eggs are now discharged from the ovary; they remain, however, for some time (in some cases three or four days) entangled in the loose stroma of the ovary, and hanging from the ovarian aperture like a bunch of grapes.

The testis resembles the ovary in form and situation. A transparent mucus distends the integument of the pinnule. The fluid becomes opalescent, then granular, and finally the cavity becomes filled with a mass of fusiform parent cells (Plate XXIII. fig. 4). The contents of these cells are at first perfectly transparent; soon, however, they lose their transparency and become granular, and at length the cells are found to contain a progeny of ten or twelve minute spherical "vesicles of evolution." Bright refractive spots, the heads of the spermatozoa, three or four in number, appear in each of these secondary cells; and finally, the walls of the parent cells and vesicles give way, and the

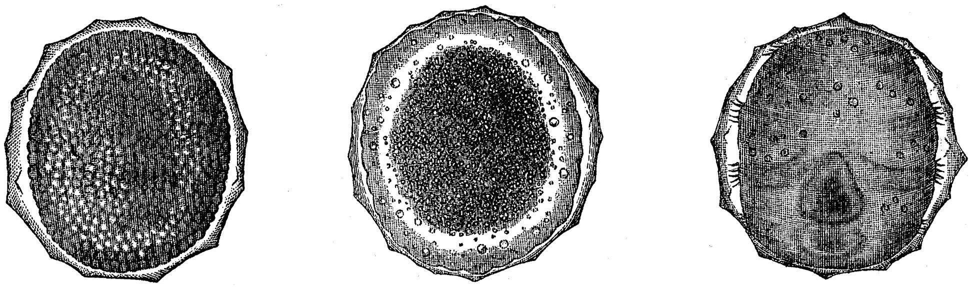
cavity of the pinnule is filled with a mucilaginous liquid charged with myriads of mature spermatozoa (Plate XXIII figs. 5 & 6).

The form of the spermatozoon is intermediate between that of a club on cards and a spade (Plate XXIII. fig. 7), with a vibratile filament of great length attached to the obtuse end. There is no special opening to the testis, so that the female may be at once distinguished by the ovarian aperture. The seminal fluid seems to be discharged by the thinning away and dehiscence of the integument. The spermatozoa are dispersed in the water. Impregnation appears to take place after the discharge of the ova, but while they are still hanging from the ovarian aperture.

An hour or two after impregnation the germinal vesicle disappears, or at all events leaves its former superficial position. The yelk-mass contracts and becomes more opaque and dense, leaving a clear space immediately within the vitelline membrane, which is thus more clearly defined, perfectly transparent and structureless, with the surface slightly and irregularly echinated (Plate XXIII. fig. 8). Consequently on the contraction of the yelk, a number of minute spherical pale yellow oil-globules are apparently pressed out into the space within the vitelline membrane (Plate XXIII. fig. 11). The appearance of the "richtungs-bläschen" may be very readily traced in the egg of *Antedon*. At a point on the circumference of the yelk a very distinct globule, about half the diameter of the germinal vesicle, with an obscure nucleus, passes out of the yelk-mass into the surrounding space. In all the cases in which I have observed it, this globule has been accompanied by two or three minute rounded granular masses. Plate XXIII. fig. 14, *a–c*, are careful representations of three groups of these globules. They remain perfectly distinct from the divisions of the yelk during the earlier stages of segmentation; at the close of this process, however, it becomes difficult to distinguish them from the ultimate divisions of the mulberry mass. In *Antedon*, yelk-segmentation is complete (Plate XXIII. figs. 9–13). Its first appearance is a slight groove passing inwards from the circumference of the yelk, immediately at the point where the so-called "richtungs-bläschen" have been extruded. If the egg be now subjected to slight pressure, a transparent nucleus may be observed in the centre; and at each stage of segmentation the nucleus may be readily detected in the centre of each segment. A few hours after segmentation has been completed, the surface of the germ-mass becomes slightly more transparent. The ultimate yelk-spherules are still sufficiently evident, giving the surface a distinctly mammillated appearance (woodcut A).

This gradually disappears, the spherules seem to coalesce upon the outer surface, remaining distinct a little longer towards the inner surface of this rudimentary germinal membrane, and a few hours later they have become entirely fused into a continuous structureless sarcode-layer (woodcut B). While these changes are taking place in the outer layer, the central portion of the germ-mass becomes resolved into a mucilaginous protoplasm sufficiently fluid towards the centre to allow of an active circulation of granules and oil-globules, but apparently continuous with, and graduating into, the lower surface of the more consistent peripheral layer.

A. B. C.



A. Usual condition of the mulberry mass immediately after segmentation has been completed. B. Appearance of the nascent pseudembryo after the coalescence of the ultimate spherules of the germ-mass. C. Pseudembryo shortly before the rupture of the vitelline sac.

In this case the development of the pseudembryo from the germ-mass resembles in every way the development of the embryo in most of the invertebrate groups; on three occasions, however, during the examination of a series of eight or ten broods, a whole brood of embryos were evolved under somewhat different circumstances. The surface of the mulberry mass became somewhat looser and more transparent, and under slight pressure a large, somewhat darker and more consistent central nucleus was observed (Plate XXIV. fig. 1). This nucleus increased in size from hour to hour, the peripheral portion of the contents of the vitelline membrane gradually liquefying and becoming absorbed into the nucleus. At length the oval outline of the pseudembryo might be traced through the flocculent mass of semitransparent semifluid yelk. The remainder of the yelk now became completely transparent and liquid, the embryo increased rapidly in size, and its form was more clearly defined through the wall of the vitelline sac (Plate XXIV. figs. 1–4). I believe, however, that this latter is an abnormal mode of development, depending probably upon imperfect aëration.

Observed during the process of development within the vitelline membrane, the embryo is at first nearly regularly oval, and the surface appears to be uniformly ciliated. I have never met with an instance in which the embryo escaped in this condition. In all the cases which I have observed, the ciliated bands so characteristic of the pseudembryonic form have made their appearance before the rupture of the vitelline sac (woodcut, C); and frequently the pseudembryo has become somewhat reniform, a depressed ciliated patch indicating the position of the pseudostome. The pseudembryo frequently, but not constantly, rotates slowly and irregularly within the vitelline sac, the rotation depending evidently upon the action of the cilia on the surface of the pseudembryo. Immediately after escaping from the vitelline membrane, the pseudembryo is about ·8 millim. in length, oval, slightly enlarged towards one extremity, and girded by four nearly equidistant transverse ciliated bands. It consists throughout of very delicately vacuolated sarcode, which becomes more and more consistent towards the periphery, where it forms a smooth firm surface, which is not, however, bounded by any definite membrane. Towards the centre the substance becomes more fluid, and is

turbid with oil-cells and granules. At this stage distinct molecular motion may be observed in the central portion, and a granular semifluid mass escapes if the larva be ruptured by pressure. The surface is dotted over with the wider ends of large pyriform lemon-coloured oil-cells immersed perpendicularly in the sarcode. Between these oil-cells the sarcode is nearly transparent, containing merely a few scattered granules. The ciliated bands project slightly above the general surface. They are greyish and granular, and appear to be rather more consistent than the surface of the sarcode, which rises up to them, sinking somewhat in the interspaces. The cilia are very long; they do not vibrate with the regular rhythmical lash of ordinary cilia, but seem to move independently, their motion regulating the rapidity and direction of the movements of the animal in the water. There is a large tuft of still longer cilia in perpetual vibratile motion at the narrower (posterior) extremity of the body. At first the pseudembryo is simply barrel-shaped, and regularly hooped by the four parallel transverse ciliated bands. Sometimes, while yet within the vitelline sac, but at all events within a few hours after its rupture, the body becomes slightly curved, somewhat like a kidney bean; and on the concave surface, the third band from the anterior extremity arches forwards towards the second band; and in the wider space thus left at this point between the third and fourth bands, a large pyriform inversion of the superficial sarcode-layer takes place (Plate XXIV. fig. 7).

This inversion is narrower anteriorly, becoming wider and deeper towards the posterior extremity. Its margins are richly ciliated. Simultaneously with the appearance of this depression, a small round aperture may be observed immediately behind it, separated from it by the fourth ciliated band, and close to the posterior tuft of cilia. This aperture is surrounded by a ring of darker granular tissue, and the outline of a short arched canal may be detected passing under the fourth ciliated band and uniting the deep posterior extremity of the larger aperture, which thus becomes irregularly funnel-shaped, with the smaller circular opening.

The large ciliated key-hole-like inversion of the sarcode is undoubtedly the pseudostome; and resembles closely in form and position the same organ in other echinoderm pseudembryos. The loop-like canal beneath the posterior ciliated band is the extremely rudimentary pseudocele, and the round aperture is the pseudoproct. The pseudembryo swims with either extremity in advance indifferently; the anterior and posterior extremities are therefore only defined at this stage by the relative positions of the mouth and anus. It swims rapidly with a peculiar swinging semi-rotatory motion. The oral surface is turned downwards in a state of rest. The pseudembryo sometimes remains for several days, increasing in size till it becomes from 1·5 millim. to 2 millims. in length, without undergoing any further change. In other cases indications of the areolated calcareous plates of the Echinoderm appear within a few hours of the rupture of the vitelline sac.

Usually not until the pseudembryo has assumed its mature and perfect form, but sometimes much earlier, several minute calcareous spicula make their appearance beneath

the external layer of sarcode. The spicula are at first blunt irregular cylinders; but shortly they fork at either end, and at length, by repeatedly dichotomizing and anastomosing, they form delicate plates of calcareous network. When definitely developed, these plates are ten in number, and they arrange themselves in two transverse rings of five each, within the wider anterior portion of the pseudembryo, the posterior row being slightly in advance of the pseudostome. These plates are at first round and expand regularly; the plates of the anterior row being arranged symmetrically above those of the posterior series (Plate XXIV. fig. 7.). They are imbedded in the substance of the sarcode, which for some time remains transparent within and without; gradually, however, the space within the plates becomes turbid and opaque, and at length a rounded brownish granular mass fills up the lower portion of the cup formed by the calcareous trellis. A series, varying in number, of delicate calcareous rings may now be detected, forming a curved line passing backwards from beneath the centre of the lower ring of plates, behind and slightly to the left of the mouth of the pseudembryo; and a large cribriform plate is rapidly developed close to the posterior extremity behind the anus (Plate XXIV. fig. 6). The rings are regular in their inner contour, but externally they are rough with minute branching spicula and excrescences.

About twenty-four hours later the pseudembryo still retains its original form, and its rapidity of movement in the water is unimpaired. The anterior wider portion has become still more bulbous and enlarged, and a thick layer of firm transparent sarcode, thickly studded with columnar oil-cells, forms a dome-shaped arch over the anterior extremity. The sarcode external to the calcareous framework is extremely transparent, and the dark granular hemispherical brownish mass within the lower tier of plates is more clearly defined; while above it and within the upper part of the space included within the plates, the outline of a second more transparent delicately granular hemisphere has become apparent. The two rows of plates are now irregularly square in outline, the plates of the lower series slightly contracted beneath, and those of the upper tier above; so that the ten plates forming the two rows, and now placed in close juxtaposition, form a delicate calcareous basket pentagonal in transverse section and slightly contracted above and below. A hollow sheaf of parallel calcareous rods, united together by short anastomosing lateral branches, is formed within each of the calcareous rings of the series passing backwards from the base of the calcareous cup. These sheaves are, as it were, *bound* in the centre by the calcareous rings, and the rods remain irregular and constantly increasing in length at either end of the sheaf, the irregular growing ends of the rods of one sheaf meeting and mixing with those of the sheaves next it. Thus we have formed what at first appears to be a continuous curved calcareous rod; a slight amount of pressure, however, is sufficient to separate the joints from one another, and to show its true structure. The base of the sheaf of rods passing through the last ring of the series abuts against the centre of the upper surface of the circular cribriform plate, now rapidly increasing in size, and becoming more defined in contour, immediately behind the anus (Plate XXIV. figs. 8, 9, & 10).

We have thus the rudiments of the "pentacrinoid stage" of the *Antedon* clearly defined and rapidly advancing in development within the body of the pseudembryo, while the latter still retains in perfection its independent form and its special organs of locomotion and of assimilation.

I have found it utterly impossible at this stage to trace the formation of the viscera of the young pentacrinoid, on account of the close calcareous network in which the nascent organs are enveloped. From its colour and position, however, there can be no doubt that the mass occupying the base of the cup represents the origin of the stomach with its granular hepatic folds, while the upper more transparent sarcode-hemisphere indicates the nascent tissues of the vault, and at a subsequent stage originates the ambulacral ring with its radial branches and the tissues of the young arms. The two rows of plates, enclosing the viscera and forming the cup at this early period, represent the *basal* and the *oral* series of plates, which are remarkably suppressed and modified during the subsequent development of the crinoid. The jointed calcareous rod is the stem of the Pentacrinoid, and the circular calcareous plate afterwards supports the round fleshy disk by which the base of the stem adheres to its point of attachment. From six to twenty-four hours later the pseudembryo becomes more sluggish in its movements, and begins to lose its characteristic contour. The anterior extremity becomes somewhat flattened, and then slightly depressed in the centre. The stem of the included crinoid lengthens, and the sarcode of the body of the pseudembryo contracts towards it. The pseudostome and pseudoproct become obscure and are shortly obliterated, the sarcode forming a thick, smooth, uniform layer over the stem and over its terminal disk. The two posterior ciliated bands disappear, the anterior bands remaining entire a little longer, and still subserving the locomotion of the pseudembryo. The anterior bands then likewise gradually disappear, the pseudembryo sinking in the water and resting upon a sea-weed or a stone, to which it becomes finally adherent.

At this stage the pseudembryo is irregularly oval and in form slightly contracted posteriorly, expanded and gibbous anteriorly, the anterior extremity flattened or slightly cupped. The posterior extremity expands into a small rounded disk (Plate XXV. fig. 1). Slightly compressed and examined by transmitted light, the Pentacrinoid larva has but little altered from the description given above; the joints of the stem are somewhat lengthened, and the cup is rather more open by the growth and slight separation of the upper portions of the plates of the upper tier. The whole of the pentacrinoid is entirely invested by a thick layer of transparent sarcode, which is merely the substance of the body of the larva which has contracted uniformly over the body and stem of the crinoid, its surface retaining, with the exception of the absence of the bands of cilia, the same character as the surface of the pseudembryo, with the same pyriform oil-cells arranged in the same way, and leaving the same interstices of nearly transparent delicately vacuolated sarcode. The head of the crinoid now becomes more regularly pyriform, and the stem rapidly lengthens. The posterior disk becomes firmly and permanently fixed to its point of attachment. The wide anterior extremity now shows a

distinct central depression, and the raised external rim indicates a division into five crescentic lobes.

The whole cup gradually expands and increases in size. The five basal plates enlarge and become more definite in form. Their upper edges are still irregular in outline, somewhat crescentic, arching upwards towards the bases of the orals; but the lateral edges are now bounded by smooth straight calcareous bands, the sides of each plate applied with the intervention of a narrow band of sarcode to the similar edges of the two contiguous plates. The narrow lower edges of the basals are rough and irregular, resting on the upper surface of the irregular ring-like rudiment of the centro-dorsal plate. The oral plates likewise undergo a change in form. They become wider inferiorly, and the sides of the plates towards the lower margin curve outwards, the lower borders thus becoming concave, the convexity turned inwards towards the centre of the body. At the same time the upper edges, which remain narrow and rounded, curve slightly forwards and inwards towards the opening of the cup. If the animal remain undisturbed in well aërated water, when the development of the skeleton has reached this stage, the five lobes (the "oral lobes") forming the edge of the calyx gradually expand, till the cup assumes the form of an open bell (Plate XXVI. fig. 1). Immediately on opening, at least five, and more usually fifteen, delicate, extremely extensile tentacles are protruded from the cup. The mouth, with the organs immediately surrounding it, is formed even before the separation of the oral lobes. It may be seen occupying the centre of the cup (Plate XXVI. fig. 3) immediately after its expansion, as a large patent aperture. When the cup is fully expanded, the transparent tissue continuous with the five oral lobes, and forming the margin of the disk, seems to curve over uniformly into the wide funnel-shaped central opening. The mouth, however, frequently contracts, though it never appears to close completely; and when contracted it is bordered by a slightly thickened very contractile rim, which projects over the cavity of the œsophagus and forms an imperfect sphincter. When this sphincter is relaxed and the mouth fully open, it is easy to see down to the very bottom of the digestive cavity, a sac-like space apparently simply hollowed out in the general sarcode-body (Plate XXVI. fig. 3).

Commencing immediately within the mouth, a series of irregularly-lobed glandular masses, of a pale yellowish-brown colour, project into the cavity of the stomach, curving in an irregular spiral down to the bottom of the cup. These glandular folds are richly clothed with long vibratile cilia. The merest film of sarcode separates their secretion from the stomach-cavity. The slightest touch, even of a hair, ruptures them and causes the effusion of a multitude of minute granules, some colourless and transparent, and others of a yellow or brownish hue. There can be little doubt from their position and colour that these lobes form a rudimentary liver. They appear very early in the pentacrinoid, colouring the lower portions of its body in the earlier stages of its growth within the pseudembryo. They increase steadily in bulk during its later stages, and with but little change of character make up a large portion of the visceral mass in the adult *Antedon*.

A wide vascular ring surrounds the mouth, occupying nearly the whole of the space between the lip and the base of the oral lobes. This ring seems to be simply hollowed out in the uniform sarcode. Its walls are not contractile, it maintains a constant diameter of about 0·08 millim. It is filled with a transparent liquid, which passes likewise into all its tubular appendages; and as granules move rapidly in this fluid, the walls of the ring would seem to be ciliated, though hitherto no cilia have been detected, even in sections and under high powers. The upper and outer margin of the ring gives origin to two classes of tubular tentacles. In a very few cases in which I had an opportunity of looking into the cup immediately after its expansion, the total number of these appendages has been fifteen, five extensile, and ten non-extensile. I have never seen fewer; and I feel convinced that these, with the vascular ring from which they spring, are developed towards the close of the pseudembryonic stage and within the closed cup; they are protruded so immediately after its first expansion.

Radially, the ring gives off five highly mobile, irritable, and extensile tubular tentacles, one opposite each of the intervals between the oral lobes. The cavity of these tentacles is continuous throughout, and immediately continuous with the cavity of the oral ring. Their wall seems to consist of a simple contractile sarcode-layer, studded with oval yellowish endoplasts. There is no definite differentiation of a contractile fibrous tissue. Under a high power, however, the sarcode appears to have a longitudinal arrangement; this may possibly be due to motion among the particles producing a play of light. The walls of these tentacles are produced into numerous delicate tubular processes (Plate XXVI. fig. 3 *e*), their cavities continuous with those of the tentacles. These processes are arranged in three or four irregular longitudinal rows. They are extensile, their walls when extended are extremely delicate, transparent, and apparently structureless. When contracted two or three delicate ring-like rugæ appear on the walls of each (Plate XXV. fig. 3). Each process is terminated by a minute three-lobed slightly granular head. At the base of each of these processes there is a delicate crescentic leaf-like fold, slightly granular, and most distinctly marked when the tentacle is retracted. When one of the extensile tentacles is wholly or partially retracted, it is thrown into obscure transverse wrinkles, which give it at first sight the appearance of being divided by a series of dissepiments. When the tentacle is fully extended these folds totally disappear. At the base of each of these five "azygous tentacles" there is a conical thickening and enlargement of the sarcode-tissue, contracting outwards towards the tentacle which is continuous with its apex, and whose cavity passes through it to unite at its base with the oral vascular ring. This conical projection is the commencement of the young arm. The azygous tentacle terminates it, and leads it out, as it were, up to the point of bifurcation. The tentacle remains persistent for some time in the angle between the two first brachial joints (Plate XXVII. figs. 1 & 3), and finally becomes absorbed and disappears. These five azygous tentacles are the first of a system of "extensile tentacles" which are subsequently developed in very extended series as appendages of the radial and brachial tentacular canals. In almost all cases,

as soon as the interior of the cup can be examined after its expansion, the number of extensile tentacles has reached fifteen; but from the one or two instances in which the ten additional tentacles have been absent, there can be no doubt that they are developed somewhat later than the five already described. They arise in five pairs, one tentacle on either side of and slightly within the base of each of the azygous tentacles, which they resemble closely in character. They commence as minute cæcal diverticula from the canal which passes through the enlarged base of the azygous tentacle, and become rapidly developed into tubular prolongations. At this stage (Plate XXVI. fig. 1), when the cup is open, the fifteen tentacles are usually fully extended, curving over the edge of the cup in the angles between the oral lobes, in threes, the azygous tentacle somewhat longer in the centre, and one of the paired tentacles on either side.

Interradially, opposite each of the oral lobes, there is a pair of short tubular tentacles, their cavities likewise continuous with that of the oral vascular ring. These tentacles appear simultaneously with the five azygous extensile tentacles, immediately on the expansion of the cup. They are flexible, but not extensile, slightly club-shaped towards the distal extremity, which is fringed on either side by a single row of short conical tubercles. The base of these tentacles is involved in the contractile sarcode ring surrounding the mouth. When the disk is fully expanded they lie in pairs up against the inner surface of the oral lobes. They are frequently, however, gathered inwards together, or singly curving over the mouth. They form part of a very characteristic system of "non-extensile tentacles," which afterwards fringe the radial and brachial grooves. At this stage, then, the oral ring usually gives off twenty-five tentacular appendages, of which fifteen are radial and extensile, and ten are interradial and non-extensile.

Imbedded in the sarcode at the base of each of the azygous tentacles, a peculiar glandular body is very early developed. At first it consists of a minute vesicle containing a transparent fluid. The vesicle gradually increases in size till it attains a diameter of about 0·08 millim. in diameter. Its contents become granular, and at length it has the appearance of a large cell with a special wall, included in a capsule formed of a firm sarcode-layer, from which the cell can be turned out unbroken.

The cell contains a number of large, irregularly-formed, transparent, slightly granular masses, which are set free by the rupture of the cell-wall. These masses are quite colourless. They are coloured by carmine more deeply than the general substance of the body, and after death they become immediately strongly coloured by the red pigment set free from the perisom. I have been utterly unable to determine the function of these bodies. They are produced in great numbers, during the growth of the pentacrinoid, along the edges of the radial and brachial grooves, and are permanent in the mature *Antedon*. The only speculation which seems to me at all feasible, a speculation which derives some support from their peculiar affinity for colouring matter, is that they are glands connected with the secretion of calcareous solution for the development and nutrition of the skeleton, analogous to the calcareous glands so constantly met

with in the pseudembryos and young of some of the other Echinoderm orders. At this early period no general body-cavity can be detected separating the wall of the stomach from the body. The stomach seems to be simply excavated in the structureless body-substance, and the organism corresponds generally with the Cœlenterate type. The external sarcode-layer still retains much the same character which it possessed in the pseudembryonic stage. Its basis is transparent and structureless, with imbedded pyriform oil-cells, endoplasts, and granules.

The stem now gradually lengthens, by additions to either end of the sheaf-like calcareous cylinders which form the axes of the stem joints, and by the addition of new rings which rapidly become filled up by the vertical tissue, at the top of the stem, immediately beneath the rudiment of the centro-dorsal plate (Plate XXVI. fig. 2). The disk of attachment becomes opaque by the addition of calcareous matter, and is firmly fixed. The centro-dorsal ring (Plate XXVI. fig. 2) is more definite in form, though it is still simply perforated in the centre, and in connexion with the sarcode-axis of the stem, and bears no traces of dorsal cirri. The basals expand and form a wide, nearly continuous cup. By the rapid expansion of the body, five diamond-shaped spaces are left at the points where the upturned angles of two oral plates are opposed to the bevelled-off upper angles of two adjacent basals. In these spaces cylindrical spicula appear, which soon become club-shaped, dichotomize, branch, and anastomose into delicate net-like superficial plates, irregularly oval, slightly produced superiorly, their upper, narrower portions resting beneath, and supporting, the gradually extending sarcode projections which are terminated by the azygous tentacles (Plate XXVII. fig. 1). The equatorial portion of the body, the band between the upper edges of the basals and the lower edges of the orals, now rapidly expands. The five young arms extend outwards, their bases carrying out with them a zone of sarcode which gives the central portion of the body a great additional width. The oral plates maintain their original position, so that they are now completely separated from the basals by this intervening equatorial band; and are left, a circle of five separate plates, each enclosed in its sarcode-lobe, on the centre of the upper surface surrounding the mouth, and enclosing the ten non-extensile tentacles only. The first radial plates begin to thicken, especially towards the upper margin, and this thickening is produced by the growth, beneath the cribriform superficial calcareous film, of a longitudinal mass of tissue of the same character as that which forms the cylindrical axis of the stem joints. On the lower surface of each arm, in linear series, immediately above the first radials, two spicula, horseshoe-shaped, with the opening above, appear almost simultaneously, and become quickly filled up with elongating sheaves of longitudinal trellis-work. These extend along beneath the extending arms, and indicate the second radials and the radial axillaries.

The upper surface of the arms now becomes grooved by the development, on either side of the central vessel, of a series of delicate crescentic leaves. These leaves are hollow, communicating by special apertures with the radial vessel, and filled with fluid from it. At the base of each of the leaves there is a pair of tentacles forming a group

with the leaf, and along with it communicating with the vessel. One of these tentacles (the distal one) is somewhat larger than the proximal; they are both slightly club-shaped, the club-shaped extremity fringed on either side with conical papillæ. They are non-extensile, and resemble in every particular the ten non-extensile tentacles early developed from the oral ring. A group consisting of a crescentic leaf and two non-extensile tentacles lies immediately at the base of each extensile tentacle, and a little lower down the arm (Plate XXVII. fig. 3 *d*). Minute spicules, some of them simple or key-shaped, and others expanding into a cribriform film, appear in the superficial sarcode-layer along the back or edges of the arms; and, usually at the base of each of the tentacles, irregularly imbedded in the sarcode-substance, there is one of the calcareous glands.

Immediately on the expansion of the equatorial portion of the cup, the wall of the stomach becomes separated by a distinct body-cavity filled with fluid, from the body-wall. The stomach seems to hang in this cavity as a separate sac, attached to the body-wall here and there by sarcodic bands and threads. As the disk expands, the radial canal may be distinctly seen rising from the oral ring, crossing the narrow disk and running along the upper surface of the arm, communicating on either side with the various tentacles and respiratory leaves, and ending at the extremity of the arm in the azygous tentacle. Beneath the radial canal a tubular extension of the perivisceral space passes along the radial grooves. This series of vessels, for which Dr. CARPENTER proposes the term "cœliac canals," afterwards extends throughout the whole length of the arms. In the mature *Antedon* Dr. CARPENTER has observed a third vessel intermediate between the cœliac and tentacular canals; but no trace of this vessel can be detected in the earlier stages in the development of the pentacrinoid.

A little later, the end of the arm shows a tendency to bifurcate, and two half rings, with their enclosed sheaves of calcified tissue, give the first indication of the first two brachials. At the stage which I have described the arm is free, from the base of the second radial; at a later stage the visceral sac extends to the bifurcation, and the whole of the radial portion of the arm becomes included in the cup and disk. The azygous tentacles go no further than the bifurcation. They remain for some time in the centre, between the two divisions of the arm, while secondary branches from the radial canal run on in the brachial grooves. About the period of the development of the second radials, a forked spicule makes its appearance in one of the interradial spaces between the upper portions of two of the first radial plates. This gradually extends in the usual way till it becomes developed into a round cribriform superficial plate.

Simultaneously with the appearance of this "anal" plate, a cæcal process like the finger of a glove rises from one side of the stomach and curves towards the plate. The plate increases in size, becomes enclosed in a little flattened tubercle of sarcode, and maintaining its upright position it passes slightly outwards, leaving a space on the edge of the disk between itself and the base of the oral plate immediately within it.

Towards this space the cæcal intestinal process directs itself. It rises up through it

in the form of an elongated tubular closed papilla. The summit of the papilla is finally absorbed, and a patent anal opening is formed. The details of these later changes belong, however, more properly to a subsequent stage.

Having thus described generally the development of the Pentacrinoid stage of *Antedon* up to a point when a marked change takes place in its structure and economy, I shall now discuss, in somewhat fuller detail, certain general considerations arising from the successive steps of the developmental process.

The relations of the Pseudembryo.—In *Antedon* the germ-mass is resolved, at all events to a great extent, into sarcode having the peculiar delicately vacuolated structure so characteristic of this zoological element. The sarcode contains multitudes of "endoplasts;" and of oil-cells and granules scattered through its substance, but these latter I must regard merely as stores of various organic compounds elaborated as secretions and excretions during the development of the organism. In the centre of the sarcode zooid there is usually a darker nucleus, indicating a special accumulation of granular matter. I have satisfied myself, however, that this condition is not essential, as in some cases in which the young were developed in clear water, with a scanty supply of nourishment, the pseudembryo became transparent throughout. Still it is conceivable that a germ of the original substance of the mulberry-mass may be retained to originate the Crinoidal embryo. At all events, the temporary organism which I have termed the Pseudembryo is entirely dependent for its form and structure upon the sarcode into which the whole or the greater portion of the germ-mass is resolved. This sarcode zooid possesses all the peculiarities of the sarcode organisms among the Protozoa and the lower forms of the Cœlenterata. Its external surface is richly ciliated, and if lightly touched with a bristle it moves off rapidly, by means of these cilia, in a direction opposite to the touch, giving evidence of a high degree of irritability and power of automatic motion, without the slightest trace of a special nervous system. During the early stages of its development, and before the differentiation of a special assimilative tract, the body increases rapidly in size; the sarcode is therefore capable, as in the case of the astomatous Protozoa, of absorption over the whole external surface, and of assimilation throughout the entire internal substance.

Whatever at this stage may be the relations of the granular nucleus of the pseudembryo, I believe the external ciliated absorbent and irritable sheet of sarcode must be regarded as a special provisional organ for the nutrition and aëration of the nascent embryo. Dr. CARPENTER * has already suggested a correspondence between the zooid pseudembryo in the Urchins and Starfishes, and the temporary embryonic structures in

* "We here find the yolk-mass converted into a structure, which is destined only to possess a transient existence, and which disappears entirely by the time that the development of the offset from it has advanced so far that it begins to assume the characters of the permanent organism. This, however, is what takes place in the higher vertebrata; for the structures first developed in the egg of the bird hold nearly the same relation to the rudimentary chick, that the 'Pluteus' bears to the incipient Echinus or Ophiura, or the 'Bipinnaria' to the incipient Starfish."—Principles of Comparative Physiology, 4th edit. p. 568.

the higher animals; and I have developed the analogy* still further, in tracing the continuity of the cavity of the pseudembryonic appendages in Asteracanthion with the vascular system of the young Starfish. The sarcode cylinder preceding and afterwards investing the embryo of *Antedon* must undoubtedly be referred to the same category of structures.

As the development of the pseudembryo proceeds, a large funnel-shaped ciliated pseudostome with an obscure intestine and a minute pseudoproct are formed; and the zooid, which at first resembled a *Plagiophrys* or *Difflugia* in simplicity of structure, may now be compared to a *Vorticella* or *Bursaria.*

The alimentary system is, however, extremely simple. The digestive tract is rudimentary, and the function of the large funnel-shaped œsophagus, with its loop-like pseudocele, seems to be to produce a rapid and special current of fresh water to the general mass of absorbent sarcode rather than to localize the assimilative function. The functional activity of the pseudembryo appears to reside essentially in the peripheral layer. During the earlier stages of its development the central portion consists of a dusky granular semifluid substance, increasing gradually in opacity, and exhibiting active molecular motion; afterwards the centre is devoted to the building up of the viscera of the embryo at the expense of this previously secreted pabulum; but during the earlier stages of the growth of the embryo, its increasing bulk does not appear to interfere in any way with the functions of its nurse. Absorption, as indicated by increase in size and weight, is at no period more rapid than when the pseudembryo is losing its special organs of locomotion and assimilation, and becoming torpid and distorted by the growth of the included organism.

The hollow cylinder of sarcode forming the independent living body of the pseudembryo, at a certain stage loses its cilia, its special organs of assimilation are obliterated, it appears to merge its distinct life in a second harmonized combination of organs which has grown up within it, and the whole layer, without the slightest change in structure, subsides into the perisom of the Pentacrinus.

Histologically the ectosarc of the pseudembryo must be regarded as having been the integument of the Crinoid throughout, its functions highly modified and exalted for a special purpose. The hard structures of the perisom, the two rows of cup-plates and the stem, are accordingly developed in the substance of this integument; and the outline of the Crinoid is thus frequently mapped out in calcareous trellis-work before there is the least trace of the differentiation of internal organs. The stem has clearly no connexion with the viscera whatever, it is a temporary appendage to the radial skeleton.

Until we have accurate details of the embryogeny of a more extended series from the various Echinoderm orders, I believe it would be premature to discuss at length the morphology of the pseudembryo of *Antedon.* At present we are acquainted with many species belonging to widely differing genera, scattered apparently irregularly through the four orders of the subkingdom, which produce independently organized pseud-

* "On the Embryology of *Asteracanthion violaceus* (M. & T.)," Quarterly Journal of the Microscopic Society, 1861, p. 99.

embryonic nurses, presenting a distinct bilateral symmetry in the arrangement of their alimentary system and natatory apparatus. A certain community of plan appears to run through the swimming group described by Professor MÜLLER; but subsequent observations would seem to indicate that so high a development of the pseudembryo is exceptional.

In genera closely approximated to those in which the pseudembryo is most highly organized, or even in allied species of the same genus, the pseudembryonic appendage is reduced to a mere rudimentary vascular tuft, or to a simple investment of sarcode. My own observations would lead me to suspect that the independent development of the pseudembryo may be greatly modified, even in the same species, under different circumstances of light, warmth, aëration, and nourishment.

The pseudembryo of *Antedon* resembles very closely what Professor MÜLLER has described as the "pupa stage" in certain Holothuridea. The young Holothuria, however, has in these instances, according to MÜLLER'S observations, passed through the phase of a pseudembryonic zooid (Auricularia), with a special mouth and alimentary canal, special natatory lobes, and a regular bilateral symmetry, before assuming the pupa form of a closed sarcode-cylinder girded with ciliated bands and devoid of special organs. In *Antedon* the "Auricularia" and the "pupa" stages are, as it were, fused into one. The "pupa" form is at once developed from the germ-mass, but it is provided with the assimilative organs of the Auricularia, though in a very rudimentary degree. Further metamorphosis proceeds very similarly in both cases. In both the organs of the young are gradually differentiated within a sarcode-cylinder, the branchial tentacles finally protruding through an anterior sarcode dome. The close analogy is highly marked in the Synaptidæ, the group whose metamorphoses have been observed by MÜLLER, in which, as in the Crinoids, the oral tentacles are highly developed at the expense of the vessels of the ambulacral region. One or two remarkable differences, however, exist. In *Antedon* no part whatever of the alimentary canal is adopted by the nascent Crinoid. In *Antedon* the development of the organs of the embryo is confined to the anterior region of the pseudembryo, the posterior portion containing the stalk, a temporary appendage. In the Holothuridea the whole pupa passes by simple metamorphosis into the body of the perfect form, the apical pole being occupied by the excretory orifice of the alimentary canal. In the Holothuridea the madreporic tubercle and the sand canal, though frequently extremely rudimentary in the mature form, seem uniformly conspicuous during the development of the young. In the pseudembryonic stage of *Antedon* no trace of this organ has been observed.

I believe that, in zoological language, the term "embryo" has hitherto been understood to indicate a young animal during the early stages of its development; an organism which is produced by the differentiation of the whole or of part of the segmented yelk, and which is a stage in progress towards the mature form of its species. Any accessory or deciduous parts have usually been termed embryonic appendages; but these embryonic appendages have always been regarded as parts of the embryo, although

temporary, yet partaking during their life, of the life of the embryo, and as affording no evidence of possessing independent vitality. I imagine that as the term Embryo has not been applied to the yelk, or to the germ-mass before the separation of the organs of the young, it would be a like misapplication of the term to apply it to any stage in the development from that germ-mass of a being whose organs do not homologate with, and never by any subsequent metamorphosis become converted into, the analogous organs of the perfect form. Again, according to the ordinary conception of a "larva," it is a stage in the development of an animal during which its external form differs to a greater or less degree from that of the "imago" or mature form, and its organs are greatly modified for the performance of certain functions at the expense of others; but the organs of the larva are essentially the organs of the imago; and the individual which is formed of the sum of these organs, and which manifests vital phenomena, is the same individual which subsequently lives as the imago. It is utterly inconceivable that the larva and the imago should exist as separate individuals at the same time. The relations of the pseudembryo are entirely different. It is developed from the germ-mass as a distinct animal form, manifesting a combination of vital phenomena, through a sum of organs which attain a distinct maturity of their own, and which never pass in combination into the sum of the organs of the perfect being. So complete is this independence, that in cases where this type of the reproductive process is carried out most fully, as in Bipinnaria, the embryo is at a certain period cast off from the pseudembryo, and both beings continue for some time to manifest independent life. I would therefore define a "pseudembryo" or a "pseudembryonic appendage" as any provisional appendage produced from the germ-mass, which manifests the functions of organic and animal life through the medium of a combination of organs which precede and do not homologate with the organs of the true embryo. This appendage may be reduced to a condition of extreme simplicity. It may exist merely as a layer of structureless sarcode, ciliated, and manifesting the form of life characteristic of the simpler Protozoa; within which the organs of the embryo are gradually built up.

In most, however, if not in all the invertebrate groups, the so-called embryo differs greatly in external form from the mature organism.

It usually commences in aquatic animals as a "ciliated germ"; and in this condition, whether within the vitelline sac or free after the rupture of the sac, it increases in size by absorption through the general surface. Very usually various lobes and fringes are produced, frequently richly ciliated, extensions of a transparent sarcodic investing layer, within which—but bearing to it only obscure relations in form—the nascent organs of the true embryo are slowly differentiated. During this period the permanent organs, so far as their special functions are concerned, are utterly inert. They are merely growing. The rudiments of the alimentary canal are being laid down, but probably the mouth has not yet "broken through." The entire zooid, however, is by no means inactive. It moves rapidly through the water, its movements beautifully characteristic, and apparently guided by an obstruction-perceiving and light-perceiving instinct.

The perfect organic and relative life of this being, closely comparable to the life of the most highly gifted members of the protozoic subkingdom, does not certainly exist in the sum of the permanent organs; it resides, I believe, simply in a pseudembryonic sarcodic layer, endowed with the same properties which this zoological element possesses when isolated, as in the Protozoa. Gradually the sarcode eliminates from the products of its own assimilation the constituents, and elaborates the tissues, of the permanent special organs; and when these are sufficiently developed, it loses its own individuality, its vital activity passing into the organs which it has produced, and performing through their medium more effectively and condensedly, functions, which, as a transient nurse-layer, it performed in a manner perfect as to its simple object of temporary nutrition, though somewhat feeble and diffuse. In respect to the essentials of this process, some of the Holothuridea among the Echinodermata seem to conform almost exactly to the ordinary Invertebrate type. The pseudembryonic sarcode-layer is here little more special or independent than it is in the embryos of the Annelids and Mollusks, and infinitely less so than in some Turbellarians; and the transition from this condition, through the Crinoids, in which a short alimentary canal is formed in the sarcode layer,—and the "Plutei" in which the "Echinoderm disk" with its accompanying permanent organs is developed within the pseudembryo and covered by its general integument, the whole substance of the pseudembryo being finally absorbed into the embryo,—to the "Bipinnaria," in which the independent life of the pseudembryonic zooid is apparently carried to its limit, is so perfectly gradual as to leave no doubt whatever of the uniformity of the embryogenic plan.

This being the case, that is to say, a vast number of invertebrate embryos combining in their earlier stages pseudembryonic appendages possessing independent vitality with the nascent organs, no special divergence from the ordinary mode of development is to be anticipated in cases in which the pseudembryo attains unusual individual independence. We find accordingly the earlier stages in the development of the pseudembryo in the Echinoderms conforming closely to the general mode of development of the "embryo" of aquatic invertebrates.

The earlier stages in the development of the Tissues of the Pentacrinoid.

The general connective tissue.—As stated above, the general transparent investment which during the earlier stages of its development makes up the greater portion of the substance of the pentacrinoid, is produced by the gradual extension and modification of the sarcode substance of the pseudembryo. The pseudembryo is moulded from the germ-mass, and at first its surface retains the mammillated structure, the result of the ultimate segmentation of the yelk. At first each spherule retains a trace of the original enclosed endoplast; this, however, shortly disappears. No cell-membrane can be detected investing these spherules at any period. An hour or two after the rupture of the vitelline sac, the mammillated structure entirely disappears, the ultimate spherules being fused into a structureless layer. The external layer is firm and consistent. If the

pseudembryo die at this stage, shortly after its death, a delicate film is sometimes separated from the surface of portions of the body, similar to the film which is observed under similar circumstances on the surface of Infusoria. I do not believe, however, that this film previously existed as a special membrane; but am rather inclined to think that it is produced after death by the coagulation of a layer of mucous excretion. Pyriform capsules of considerable size, about 0·03 millim. in diameter, are imbedded here and there in the superficial layer. These cells are of a pale yellow colour, full of a yellow fluid, which when the cell is crushed escapes as a round refractive globule. The wide end of the capsule is superficial, the narrower extremity passes inwards and ends in a delicate thread-like process, which is lost in the substance of the sarcode.

I have been able to detect no special wall to these capsules, the fluid of which seems simply to be enclosed in a pyriform space in the continuous sarcode: I regard these as reservoirs of oil.

The peripheric layer is nearly free from granules; but passing from without inwards, minute granules, compound granular masses, and endoplasts become more numerous; the sarcode at the same time apparently losing in consistency, till at length, towards the inner surface of the consistent perisomatic layer, it becomes densely granular, and no distinct line of demarcation can be detected between the sarcode which still retains a certain consistency, and the central semifluid protoplasm, in which the granules exhibit active molecular motion. The outer layer, when compressed and examined with a high power, exhibits between the endoplasts and oil-cells a very finely vacuolated structure. Minute spaces, somewhat like the lacunæ of bone, filled with a clear liquid, are scattered through the sarcode; and uniting these there is a system of exceedingly delicate tubules which may be compared to the canaliculi; they are much less numerous, however, only about six or eight apparently radiating from each lacunar space. Even while under observation, the size of these spaces appears to vary, one or two which were prominent in one part of the field gradually contracting and becoming indistinct, while others previously scarcely visible seem to expand into view. I believe that this appearance is caused by the circulation of fluid through the system of vacuoles and vessels by movements depending upon the general contractility of the body-substance. Near the close of the free stage, when the embryo is beginning by its growth to distort the form of the pseudembryo, the integument of the wider anterior extremity of the pseudembryo immediately above the mouth of the embryo seems to become columnar in structure and opaque with closely packed long oil-cells, arranged vertically, and forming a kind of dome. In the earliest fixed stage this dome gradually splits up into the five oral lobes, each with its enclosed oral plate.

The devlopment of the Skeleton.—To make the description of the development and relations of the parts of the calcareous skeleton of the pentacrinoid stage of *Antedon* intelligible, I shall in the first place describe very briefly the arrangement of the hard parts in the mature *Antedon* and in some nearly allied forms. I shall touch on this

part of the subject lightly, as Dr. CARPENTER is preparing an elaborate memoir on the skeleton of *Antedon*. I adopt, in concert with Dr. CARPENTER, a nomenclature differing very slightly from that proposed by M. DE KONINCK in his valuable work on the fossil Crinoids of the Carboniferous System of Belgium. I accept for convenience of description the division of the body of a Crinoid into three parts, the stem, the head, and the arms. The head consists of two hemispheres, a dorsal or apical, and an oral hemisphere. The former I shall term the cup of the Crinoid, and the latter the disk. It must be remembered, however, that all the radial portions of the head belong morphologically and physiologically to the arms. In the earlier stages of development the radial plates of the cup, and the radial vessels of the disk, *form* the budding arms; and it is only at a later period that a distinction is produced between radial and brachial portions, by the development of the visceral mass and the extension of the space for its accommodation.

The mature Antedon has no true stem. The cup is closed beneath by a large circular plate hollowed out above into a small rounded chamber. The inferior convex surface of this plate in *Antedon rosaceus* is pitted with a series of small rounded depressions perforated in the centre with minute channels communicating with the cavity of the plate. Into these depressions are inserted a number of jointed calcareous cirri. I shall term the circular plate the "centro-dorsal plate," and the appendages the "dorsal cirri." The centro-dorsal plate in *Antedon* does not belong to the cup. It represents a coalesced series of the nodal stem-joints in the stalked Crinoids.

In *Pentacrinus* (*Neocrinus*) *asterias* (L.), the stem grows by additions immediately beneath the row of basal plates of the cup. These plates are five in number, interradial, wedge-shaped, their outer wider ends knob-like, heading and corresponding with the salient angles of the pentagonal stem. Their inner narrower ends nearly meet in the centre, each being only slightly truncated and emarginated, so that the five grooved ends may unite in forming the walls of a canal, which is continuous with the central canal of the stem, and through which the central sarcode-cylinder of the stem passes to branch to special perforations in the first radials. The lower surface of each basal plate is hollowed by a longitudinal groove crenated on the edges, and the five grooves are so arranged that when the basals are in position, they form together a star-like mould, in which the joints of the stem are formed. This cavity holds from three to four stem-joints at a time; one extremely small at the bottom of the mould, the others gradually increasing in size and gradually forced out and added to the lengthening stem, by the growth of those behind them.

The joints developed in this position are all nodal, that is to say, they subsequently bear whorls of cirri. The internodal joints, varying in number in different species, are developed afterwards between these, each new internodal joint originating apparently immediately beneath the nodal joint.

The dorsal cirri represent a varying number of compressed whorls of the stem-cirri of stalked species which possess such appendages.

The centro-dorsal plate with its dorsal cirri in *Antedon* is therefore the homologue of the stem with its cirri in the stalked Crinoids.

The true cup in the mature *Antedon* consists inferiorly of a delicate rosette of more or less fully coalesced small cribriform calcareous plates; which have been shown by Dr. Carpenter, in a series of beautiful observations, to be the remains of the row of five basal plates which occupy so prominent a place in the cup of the Pentacrinoid.

This rosette is completely concealed in the cavity of the ring formed by the first five radials. Around the basal rosette, and alternating with its segments, five elongated calcareous blocks, triangular in transverse section, the first radial plates, form a column within the base of the cup. In *A. rosaceus* these plates are entirely concealed by the centro-dorsal plate and by the series of second radials. In some species of the genus *Antedon*, they project beyond the centro-dorsal plate, forming above its upper edge a closed ring which supports the series of second radials. The centro-dorsal plate, the basals, and the first radials are immoveably cemented together; they do not, however, coalesce, and may be easily separated after boiling in weak caustic potash. A ring of five second radial plates placed in close contact, form, externally, the base of the cup in *Antedon rosaceus*, resting within upon the upper surfaces of the first radials, and externally upon the edge of the centro-dorsal plate.

Resting upon the second radials, we have next a row of five triangular axillary radial plates, each bevelled above into two diverging surfaces for the articulation of the first brachial joints. The axillary radials are not in immediate contact laterally, they are separated by minute wedge-shaped prolongations downwards of the perisom of the disk. In *Antedon rosaceus*, the basals, and the first, second, and axillary radials form the whole of the skeleton of the cup.

In certain species of *Antedon*, as in *A. Milleri* (Müller, sp.), a series of five minute interradial plates are intercalated between the angles of the axillary radials, and in other forms, as in *A. Solaris* (Lam., sp.), and *A. tessellatus* (Müller, sp.), the whole of the perisom of the disk is covered with a pavement of irregular flat plates. We are unacquainted with the development of *Pentacrinus* (*Neocrinus*) *asterias* (L.), but in the mature form the perisom of the disk is continuously tessellated, and some of the plates pass irregularly downwards between the axillary radials. In *Pentacrinus* (*Neocrinus*) *decorus* (nob.), the surface of the disk is rough with irregularly scattered blocks, like fragments of perforated bricks; and these descend into the spaces between the axillary radials, though without any regular arrangement.

The basal and oral plates.—The first portions of the skeleton which appear are the two rings of five plates each, the plates of the upper ring directly superposed on those of the lower, which form the trellised basket, completely enclosing the viscera of the Pentacrinoid during the early stages of its growth within the pseudembryo. The plates of the upper tier subsequently extend into the five oral lobes, and remain as five valve-like interradial oral plates during the greater part of the pentacrinoid stage.

The lower series are the basals. These are permanent, with some remarkable modifi-

cations in form, in the mature *Antedon.* These ten plates appear simultaneously as delicate spicula imbedded within the firm peripheric layer of the pseudembryo, usually only a few hours after its escape from the vitelline sac, and before there is any trace of the permanent organs of the embryo.

The spicula are hollow throughout. They are at first simple and cylindrical; shortly they become club-shaped at each end; each thickened end then divides into two diverging branches, equal in length to the original rod; these fork in their turn, till on their second bifurcation their branches meet and coalesce with the corresponding branches from the opposite end of the original spiculum. By thus constantly branching and anastomosing on one plane, the spiculum extends into a delicate net-like plate, the meshes of which are at first irregularly hexagonal, but afterwards become rounded. The extending calcareous tubes are constantly closed, and constantly hollow to the end. They appear to grow by the molecular removal of calcareous matter from the back of the growing point, and its deposition in advance. At first all the ten plates are round; but as they expand they become irregularly square, their edges during the free condition of the embryo remaining rough with sprouting spicules.

About the time of the fixing of the pentacrinoid, the basals, which have now assumed a somewhat definite form, narrower beneath and expanding above, have their lateral edges bounded by straight lines, so that the edges of two adjacent plates are closely applied to one another. Even after their edges have become thus defined, the plates go on steadily increasing in size, apparently by interstitial growth. The upper edges of the basals still remain rounded and rough. Their lower edges are likewise irrregular, but these soon become obscured by the growth of the centro-dorsal ring. The oral plates extend principally upwards into the oral lobes, where they become lengthened and somewhat contracted, their edges fringed with diverging pointed spicules (Plate XXVI. fig. 1). As development proceeds they change somewhat in form. The upper angle is slightly depressed, and the sides at the inferior angles are raised, the raised edges at that stage lying up against the sides of the second radials. Absorption of the inferior portion of the oral plates commences about the time of the appearance of the first brachial joints and of the anal plate (Plate XXVII. fig. 1). Both basal and oral plates consist at first of a delicate cribriform calcified film, formed by the lateral extension of a single layer of calcareous tubing only. As they increase in size, however, they gradually thicken, and this thickening is effected by the network sending in from its inner surface irregular processes which branch and unite to form a second layer not quite so regular as the first, but resembling it in general character. This process is repeated till the plates have attained the required thickness. In the oral plates the thickening is very slight, and is confined to the lower portion of the plates.

The stem.—As described above, shortly after the appearance of the spicula indicating the basal and oral plates, a chain of six or seven calcareous rings may be observed curving from the centre of the space between the bases of the basal plates; behind, and usually somewhat to the left of the pseudostome and pseudocele, and abutting against a round

cribriform plate which makes its appearance at the same time close to the posterior extremity of the pseudembryo, behind and below the pseudoproct. Immediately beneath the basal plates an irregular calcareous ring is early formed, considerably wider and broader than the ordinary rings of the stem. This ring, which is subsequently developed into the permanent centro-dorsal plate, gradually thickens and becomes more regular in form, maintaining its position at the top of the stem, the lower edges of the basal plates resting on its upper surface. During the earlier stages of the growth of the pentacrinoid it is simply a circular band of the ordinary calcified areolar tissue, enclosing a sheaf of the peculiar fasciculated tissue of the stem, gradually enlarging, with a central aperture continuous with the bore of the tube-like stem-joints. It is not till some time after the latest stage described in the present memoir, that the rudiments of the first dorsal cirri appear round its lower contour. The rings which originate the ordinary stem-joints commence as small curved hollow spicules. At first they may often be seen open and imperfect; afterwards they completely close (Plate XXIV. fig. 6). The inner surfaces of the rings are smooth, the outer roughened with projecting branches. I have only once or twice seen the rings of the stem in this early simple stage. Very soon after their appearance, usually before the pseudembryo has attained its full size, a hollow sheaf of calcareous rods united by minute calcareous trabeculæ arises within each ring. The stem-joint increases in length by additions to each end of these cylinders. The centre of the cylinder is occupied by a consistent sarcodic thread running through the whole length of the stem. At this stage no fibrous tissue can be detected, either mixed with the calcified tissue or in the outer perisom. Additions are made to the length of the stem by the formation of new rings immediately beneath the centro-dorsal plate, the new rings becoming, as in the former case, gradually filled up by cylinders of linear calcified tissue. As the calcareous axis of the stem increases in width, the original rings girding the centre of the joints expand. They remain permanent during the whole of the fixed stage, and give the stem of the Pentacrinoid its characteristic beaded appearance. The terminal plate of the stem is formed on the same plan as the basals and orals. It is developed as a simple round cribriform plate within the posterior extremity of the pseudembryo; and when this extremity becomes expanded into a disk of attachment, it supports and forms the skeleton of the terminal sucker. Afterwards it becomes thickened by irregularly deposited calcareous matter. The layer of soft tissue between the calcareous disk and the point of attachment seems to be at length absorbed, and the stem is permanently fixed by amorphous cement.

The first and second radial joints and the axillary radials.—Shortly after the fixing of the Pentacrinoid and the opening of the cup, a third series of five plates make their appearance as minute branching spiculæ occupying the spaces left by the bevelling off of the upper angles of the basal plates and the lower angles of the orals, thus forming an intermediate series between the basals and orals, and alternating with them. The spicula indicating the origin of these plates, the first radials, branch and extend in the manner already described, till at length they form diamond-shaped films consisting of a

single layer of cribriform calcified tissue. The plates shortly begin to thicken; but their mode of growth at once distinguishes them as fundamentally different in structure from the basals and orals. Processes are sent inwards from the inner surface of the superficial film as before; but the added tissue is longitudinal and fasciculated, resembling precisely in structure and mode of growth the inner cylinder of the joints of the stem; and, as in the case of the stem, tubular perforations are formed in it for the passage of the sarcode-cords, which subsequently extend in like channels through the joints of the arms and pinnules. The second radial joints and the radial axillaries rapidly succeed the first radials, and are developed nearly in the same way. They first appear as horseshoe-shaped spicula, or imperfect rings, which have the same relation to the joints which the stem-rings have to their included cylinders. The spicula soon become filled up with lengthening fasciculated tissue; the joints at this period are slightly grooved longitudinally on their upper surfaces to accommodate the radial vessels.

The anal plate, the interradial plates, and the plates and spicula of the perisom.—Upon the appearance of the second and third radial joints, the perisom between and somewhat above two of the first radials rises into a rounded papilla, towards which a cæcal process of the digestive cavity is directed. On the outer side of this papilla a branching spicule appears which rapidly extends into a round plate. This, the anal plate, grows, and afterwards thickens precisely on the model of the basal and oral plates; it contains none of the fasciculated tissue proper to the radial system. The basal and oral plates, the first and second radials, the radial axillaries, and the anal plate seem to complete the series of essential parts entering into the cup of the pentacrinoid. In one or two cases however, I have observed about the time of the first appearance of the anal plate, a series of five minute rounded plates developed interradially between the lower edges of the oral plates and the upper edges of the basals. These interradial plates sometimes remain permanent in the mature *Antedon rosaceus*, and they appear to be constantly present in some species, as for instance in another and a rarer British form, *Antedon Milleri* (Müller). They usually occur, finally, in groups of three or five. They are irregular in form, and they resemble the anal plate in structure and mode of growth. Simple and key-like spicula and small round cribriform plates are imbedded irregularly in the perisom of the arms, often almost covering the second and third radial joints with a dermal calcified layer, but never overlying the basal or oral plates of the body.

General remarks on the Skeleton.—The skeleton of the pentacrinoid is composed of two systems of plates, which I shall term respectively the *radial* and the *perisomatic* system, thoroughly distinct in their structure and mode of growth. The radial system consists of the joints of the stem, the centro-dorsal plate, the radial plates, and the joints of the arms (and subsequently of the pinnules). The perisomatic system includes the basal and oral plates, the anal plate, the interradial plates, and any other plates or spicula which may be developed in the perisom of the cup or disk. In the recent *Pentacrini*, and in certain species of *Antedon*, the disk is paved or studded with plates belonging to the perisomatic system, and a double series of like plates fringe the radial

and brachial grooves. The joints or plates of the radial system may be at once distinguished by their being chiefly made up of the peculiar fasciculated (or radial) tissue of parallel rods which I have already described, and by their being perforated for the lodgment of a sarcodic axis. At first each radial element appears to consist of two parts. A stem-joint always commences with an annular spicule, within which the cylinder of "radial" tissue seems to arise. An arm-joint begins with a crescentic spicule, and a radial plate with an expanded single cribriform film. From the strong contrast which these superficial portions present to the tissue which is afterwards developed beneath them, I am inclined to refer the outer rings and films, even of the brachial joints and radial plates, to the perisomatic system, and to regard the radial system of plates as composed essentially of the "radial" tissue alone. The plates and joints of the radial system are singularly uniform in their structure and arrangement throughout the whole of the crinoidal series.

They seem to form, as it were, an essential skeleton whose constant general arrangement stamps the order with its most important and prominent character. In the Pentacrinoid the radial system of radial- and arm-joints supports the extensions of the radial vessels, and the radial vessels with their œsophageal vascular ring clearly arise in connexion with the disk, on the oral aspect of the animal. The radial plates arise at the opposite or apical pole. The first portion of the radial system which appears is the stem. When the sarcode-axis of the stem enters the cup, passing through the centro-dorsal plate and between the lower edges of the basals, it splits into five threads which enter the first radial plates, and after a somewhat singular distribution in the walls of the cup, which is not apparent till a later stage, they follow out the growing arms, the arm-joints being moulded round them as they extend. The perivisceral sac lies in the cleft formed by the five radial branches of the stem. The plates of the perisomatic system commence as simple cribriform films imbedded in the outer layer of the perisom, and thicken by a repetition inwards of the same diffuse areolar tissue. They are essentially variable in number and in arrangement; most of the minor structural modifications throughout the group depend upon the multiplication or suppression of plates of this series. Even in the same species they are by no means constant. In *Antedon rosaceus* the perisom of the disk is usually naked, but specimens from certain localities have well-defined groups of perisomatic interradial plates developed in the angles between the radial axillaries, and in some individuals rows of similar plates are imbedded along the margins of the radial grooves in the perisom of the disk. The entire body of the Pentacrinoid is, at first, while yet included within the pseudembryo and during its earliest fixed stage, surrounded and enclosed by plates of the perisomatic system alone, and it is quite conceiveable that plates belonging to this system may expand and multiply so as to form a tessellated external skeleton to the mature animal, the radial system being entirely absent, or represented only in the most rudimentary form. I believe that all the modifications of the skeleton which characterize the principal divisions of the Echinoderm subkingdom will be found to depend mainly upon the relative development or suppression of the radial and perisomatic systems of plates.

With reference to the form and position of the oral plates, Professor ALLMAN has suggested some interesting analogies between this transition stage of *Antedon* and the permanent condition of the fossil genera *Haplocrinus*, *Coccocrinus*, *Stephanocrinus*, and *Lageniocrinus*. I thoroughly agree with Dr. ALLMAN, that the oral plates of the Pentacrinoid are in all probability homologous with valve-like plates surrounding the mouth only in all crinoidal genera in which such plates occur. In *Antedon rosaceus* they disappear during the later stages in the growth of the Pentacrinoid young, and in all known species of the genus *Antedon*, even in those with a tessellated disk, they are wanting in the mature form. In *Pentacrinus* (*Neocrinus*) *asterias*, (L.), the mature form to which the fixed stage of *Antedon* is evidently most analogous, they are said to remain permanent. The evidence on this point is as yet extremely defective. It rests entirely upon the descriptions and sketches of M. DUCHASSAING *, which are sufficiently graphic, but by no means technically exact. In two nearly allied species, *Pentacrinus* (*Neocrinus*) *Mülleri* (Oersted) and *P.* (*N.*) *decorus* (nob.), in both of which I have had an opportunity of examining the perisom of the disk, the oral plates are totally absent.

Almost all Dr. ALLMAN'S illustrations are necessarily taken from a small aberrant family of Crinoids, the Haplocrinidæ, of whose structure we know as yet very little. With the exception of *Stephanocrinus*, which only doubtfully belongs to the group, all the genera are Devonian, preceded by the peculiar Cystideans of the Upper Silurians, and ushering in the carboniferous Blastoids.

Notwithstanding Professor MÜLLER'S discovery of rudimentary free arms, I cannot help still leaning to the view that the triangular interradial valves in the Haplocrinidæ may, like the pointed upper tier of interradial plates in the Pentremites, surround not only the mouth, but ovarian and anal openings; a discussion of the homologies of the fossil Crinoids is however foreign to the object of the present memoir.

The development of the assimilative and vascular systems, so far as it has been possible to observe it at this early stage, has already been described in detail.

EXPLANATION OF THE PLATES.

PLATE XXIII.

Fig. 1. Portion of the ovary under slight pressure, showing ova in various stages of development, $\times 40$ linear.

Fig. 2, *a–o*. Ova in various stages, from the first appearance of the germinal spot 2, *a* to the maturity of the egg 2, *o*, $\times 40$ linear.

Fig. 3. Yelk-granules, $\times 120$ linear.

* Quoted by M. DE KONINCK, "Recherches sur les Crinoïdes du terrain Carbonifère de Belgique," p. 53. Brussels, 1854.

Fig. 4. A group of parent cells containing vesicles of evolution, and forming a portion of the tissue of the testis, ×40 linear.

Fig. 5, *a–e*. Parent cells with vesicles of evolution in various stages of development, ×40 linear.

Fig. 6, *a–c*. Mature vesicles of evolution containing spermatozoa, ×80 linear.

Fig. 7. Spermatozoa, ×120 linear.

Fig. 8. Egg shortly after impregnation, ×40 linear.

Figs. 9–13. The process of yelk segmentation, ×40 linear.

Fig. 14, *a–c*. Further enlarged views of the earlier stages of yelk segmentation, showing three groups of the "direction vesicles," ×80 linear.

PLATE XXIV.

Figs. 1–4. The development of the pseudembryo within the vitelline membrane, ×40 linear. In this case the development is somewhat abnormal.

Fig. 5. Dorsal aspect of the pseudembryo shortly after the rupture of the vitelline sac, ×40 linear.

Fig. 6. Dorsal view of the pseudembryo a little more advanced, ×40 linear.

Fig. 7. Ventral aspect of the pseudembryo a little later, showing the pseudostome and pseudoproct, and the rudiments of the cup plates of the embryo, ×40 linear.

Figs. 8, 9, 10. Ventral, dorsal, and lateral aspects of the pseudembryo shortly before the disappearance of the ciliated bands, ×40 linear.

PLATE XXV.

Figs. 1–3. The pseudembryo losing its special organs of assimilation and locomotion and passing into the "pentacrinoid stage," ×40 linear.

PLATE XXVI.

Fig. 1. Pentacrinoid larva immediately after the complete separation of the oral valves, expanded, ×40 linear.

Fig. 2. Pentacrinoid in the same stage, the cup closed, ×40 linear, but afterwards slightly reduced to suit the size of the plate.

Fig. 3. A portion of the oral disk of the same stage seen from above, in a state of complete expansion: *a*, patent oral aperture bounded by a ring of contractile tissue, and showing yellow richly ciliated granular folds, arranged somewhat spirally on the walls of the digestive cavity; *b*, central ring of the radial vascular system; *c*, non-extensile tentacles in immediate connexion with the vascular

ring, ten in number, and laid up in a state of complete expansion in pairs against the inner surfaces of the oral valves *f*; *d*, first pair of extensile radial tentacles; *e*, azygous radial extensile tentacle leading out the growing arm to its bifurcation, and giving off pairs of tentacles of the same series from its base. ×40 linear.

PLATE XXVII.

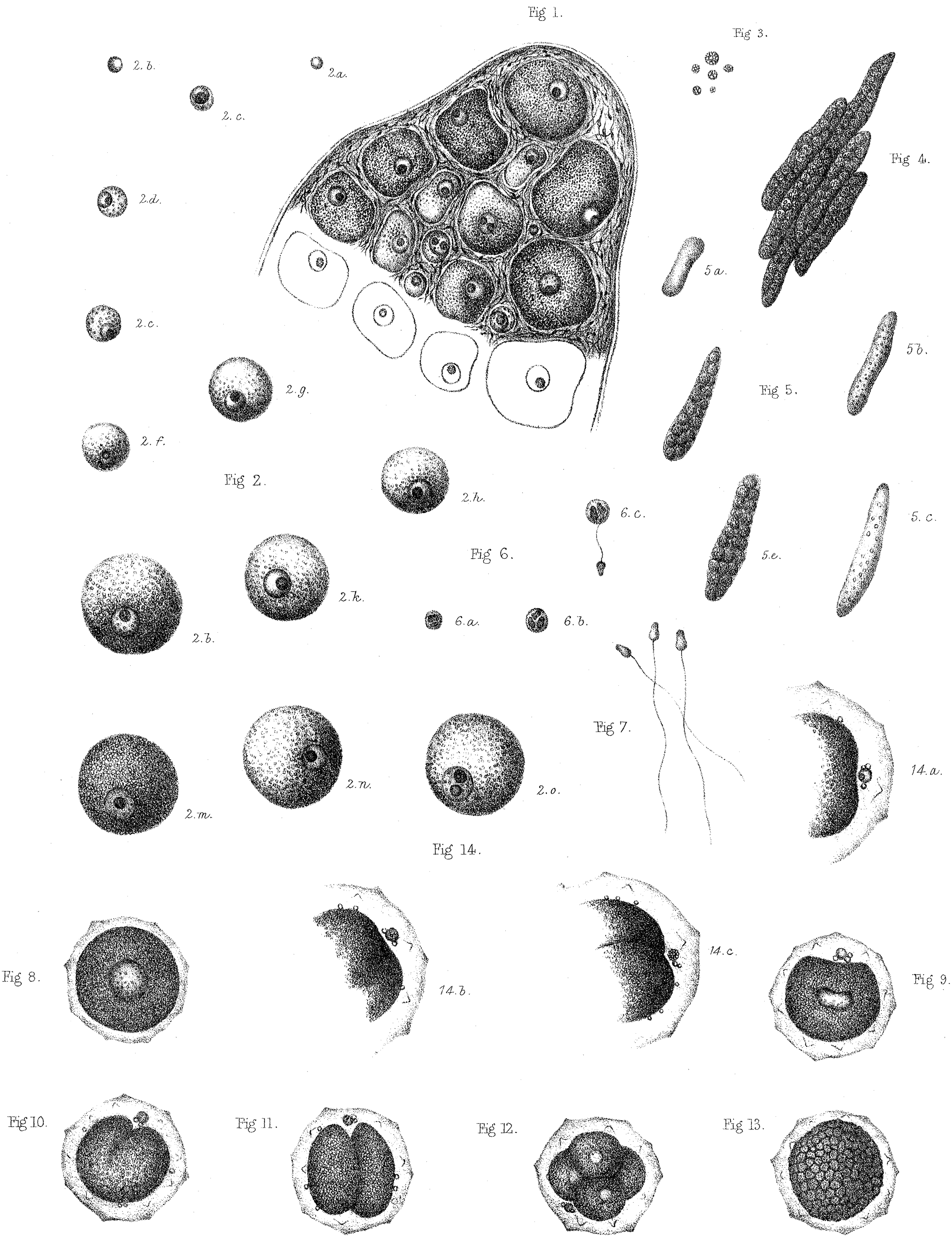
Fig. 1. Pentacrinoid larva immediately before the expansion of the ventral disk: *a*, centro-dorsal plate; *b*, series of basal plates; *c*, first radial plates; *d*, second radial joint; *e*, third radial; *f*, first brachial joint; *g*, anal plate; *h*, stem-joint; *k*, cribriform plate supporting the disk of attachment; *l*, granular visceral mass; *m*, cæcal process passing from the stomach towards the papilla which indicates the position subsequently occupied by the anal tube; *n*, oral valve and plate. ×40 linear, slightly reduced.

Fig. 2. An example in a somewhat earlier stage, expanded, and showing the arrangement of the non-extensile tentacles in connexion with the oral vascular ring, ×40 linear, considerably reduced.

Fig. 3. End of an extending arm further enlarged: *a*, *b*, and *c*, first, second, and third radial joints; *d*, superficial spicules and small cribriform plates of the perisomatic system; *e*, lenticular "gland"?; *f*, radial vessel passing out on the arm to terminate in the azygous extensile tentacle *h*, after giving off the second pair of extensile tentacles *k*, *k*; *g*, leaf and pair of tentacles of the non-extensile tentacular system. ×40 linear.

Fig. 4. Pseudembryo uncompressed and observed by reflected light: *a*, pseudostome; *b*, pseudoproct; *c*, *c*, *c*, *c*, ciliated bands. ×40 linear.

All the figures, except Plate XXVII. fig. 4, have been drawn from specimens under slight pressure, and with a special view to the details of internal structure. The contour has been thus in some cases to a certain extent lost, and the figures, especially those of the pseudembryo, must be understood to represent individuals slightly flattened.



Wy. T. ad nat. del.

Edwin M. Williams. FLS. sc.

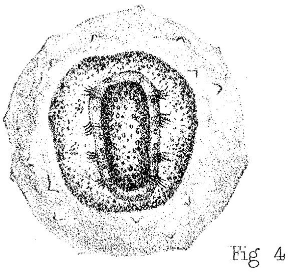


Fig 4.

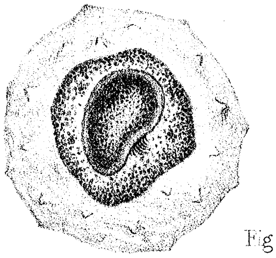


Fig 3.

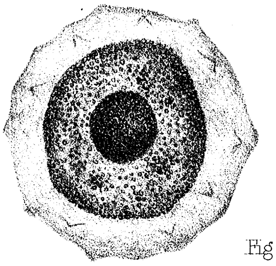


Fig 2.

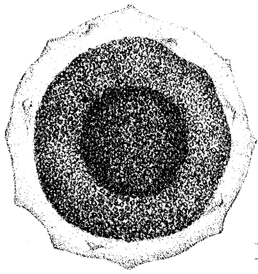
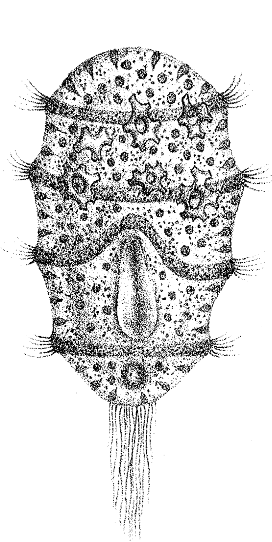


Fig 1.

Fig 7.



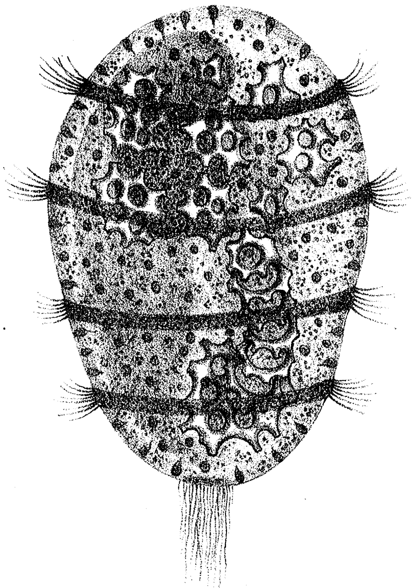


Fig 6.

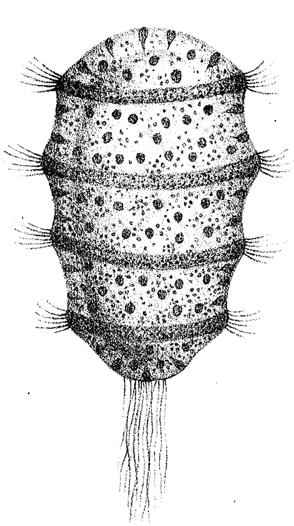
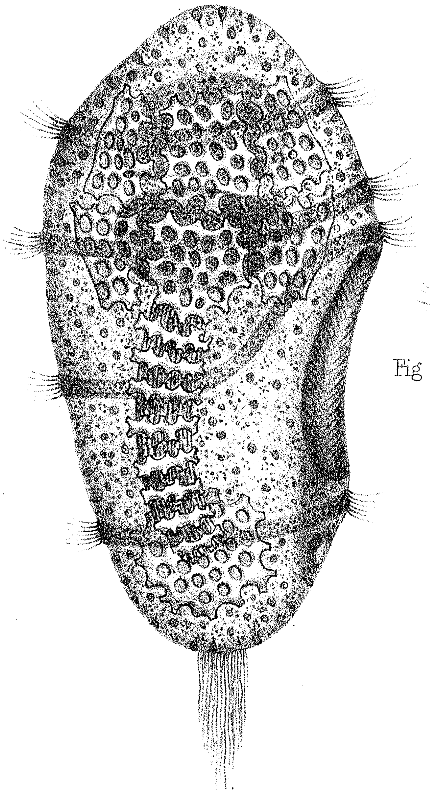


Fig 5.

Fig 10.



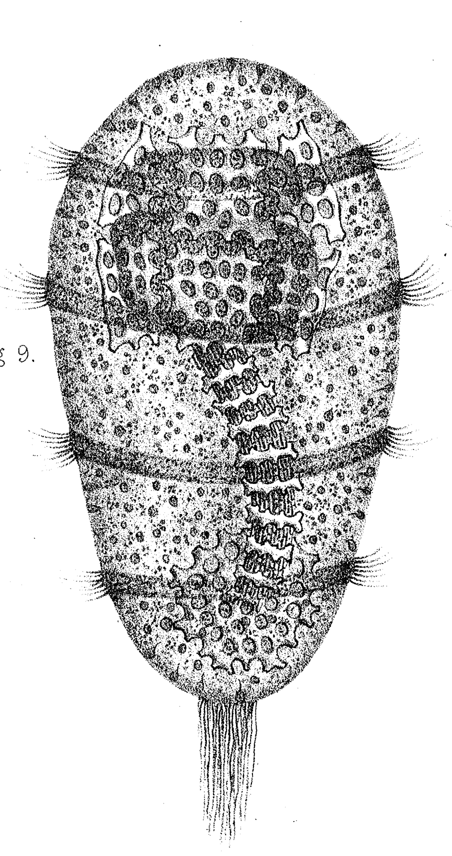


Fig 9.

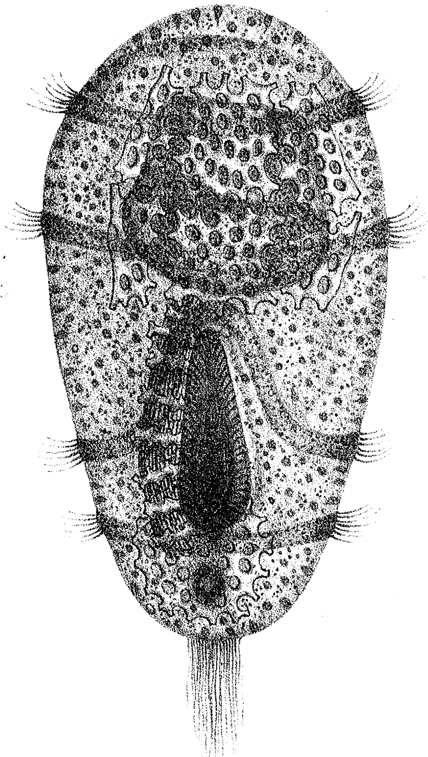


Fig 8.

Wy. T. ad. nat. del.

Edwin M. Williams. F.L.S. sc.

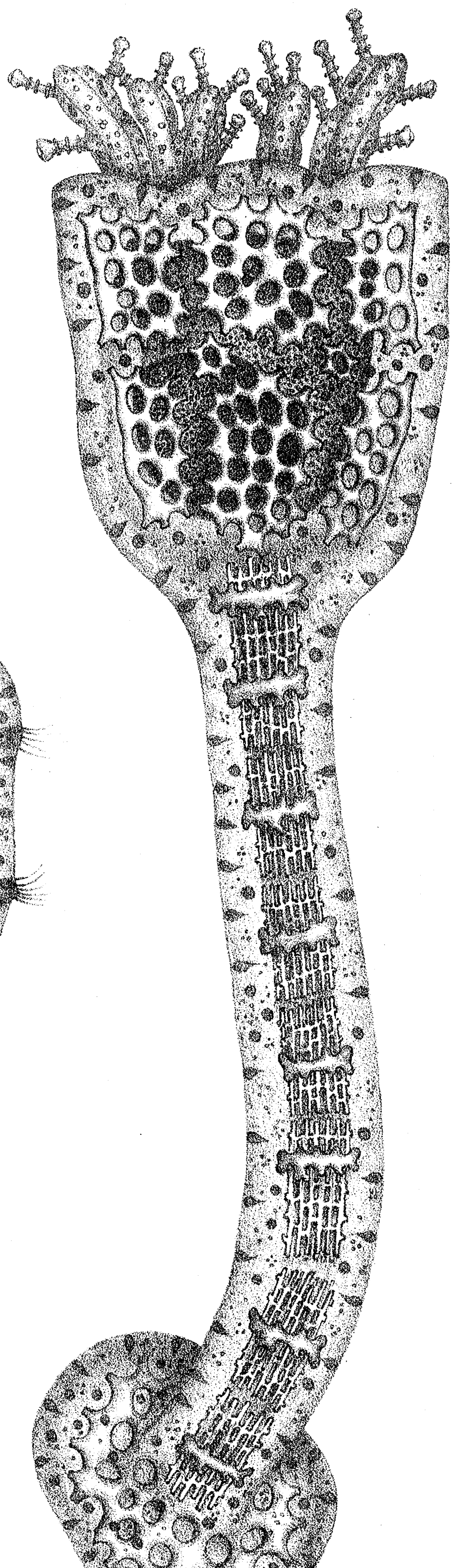


Fig 3.

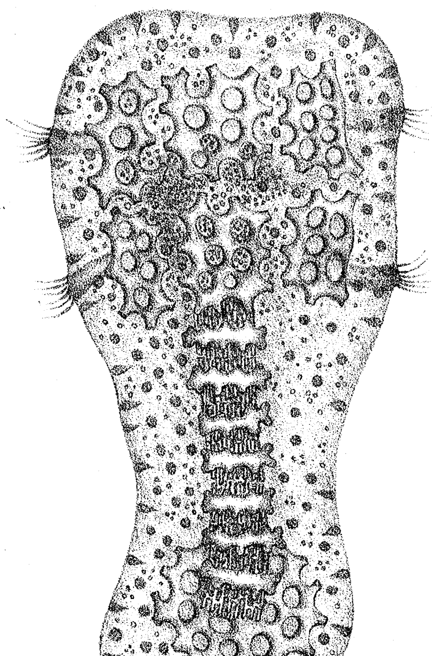


Fig 1.

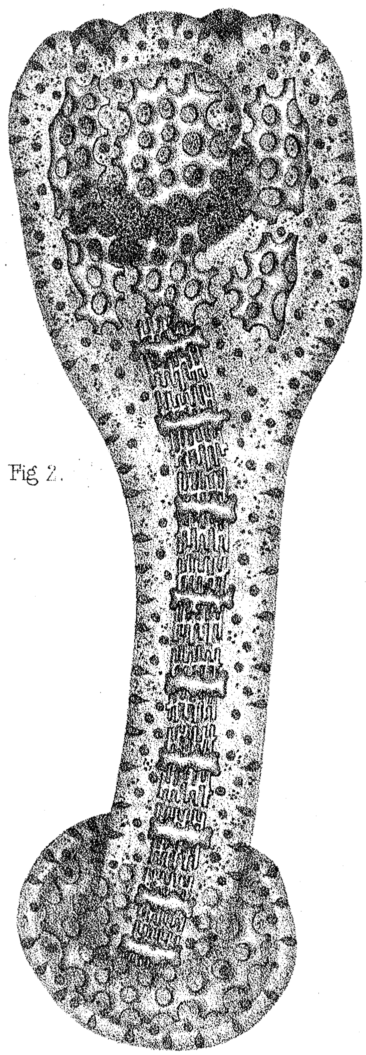


Fig 2.

Wy. T. ad. nat. del.

Edwin M. Williams. F.L.S. sc.

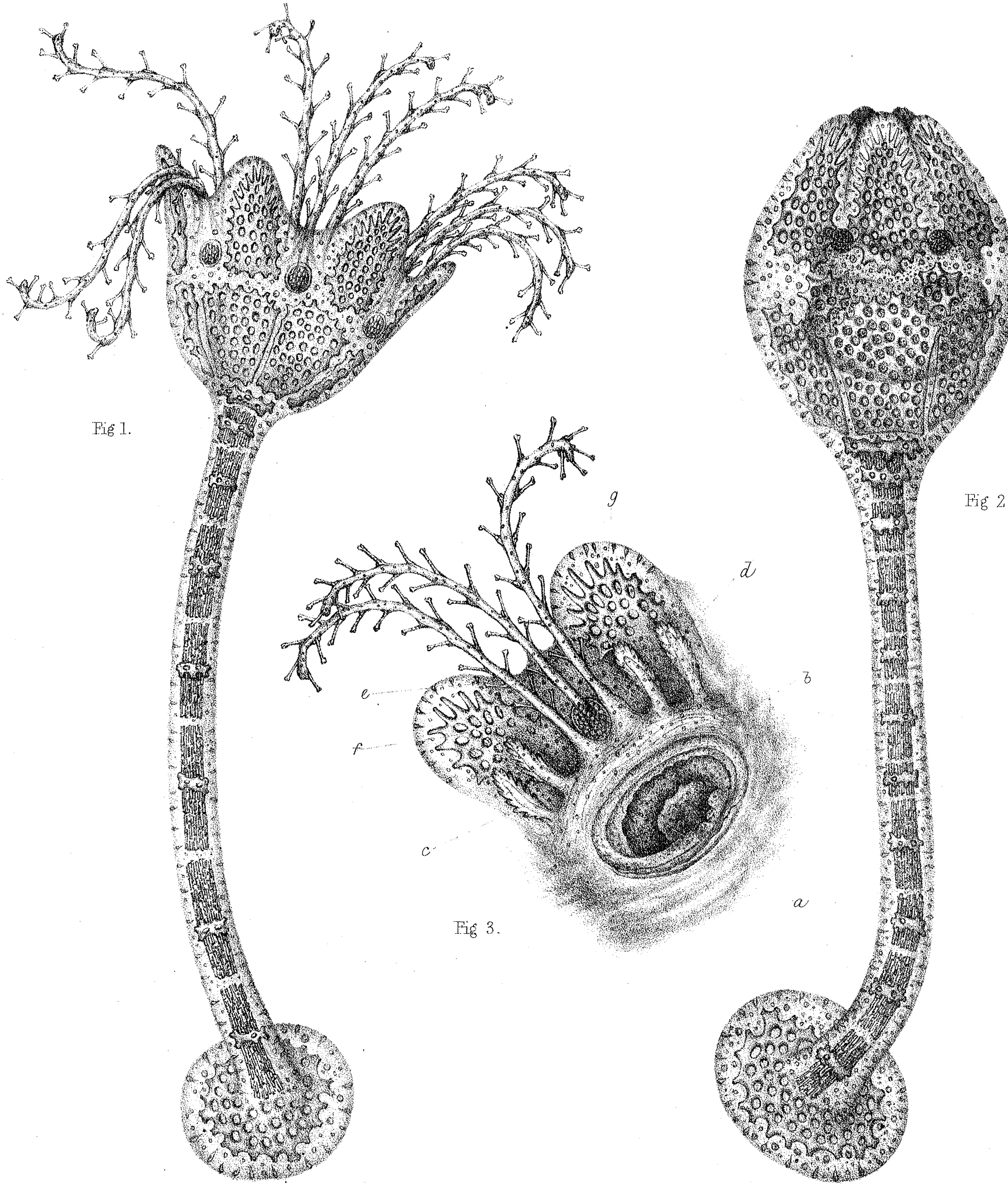


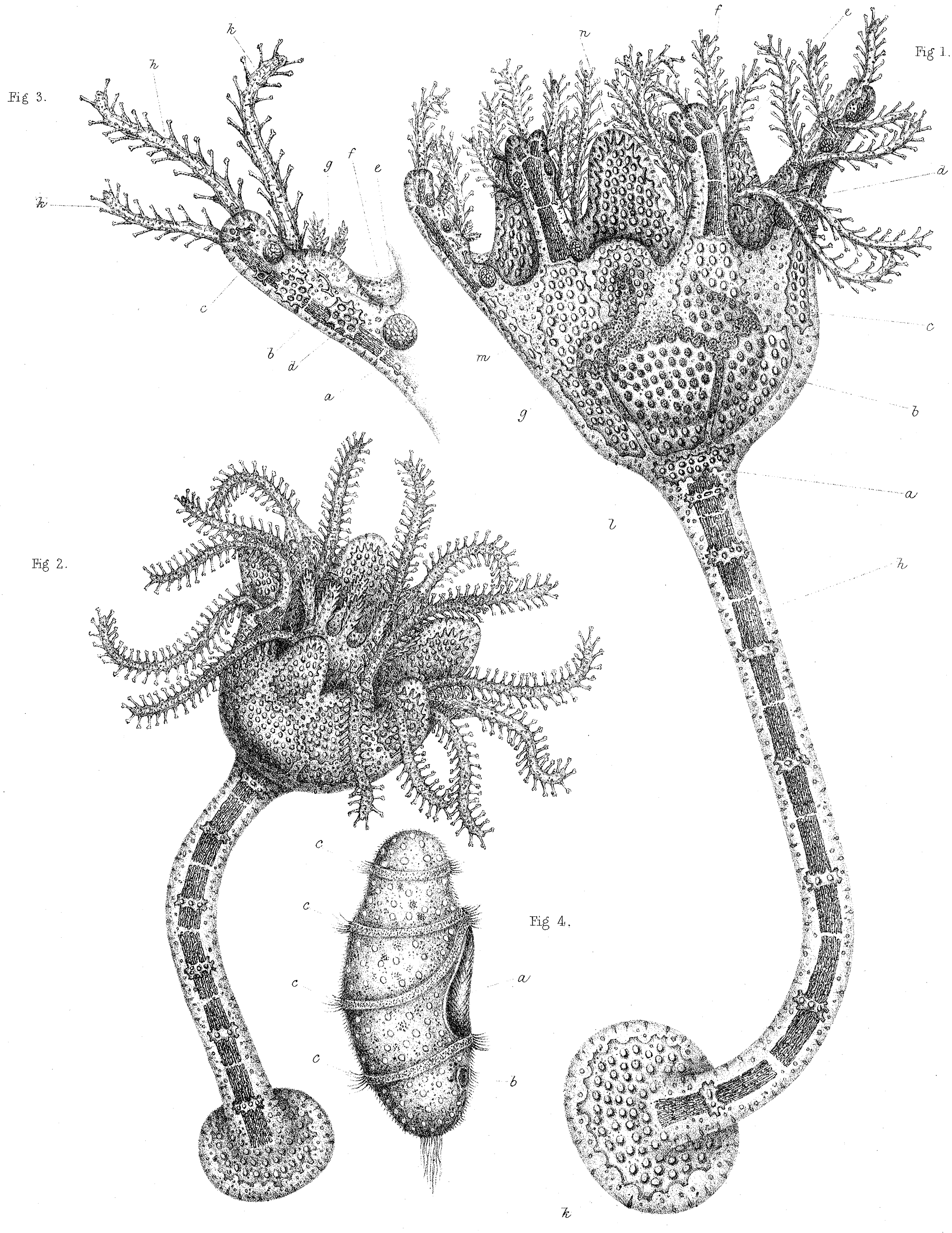
Fig 1.

Fig 2.

Fig 3.

Wy. T. ad nat. del.

Edwin M. Williams F.L.S. sc.



Wy. T. ad. nat. del.

Edwin M. Williams. F.L.S. sc.