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ON THE DEVELOPMENT OF MANICINA AREOLATA.

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DURING the spring of 1887 the Marine Laboratory of the Johns Hopkins University was stationed on the island of New Providence, Bahamas. As soon as possible after my arrival, March 10, I endeavored to find out what corals were breeding. Of half a dozen species examined only one was with eggs. This was the so-called Chenille stone, or *Manicina areolata,* one of the commonest corals in the Bahama waters. The breeding continued to be very active until the middle of April, when it began to decline, coming to a close before the first of May.

The coral is found in large numbers in water of easy wading depth, lying with its pedicel buried in the sand. It lives very well in small aquaria, if care be taken to change the water twice a day. In rearing the larvæ I was compelled to employ the same tedious method as Lucaze Duthiers: every morning and evening I transferred them, one or two at a time, by means of a pipette, to a dish of fresh water. When' once the larvæ had become attached, the matter was simplified by transferring the entire dish to a bucket of fresh water. For preserving the larvæ, Perenyi's fluid proved the most generally useful reagent. Osmic acid specimens were also of very considerable value in elucidating special points. For the anatomy of the adult, absolute alcohol gave the most satisfactory results. I take this opportunity of thanking Professor Brooks, the director of the Marine Laboratory, for his advice and constant suggestions, which have been of the greatest value to me during the course of this work, both at the seaside and in the Baltimore laboratory. I am also indebted to Mr. C. S. Hodge, of this laboratory, who very kindly took upon himself a part of the task of cutting the sections.

I. SYSTEMATIC DESCRIPTION OF MANICINA.

Milne Edwards makes Manicina the sixty-fourth genus in the family Astræidæ. Like Meandrina, this coral grows by incomplete fission, the calicles remaining connected so as to form meandering valleys, in which the limits of a calicle are not distinguishable. The shape of the colony ordinarily met with is subturbinate (see figures on Plate I), there being a well-marked pedicel. With increasing age the pedicel becomes less and less evident, until the corallum finally assumes the shape of a convex mass with a flat basal surface. The basal surface has two diameters, the longer about three inches, the shorter two inches, and the vertical height of the corallum is about equal to the shorter diameter. The distinguishing features of the genus, besides its growth from a pedicel, are as follows: The columella is spongy and very well developed. The septa are thin, closely set, and have strongly marked granulations on their sides. The edges of the septa, both within and over the exterior of the calicles (costæ), are finely and regularly toothed. "The genus was instituted by Ehrenberg for certain of Lamarck's Meandrinæ, characterized by growing from a pedicel or central point of attachment" (Dana). In the species Manicina areolata, the septa can be divided into three cycles, and each septum has in the neighborhood of the columella a large and rounded lobe.

The animal is of a brownish color, and when expanded, extends high above the skeleton. In this condition the tentacles are moderately long, and are closely set round the periphery of the oral surface. In the pedunculate forms, both in the expanded and contracted condition of the animal, the upper part of the lateral surface of the skeleton is covered by the polyp. The pedicel, which includes the skeleton below this region, is usually disfigured by small annelid tubes and other incrustations.

The young, after the swarming life is over, affix themselves to some solid substratum, such as a piece of rock or a shell. To this they remain attached until they have reached a diameter of about half an inch. Until the diameter is one-third of an inch, the animal remains a single polyp, circular or oval in transverse section, and with a flat or irregular surface of attachment. The multiplication by fission then begins, and with it the formation of the pedicel. When the latter has become apparent, the coral is broken off from the rock to which it was attached, and henceforth lives free in the sand.

II. GENERAL SKETCH OF THE DEVELOPMENT FROM SURFACE VIEWS.

Lacaze Duthier's figures of Astroïdes (1) apply so well to Manicina, that I have thought it unnecessary to give a series of such views. The chief point of difference is that the larvæ are red in the former genus, but colorless in the latter.

Manicina is hermaphrodite. Normally, it would appear, the mother gives birth to larvæ, which pass out by the mouth. But the first two batches of corals I kept poured out an abundance of eggs and semen. Each batch numbered eight corals, was distributed into four aquaria, and was kept for only a day. The first set laid on the night of the 15th, the second, on the 17th of March. I was not able to try a third batch until the 20th, when I was surprised to find that all the corals had given birth to larvæ a little more advanced than the planula stage. The throwing out of eggs and spermatozoa was probably abnormal, as the eggs which I watched underwent very irregular changes, and finally broke up. In connection with this ejection of eggs and semen, it may be interesting to note that though after March 20 the corals always ejected larvæ when kept in aquaria, the stage of development in which the larvæ were born became much more advanced as the season grew older. The larvæ born March 20 and 21 were without cilia, and at the stage represented in Fig. 4, Pl. II. Those born April 5 were ciliated and as far advanced as Fig. 20, Pl. IV.

The larvæ I obtained during March lay, for a day or two after birth, motionless on the surface of the water. They then acquired cilia, and began to swim feebly about at the surface, often collecting in rows at the sides of the vessel or in groups away from the sides. Lucaze Duthiers noticed the same habit in Astroïdes. At the end of a week the larvæ are rapid swimmers, now spending most of their time below the surface of the water. Often they creep along the bottom and sides of the dish like little worms. Though they are constantly lengthening or shortening their bodies, the general shape is that of a pear, with the mouth at the small end. The broad end is usually, though not invariably, directed forwards in swimming. While creeping over the glass they frequently fasten themselves by their broad ends for from one to ten minutes, becoming free again of their own accord. The larvæ continued to swim about without any change in form until the middle of April. By this time, as subsequent examination showed, they had acquired six mesenteries (three pairs) and two long mesentrial filaments (Fig. 19, Pl. III.). A large number now began to attach themselves. Supported on the broad end, they stood nearly erect, spinning slowly around. The long axis began to shorten, and by the time they had assumed the shape of an oblate spheroid, eight meridional constrictions had appeared, marking the number of mesenteries. The long or, rather, oral-aboral axis continued to shorten until the little coral had assumed a disk-like shape with a flat basal surface and a convex upper surface, the latter marked with the meridional constrictions (a transverse section of this stage is shown in Fig. 34, Pl. V., and a longitudinal in Fig. 38). The whole process of fixation occupied several hours. All the larvæ did not become attached at the same time. On the contrary, many continued to lead a free life until the first part of May.

The lot of larvæ I got on the fifth of April were born in a more advanced state than their predecessors, and developed after birth more rapidly. So much so, that by the middle of April as many of this batch became attached as of the larvæ born March 20. Indeed, the first fixed larvæ I obtained, April 9, were from this lot, and had taken only four days to go through the metamorphosis, which in all the other larvæ required from two to four weeks. This great amount of difference amongst the larvæ, as to the time required to reach a certain stage of development, made it a matter of some trouble to pick out a consecutive series of stages. When I began to section, I found that inferences based on the length of the larva's life were only true within wide limits.

The stage with eight mesenteries is followed in a day or two by the stage with twelve. At this period the first deposition of the skeleton makes its appearance as a circular patch of calcareous matter on the basal surface of the attached polyp. I was not able to rear the young corals beyond this point; though I kept a few alive until the first of June. The death rate increased very much as soon as the larvæ became attached.

III. EARLY STAGES, INCLUDING THE FORMATION OF LAYERS.

The diameter of the unsegmented egg was about two-thirds the long diameter of the blastosphere (Fig. 2, Pl. II.). There was a very large centrally-placed nucleus, and the body of the egg was filled with vesicles, resembling in this respect the endoderm of the subsequent planula. The only observations on the segmentation were made on the eggs accidentally (?) discharged March 21. The spermatozoa played round each egg in large numbers. After fertilization the spherical egg became oval, and then divided into two equal blastomeres, which remained connected by a bridge of tissue. The division into four then followed. So far the segmentation was quite regular, but irregularities now began to crowd in, which led to the production of a grotesquely shaped mass comparable with the irregular planula described by Metschnikoff for Oceania (2). (I have observed a precisely similar segmentation and planula in an allied medusa, Turritopsis.) The irregular mass did not develop any further.

The normal segmentation which goes on in the body of the parent results in the formation of a blastosphere with a very large cavity (Fig. 1). The blastosphere is markedly bilateral, and is without cilia. The cells contain a large number of very distinct vacuoles, pretty evenly distributed through the cell body. In older blastospheres, Figs. 2 and 3, the formation of the larval or primitive endoderm has begun. The blastosphere cells are columnar, the nucleus is peripherally placed, and the vacuoles are concentrated in the central end of the cell. The cells are evidently delaminating, the inner vacuolated ends being split off to form the endoderm. The nuclei of the endoderm segments are very hard to make out. The delamination takes place irregularly over the general surface of the blastosphere, and is of a peculiarly complex character in certain spots. In the cell groups *m* and *m'*, Fig. 2, for instance, the lines of the transverse divisions of the several cells are continuous, and seem to indicate that the whole group must have divided transversely while it was yet a single cell: before it had been split up by the longitudinal divisions. But the latter show that the transverse divisions did not precede them. Such a cell as *n*, Fig. 3, throws light on the matter. This cell has begun to divide longitudinally, but even in the peripheral part of the cell, though the longitudinal constrictions are evident enough, the segments are far more intimately connected than are, say *n*, and the adjacent cells. In another cell, *n'*, the longitudinal division is apparently perfect; but on comparing the close apposition of the new segments with the marked space between *n'* and the adjacent cells, I am inclined to believe that the halves of *n'* are still connected by bridges of tissue, much as the blastomeres in many segmenting eggs remain connected after they are clearly marked off. In the group *m'*, then, Fig. 2, it is probable that the longitudinal constrictions were the first to appear in the mother cell, but that before they became complete divisions a general transverse constriction took place.

Delamination appears to be the exclusive means by which the endoderm is formed. I looked in vain for cells migrating from the surface. Whenever there appeared to be such, examination of the next sections showed that the cells in question had been cut obliquely, the peripheral end with the nucleus having been severed from the rest of the cell body. The cell *a*, Fig. 2, for instance, is merely the central portion of a constricted cell like *b* in the same figure. The delamination and accompanying longitudinal division often give rise to spheroidal cells, such as *x*, Fig. 3. These cells are always at the surface of the blastospheres. Whether their fate is different from that of the general ectoderm cells, I do not know.

The cavity of the blastosphere having been filled up by the endoderm segments, a solid planula, Fig. 4, is formed. On studying this figure, a median longitudinal section, we see that the longitudinal division of the superficial cells, which was active in the blastosphere, has given rise to a layer of columnar cells, the ectoderm. The inner ends of these cells are not distinctly marked off from the solid endoderm. The endoderm, when the living larva is compressed or when pretty thick sections are examined, appears made up of a quantity of vesicles, which look something like fat cells. When thin sections are examined (Fig. 4), it is found there exists a continuous protoplasmic matrix binding the vesicles together, which are now seen to be identical with the vacuoles present in the endoderm segments of the blastosphere cells. There is, however, a difference in their appearance, which is best shown in Figs. 9 and 10. In the blastosphere cell, the protoplasm in which lie the vacuoles is pretty uniform; but in the endoderm of the planula, the protoplasm immediately round each vacuole is denser than the intervening stroma, and forms a more or less differentiated shell for the vacuole. The shell stains much more deeply than the stroma. What the contents of the vesicle is, I cannot say. Carmine and hæmatoxylin do not affect it, and in these young stages I did not try osmic acid.

The endoderm contains, besides the vacuoles just mentioned, a number of "yellow cells" and scattered nuclei. No cell boundaries can be made out, and there is every indication that the layer is a plasmodium. A stage between Figs. 2 and 4 would go far towards elucidating the intricate structure of the solid endoderm, but I did not succeed in obtaining such.

While the embryo is still solid, the œsophageal invagination makes its appearance, Fig. 4. The larva is very narrow except at its base, where it is slightly dilated. At this stage it swims feebly about, the cilia having commenced to develop.

The formation of the permanent layers is illustrated in Fig. 5. In the region *d* the layers are in the condition characteristic of the earlier larva. But in the neighborhood of *c* the ectoderm cells have become much more clearly marked off from the endoderm. Their inner ends form a ragged line which gradually becomes more uniform, until the ectoderm is bounded internally by a smooth limiting surface, as at *a*. Though the bounding surface is smooth in this region, the supporting lamella has not yet formed. A little later it appears as a delicate membrane between the two layers (from *a* towards the mouth). While it is still very thin it resembles an ordinary cuticle. It appears between the layers, and is not formed by the direct metamorphosis of the ends of ectoderm or endoderm cells. As to the much-discussed question of which layer secretes the membranes; in early stage, such as Fig. 5, it is impossible to decide whether the secretion is the peculiar property of either layer. But in later stages, it is found in places where it can only be endodermic, and in others where it is evidently ectodermic. I shall return to this point further on. The various steps in the formation of the permanent layers can often be observed, with but few gaps, in a single section. Fig. 5 is such a section, with a few additions from another.

The permanent endoderm is formed from the larval endoderm by a differentiation of a peripheral layer from the central portion, Fig. 5. The peripheral layer is not formed continuously over the whole surface, but in spots here and there. It is at first marked off from the central portion only by its somewhat greater density, but it gradually breaks its connection with the latter by the acquisition of a smooth limiting surface, Figs. 5 and 10. Cell boundaries soon appear. The permanent endoderm as thus formed is a single layer of vacuolated cubical cells, except in the immediate neighborhood of the œsophagus, round the sides of which the cells are massed so as to fill up, more or less completely, the space between it and the body wall. This is especially noticeable on the left side of Fig. 5.

The œsophageal invagination as seen in Fig. 5 is much dilated at its base. Here the ectoderm has preserved its intimate connection with the endoderm, the ectoderm cells not even having acquired a smooth bounding surface. In Fig. 6 this even surface has been acquired, but at no time is a supporting lamella secreted over this area. The absence of the lamella clearly facilitates the absorption by the endoderm (or yolk) of the base of the invagination. The details of the absorption are as follows. The dilated bottom of the invagination, shown in transverse section in Fig. 10, is broken through at one point. Through this breach the yoke passes into the lumen, Figs. 8–10, and the base of the œsophagus thus enclosed above and below by yolk is absorbed. It is, I think, possible to recognize the base after it has passed into the yolk, though of course the histological structure is gone. In Fig. 8 is seen a curved mass of tissue extending from the left side of the œsophagus nearly to the right. Though in structure like the yolk, it stains a much deeper hue, and is therefore well defined. On comparing this figure with Figs. 6 and 10, there seems to be no doubt that the mass in question really represents the ectoderm base of the œsophagus.

The central portion of the larval endoderm remains as a food-yolk. In Fig. 5 it still exists as a continuous structure, but as more and more of the protoplasm is drawn into the layer of permanent endoderm, the vesicles lose their connection with each other. By the time the layers are definitely established, Figs. 6 and 8, the yolk is a loose mass of vesicles, the shells of which have begun to disintegrate. The shell is extremely dense, and in this and subsequent stages seems to be fatty, as it stains very dark with osmic. Remnants of the yolk are found in stages as late as Fig. 19.

Though the formation of the supporting lamella and the differentiation of the permanent endoderm very often take place at about the same time, this is not always the case. In many larvæ the supporting lamella is entirely formed, and the œsophagus has opened centrally, while the endoderm is still solid, Figs. 10 and 12.

The "yellow cells," which later are found in such abundance, appear for the first time in the planula, Fig. 4. I have not seen them actually entering the planula, but in this and slightly older stages, Fig. 5, a few occur in the surface ectoderm, whereas in older larvæ and in the adult they are confined to the inner layer of the body.

COMPARISONS.

a. Germinal Layers.

Among the many ways in which the germinal layers are formed within the Cœlenterates, Metschnikoff (2) has decided that one represents the manner in which the earliest metazoa were formed. In this so-called "mixed delamination" a solid endoderm is built up both by delamination and by the migration of superficial cells into the interior. *Polyxenia* (Metschnikoff) and, better, *Aurelia* (Götte) are good examples of this process. Accepting this type as ancestral, *Manicina* has diverged along the same path as certain Trachomedusæ (Geryonia, Liriope);

i.e., none of the blastosphere cells migrate into the interior, but the endoderm is formed exclusively by delamination.

Though the way in which the solid larva was originally formed seems preserved in but a few species, the solid larva itself may fairly be considered as typical for the Cœlenterates. It is especially well preserved in the Hydroids and Anthozoa. In the latter group it is nearly universal among Alcyonarians, and occurs in the majority of the Zoantheria. The Alcyonarian which comes nearest to *Manicina* in the formation of its layers is Renilla (3). In this genus, though the blastosphere has a very small cavity, the endoderm is formed by delamination, as in the coral. As regards the structure of its larval endoderm, however, Renilla differs from Manicina. In the former the endoderm is made up of a mass of cells, of which the peripheral layer becomes the permanent endoderm, while the central cells go to pieces, and are probably eaten, amœboid fashion, by the peripheral cells. In Manicina, on the other hand, the larval endoderm is a plasmodium, and in the entire process which leads up to the formation of the adult endoderm it would seem that a prominent physiological part is played by the "vesicles," which in all probability contain some kind of yolk. Owing to the plasmodial nature of the solid endoderm, the complete transformation of the latter into the permanent layer must require less time in Manicina than in Renilla. For in Manicina there is no large accumulation of yolk cells which must slowly be devoured, amœba fashion, by the peripheral cells. On the contrary, when the time for the formation of the permanent endoderm has arrived, the general protoplasm is merely drawn towards the periphery, and after it has there broken up into cells, there remains but little nutriment in the loose yolk mass. Just how the yolk is ingested after the cellular endoderm is formed, I am unable to say. It is not devoured, amœba fashion, by the endoderm cells at large, though in the region of the œsophagus, Figs. 6 and 8, connection is maintained for a considerable time between the yolk and the endoderm, which elsewhere is completely formed.

Amongst the corals and actinias, two or three forms have been described as undergoing invagination, notably *Cerianthus* (Kowalevsky 4) and *Actinia* (Jourdan 5). While the mere recurrence of invagination in a cœlenterate group can scarcely be said any longer to have a phylogenetic significance, these two forms are especially interesting, as E. B. Wilson has remarked (3), because in each of them a yolk mass appears after the layers have been completely formed. I have not seen Kowalevsky's figures, but the yolk shown in Jourdan's figure 119 is precisely like the yolk of a young Manicina (making allowance for difference in thickness of the sections). The *à priori* improbability that the endoderm would first secrete a yolk (Kowalevsky) and then swallow it again, taken together with the similarity of the yolk in question to that of Manicina, might tempt one to believe that both authors had mistaken a stage like Fig. 12, Pl. I., for a true gastrula. But Kowalevsky's statements on this head are so definite as to preclude this supposition.

b. Supporting Lamella.

The only two authors who have described in detail the formation of the supporting lamella are Jourdan (*l.c.*) and Wilson (*l.c.*). Jourdan's observations were made on a coral, Balanophyllia, and an actinia, Actinia equina. He draws a sharp distinction between the "membrana propria" and the jelly.

The former answers to the German *Stutzmembran.* It is a firm limiting membrane which appears between the two layers and extends into the mesenteries to form their axial bands. This is what I have spoken of as the supporting lamella (comp. any of figures on Pl. IV.). Its origin Jourdan was unable to trace with any certainty. The jelly, on the other hand, which eventually becomes fibrous, is formed outside the membrana by the superficial ectoderm cells. The inner ends of these cells break off and fuse together to form a granular mass, in which fibres subsequently appear (*l.c.* Figs. 119 and 129).

The supporting lamella described by Wilson is evidently the same thing as Jourdon's membrana. Its origin according to Wilson is double. In the mesenteries it is a simple cuticular secretion of the ectoderm cells. But in the body wall it is formed in a manner similar to that just described for the jelly: the inner ends of the ectoderm cells become swollen, constrict off, and form a granular layer which condenses to a smooth membrane.

In Manicina there is first formed a very distinct membrane as described. In later larval stages, at various spots, especially in angles, a thin fluid jelly accumulates. This is noticeable in

Figs. 16 and 17, beneath the right-hand mesenteric filament, and in Figs. 44 and 45 at the angles of the œsophagus. It is always to be found in the axis of the larval filament, Fig. 26. The distinction between the supporting membrane and the more fluid jelly, which is noticeable in larval stages, is lost later in life. In the older larvæ, Fig. 39 for instance, the supporting membrane throughout its whole extent has become considerably thicker than in younger stages, though the jelly in the axis of the filament is still to be distinguished from the more membrane-like band of the mesentery. In the adult the axial band of the mesentery is so much wider, while the jelly in the axis of the filament is at the same time denser than in larval stages, that all distinction between the two structures is lost. Compared with an actinia the whole mesodermic skeleton of the adult Manicina is very scanty and membrane-like, but in certain places it reaches a more generous jelly-like condition, for example, in parts of the mesenteries, Fig. 51. Here the supporting substance is merely the thickened primitive membrane.

There indeed seems to be no difference between the supporting membrane proper and the jelly, except in the mere quantity of the secreted substance and in the percentage of water. What applies to the origin of one should explain the origin of the other. Now as regards the membrane proper, I am quite sure that in Manicina it is formed as a cuticular secretion, and not by the direct conversion of the ends of ectoderm cells into granular matter, which subsequently condenses to a membrane. Turning now to the question as to which layer secretes the membrane, we see from the figures (14, 17, 26, 45) that after the mesenteries are formed, the lamella is much more intimately connected with the endoderm than with the ectoderm: where the layers are forced apart, it always sticks to the endoderm. But even here the ectoderm is provided with a well-defined limiting membrane, which if thinner than the lamella, is essentially like it. I conclude from this and other facts to follow that when the lamella lies between the two layers, both layers share in secreting it. That the endoderm cells can secrete the lamella, is plain from its occurrence in the axis of the mesenteries, and in the axis of the genital bands of a Cubomedusa (6). On the other hand, the same argument can be used to prove the ability of the ectodermal cells to secrete this substance, for in the velum of Hydromedusæ there is a well-defined lamella, which is formed *in situ*. In Cunocantha (7) I have pointed out that when the velum is developing, the ectoderm cells range themselves so that their bases will secrete a continuous membrane.

IV. Formation of the First Pair of Mesenteries and Filaments.

I was led to pay especial attention to the filaments by E. B. Wilson's interesting discovery that the dorsal pair of filaments in the Alcyonarian polyps are ectodermal lobes (8). Relying on the histological similarity between this pair of filaments and the *flimmerstreifen* of an actinian filament, Wilson suggested that perhaps in the latter the *flimmerstreifen* were ectodermal, and only the median *nesseldrusenstreif* was endodermal. I find, however, that the filaments of *Manicina* are as to origin like the dorsal pair in the Alcyonaria. They are simple ectoderm lobes which grow down from the œsophagus.

The œsophageal invagination in the earliest stages is symmetrically placed, Figs. 4 and 5. It very soon, however, begins to travel towards one side of the larva. This is shown in the transverse section, Fig. 7, and still better in the longitudinal section, Fig. 6 (the endoderm in these two larvæ is in different stages of development). The lateral motion of the œsophagus has compressed the endoderm on its left into a compact mass, which completely fills the space between the œsophagus and body ectoderm. On the right hand the endoderm has been stretched, until it forms a single layer of cells. The narrow lumen of the œsophagus is bilateral (it is doubtful whether this is true in all larvæ at this stage), and its dilated extremity has no longer the symmetrical bulb-like shape of Fig. 5. In Fig. 8 the lateral movement has gone a step farther, and meanwhile the œsophagus has opened centrally. The movement of the œsophagus is continued until in one meridian there is nothing left between the œsophageal and superficial ectoderm but the supporting lamella, Figs. 11 and 12. (In Fig. 11 the lamella has not yet appeared, but both stomadoeal and body ectoderm have smooth, limiting surfaces.) The intermediate stages show that the lateral movement of the œsophagus travels from above downwards, and that the endoderm has consequently been pushed down in this meridian. This is proved by Figs. 9 and 10, transverse sections from a larva in which the œsophageal movement had gone farther than in Fig. 8. Fig. 9 is about at the level *a* in Fig. 8, and Fig. 10 is at the level *b*. In this larva then the œsophagus was closely pressed against the ectoderm at the level *a*, but was separated from it by endoderm at a lower level *b*. In the later stage, Fig. 11, the lowest part of the œsophagus has completed the journey. The meridian in which the œsophagus is thus pressed against the ectoderm, is that of the first mesentery. (Though Figs. 9 and 10 are from the same larva, both the supporting lamella and endoderm are much farther advanced in the lower section than in the upper.)

The larva from which the longitudinal sections, Figs. 12 and 13, were cut, was very backward in forming the permanent endoderm. Fig. 12 is taken through the line *a* and *b* in Fig. 11, and is in the plane of the first pair of mesenteries. It is only on the left side that the œsophagus is in contact with the body ectoderm. But the right side is following suit, and in a slightly older stage, Fig. 12, is in the same manner applied to the surface ectoderm over a narrow tract. Fig. 13 is to one side of *a* and *b* in Fig. 11, and is consequently out of the plane of the mesenteries.

My next stage after Fig. 12, is the larva from which the series of transverse sections, Figs. 14 to 17, was taken. It is this stage which proves the meridians, along which the œsophagus is applied to the body ectoderm, to be really those of the first pair of mesenteries. Fig. 14 is the uppermost of the series, and is through the body of the œsophagus, the lumen of which is exceptionally large. On the right side the œsophagus is separated by jelly alone from the surface ectoderm. Following down the series of sections, we see that in this meridian the œsophageal ectoderm sends down a slender lobe, which, like the œsophagus above it, divides the endoderm and rests on an accumulation of jelly (right side of Figs. 15, 17). This lobe is a mesenterial filament. It is considerably shorter than the filament on the opposite side, Fig. 17, and is probably the second one of the first pair. The right side of this larva is practically in the condition shown in Fig. 12, except that the œsophagus has formed a filament.

On the left side of the larva, Fig. 14, matters are more advanced. On comparing this side with Fig. 12, we see the œsophagus has moved away from the surface ectoderm, but while doing so has remained connected with it by a band of supporting lamella. Running through the series of sections, it is found that in this meridian also an ectoderm lobe has grown down from the œsophagus. This lobe is the primary filament. It is much wider at its start, near the œsophagus, than its fellow on the opposite side, but soon dwindles to about the same size. Like the œsophagus above it, this filament is in a more advanced condition than the filament on the right side. Since we know that the left side of the œsophagus itself has passed through the condition which exists on the right side, we are pretty safe in believing that the left filament has likewise passed through the condition in which the right filament is found. The lack of a fairly intermediate stage between Fig. 12 and the larva we are studying, is to a certain extent supplied by the larva from which Fig. 11 was taken. In this individual, which was sectioned transversely, the œsophagus extended so much farther down in the meridian of the first mesentery than round its general lip, that in this meridian it formed a very evident though not a very long lobe. This lobe, which becomes the primary filament, is shown in Fig. 11, and is to be found in the sections immediately below the one figured, growing smaller towards its end.

On comparing the first and second filaments in Fig. 17, it is clear that the endoderm, which at a higher level grew in between the œsophagus and body ectoderm, has likewise forced its way beneath the primary filament, and thus given rise to the first mesentery. The mesentery is continued from the level of Fig. 17 downwards, as a very slight endodermic ridge on which rests the filament. The axial band of supporting lamella is continuous with a thinner lamella, separating the filament from the endoderm. Immediately beneath the opening of the œsophagus the mesentery is much more elevated than at a lower level. The elevation of the mesentery in this region is connected with the first appearance of an intermesenterial chamber.

In the larva we have been studying the first pair of intermesenterial chambers has been marked off. Round the œsophagus, however, they are still solid, Fig. 14, though at a lower level the hollowing out of the solid endoderm has begun. At this level, Fig. 15, which is just beneath the opening of the œsophagus, the endoderm on one side of the first mesentery exhibits a small cavity. The cavity, when traced through the series of sections, is found to open into the cœlom in Fig. 16, forming, as it does so, the cave or bay which underlies one-half the primary filament in the figure. It is thus (comp. Figs. 14 and 15) in the larger of the two primary chambers that the excavation of the solid endoderm begins, and, as I learn from other series, the excavation of this chamber is nearly completed before that of the smaller begins. The excavation starts, as we have just seen, in the immediate neighborhood of the first mesentery. From this spot it gradually extends across the chamber to the second mesentery, travelling all the while from the lip of the œsophagus upwards.

The second mesentery, which exists in its embryonic condition in Fig. 14, follows the example of the first. In Fig. 18 it is completely formed, and in the series of longitudinal sections, Figs. 20–23, which I shall describe later, the second mesentery is in the condition in which the primary is in Fig. 14; *i.e.*, in the immediate neighborhood of the second mesentery the larger of the two intermesenteric chambers is solid, while the smaller chamber is entirely solid.

In the larva from which the transverse section, Fig. 18, was made, the various processes which have been described are now completed. The œsophagus is swung by two complete mesenteries. Both intermesenteric chambers — the larger on the left, the smaller on the right — have been hollowed out. Below the œsophagus, the mesenteric ridges extend the whole length of the larva, and the first pair of filaments about half the length. The section is slightly complicated by other features, of which I shall now speak.

In the larger of the two chambers, Fig. 18, the second pair of mesenteries, 3 and 4, has appeared. The axial bands of supporting lamella as yet cause no elevation of the endoderm, and at a level slightly below the œsophagus are entirely lost. In Fig. 18 *a*, above Fig. 18, the axial band numbered 4 stretches across to the œsophagus, and still higher up 3 does likewise. In this section the position of the œsophagus is eccentric. This is very often the case at the extreme upper limit (the appearance is not due to oblique sections), and hence one mesentery usually runs out before its fellow (2 before 1). The mode of origin of the second pair of mesenteries is thus entirely different from that of the first pair. All the subsequent mesenteries are formed after the fashion of the second pair.

The outer wall of the larger intermesenterial chamber in Fig. 18 is made up of unmistakable endoderm, but the inner or œsophageal wall has an ephithelium precisely like that of the œsophagus. Both are composed of very slender elongated cells with a median thickening, in which lies the nucleus; the peripheral end is enlarged and flattened, so that by the juxtaposition of many such cells a continuous cuticle can be formed. The cells in question resemble the well-known "supporting cells" of the Hertwigs (9). Besides the supporting cells, glandular cells are found. These are slender and full of granules, the latter staining very deeply with hæmatoxylin. The epithelium of the œsophageal wall of this chamber is, moreover, sharply marked off from the rest of the epithelium. It is directly continuous with the œsophageal ectoderm round the lip of the œsophagus, and is evidently a tract of ectoderm. Any doubt which might cloud this point is removed by later stages, such as Figs. 44 and 45, where the epithelium, which is claimed as ectoderm, overlaps, at its upper limit, the endoderm. It is clear that in this stage, Fig. 18, the œsophageal ectoderm has been reflected round that portion of the lip (free edge of œsophagus) which belongs to the larger chamber, and has then run up along the outer surface of the œsophageal tube, driving the endoderm before it. The direction of growth is reversed, but otherwise the ectoderm is acting in precisely the way which it chose in forming the first pair of filaments. In the smaller chamber of Fig. 18, the epithelium forming the œsophageal wall does not differ from the rest of the endoderm. In a later stage, when the third pair of mesenteries has appeared, the ectoderm is also reflected round the lips of this chamber, and runs up along the œsophageal wall, Figs. 36 and 39.

The reflection of ectoderm, which leads to the condition shown in Fig. 18, commences as soon as the excavation of the primary (larger) chamber begins, and follows close on the heels of the latter process. The object of the reflection of ectoderm, as will be shown later, is to provide filaments for the young mesenteries before the latter are complete; *i.e.*, continuous from body wall to œsophagus. Bearing this in mind, it is probable that the reason why the ectoderm is reflected into the primary chamber at such an early date, is that the second pair of mesenteries will be formed in this chamber. The series of longitudinal sections, Figs. 20–23, illustrates the early reflection of ectoderm round the lip of the larger chamber. The larva from which this series was made was at a stage intermediate between Figs. 14 and 18. The supporting lamella of both of the first pair of mesenteries were complete, as in Fig. 18; but the intermesenterial chambers were far from perfect. The smaller chamber was entirely solid, and the cavity of the larger was only partially formed. In spite of the difference in age, it will do to refer the planes of the longitudinal sections to Fig. 18. The section, Fig. 20, thus is taken through the mesenteries 1 and 2, and the corresponding filaments. The next three figures represent a series of sections to the left of this plane, the one farthest to the left lying in the plane *a–b* of Fig. 18. Finally, the left-hand mesentery in Fig. 20 is the primary mesentery, 1 in Fig. 18. With this orientation it is seen, on glancing through the series 20–23, that only in the neighborhood of the primary mesentery has the intermesenteric chamber been hollowed out. In all the sections the endoderm is solid on the right side of the œsophagus. Now, in Fig. 23, the intermesenteric chamber (to the left of œsophagus) is in the state in which it was formed. The ectoderm has not yet been reflected round the œsophageal lip. But in the sections nearer to the mesentery, Figs. 21 and 22, the ectoderm *has* been reflected, and has driven the endoderm before it. The reflection of ectoderm, as I have said, follows very closely the excavation of this chamber. As the latter proceeds from mesentery 1 to mesentery 2 (Fig. 18), so does the former; and by the time the chamber is completely established, the ectoderm is reflected all the way from 1 to 2, as is seen in Fig. 18.

In the larva which was used to show the earliest appearance of the primary intermesenteric chamber, Figs. 14–16, the reflection of ectoderm had already begun to take place round one edge of the primary œsophageal lobe (Fig. 16, left).

To sum up the more important events described in this section:

To form the first mesentery the whole œsophagus moves laterally, until in the meridian of the mesentery there is only supporting lamella between the œsophageal and surface ectoderm. The œsophagus now grows downward in this meridian as a lobe of ectoderm, which represents the primary filament, and which pushes the endoderm before it. On the opposite side of the animal, along the line of the second mesentery, the œsophagus becomes applied to the body ectoderm in the same manner, and a lobe grows down from it to form the second filament. The mesenteries as such are formed by the ingrowth of the endoderm between the body ectoderm and œsophagus above, and between the body ectoderm and the filaments below. The primary pair of intermesenterial chambers are at first solid. The larger chamber acquires its cavity before the smaller, the excavation travelling from the lip of the œsophagus upward, and from the first toward the second mesentery. The excavation of the primary chamber is closely followed by the reflection of ectoderm into this chamber, the reflected ectoderm running up the œsophageal wall, and driving the endoderm before it. The second pair of mesenteries appear in the larger chamber as longitudinal ridges of the supporting lamella, which cause no elevation of the endoderm.

V. Histology of the Larvæ.

It may now be advisable to describe the histology of the larvæ, going when necessary beyond the stages already studied.

a. The Surface Ectoderm.

The ectoderm at the time when the supporting lamella is formed, Figs. 5 and 6, consists of columnar cells, the protoplasm of which shows a great tendency to break into small polygonal balls. While the ectoderm is in this condition the mucus cells appear (*m*, Fig. 6, Figs. 7, 8), as pear-shaped bodies in the peripheral ends of the columnar cells. The contents of the pear-shaped body stains a deep blue with hæmatoxylin, and is thus distinctly marked off from the surrounding cells. It appears to be fluid from the start, as even in such young stages as Fig. 7, many of the mucus cells have poured out their contents, which adheres to the mouth of the cell as a little mass of a blue color. This tendency of the mucus cells to eject their contents, presumably when the killing fluid touches the larva, is very noticeable in older stages such as Fig. 27, which are often completely covered by a thin layer of mucus. The mucus cells increase in size and number, until they become the prominent feature of the ectoderm (Figs. 7, 20, 27). In their final condition, Fig. 27, they are large, clear sacs, in which a few strands of protoplasm may be seen in carefully prepared osmic specimens. The nucleus of the original cell in which the sac developed cannot be made out in sections.

The mucus cells develop over the general surface of the larva, but are not found at the aboral end. Here their place is taken by a slender elongated cell, full of granules which stain even deeper with hæmatoxylin than does the mucus cell. The granular gland cell is easily recognized in its earliest stage, and is formed from the embryonic ectoderm cell by a deposition of granules throughout the length of the cell. The granular cells, though especially grouped at the aboral end of the larva, are found here and there over the general surface.

The remaining cells of the embryonic ectoderm become for the most part transformed into slender "supporting cells." Thread cells, *n.c.*, are first noticed in larvæ at about the stage of Fig. 14. Whether the ectoderm contains any muscle cells, I do not know. The larvæ can alter their shape to a great extent, but the fibres are probably all endodermal.

For the study of nervous elements, *Manicina* in all stages is a very unfavorable subject. Even the ganglion cells which show so plainly in sections of actinian larvæ, I was not able to make out in the coral. There is, however, a finely granular stratum at the base of the ectoderm, which is very thin over the general surface, Fig. 26, but at the aboral end of the swimming larva is thick and easily seen, Fig. 20. When the living larva is compressed, this accumulation of granular substance is very noticeable. It is perfectly clear, and until I began to section I thought it was jelly. When carefully examined, the granular layer in this region is found to consist of a mass of fine fibrils. It is very probably nervous. The fact that the cœlenterate planula in general swims with its aboral end in front, taken together with the occurrence of a bunch of long cilia on this end of many actinian larvæ, suggests the existence of some such primitive nervous centre as I take this accumulation of granular matter to be.

When the various elements of the ectoderm have been completely differentiated, Fig. 26 (from a stage a trifle older than Fig. 29), a finely striated cuticle is secreted, in all respects like that described by the Hertwigs for the actinias (9. Taf. III.). The cilia with which the body ectoderm is completely covered, and with which the œsophagus and filaments are likewise provided, I have not represented in the figures.

b. Œsophagus and Filaments.

The œsophagus and young filaments, Fig. 20, have the same structure as the superficial ectoderm, except that mucus cells are absent, and the granular gland cells more abundant than over the general surface. As a rule it is only in the youngest stages that the reflected ectoderm, Fig. 18, contains gland cells, and even then they are rare. In later stages, Fig. 24, mucus cells are found in the upper part of the œsophagus immediately round the mouth, and very large thread cells, Figs. 24 and 27, appear in considerable numbers in the œsophageal epithelium, extending down into the filaments. The histology of the filaments will be treated in detail in a special section.

c. Endoderm.

The endoderm, after it has once formed, remains about the same during larval life. I am not sure whether it is ciliated. The cells are cubical or columnar, and contain one or more large and distinct vacuoles. The protoplasm is granular and coarsely reticular. The cell outlines can only be distinguished with a little care. The number of yellow cells steadily increases with age. A few very fine muscle fibres can be made out here and there, especially in the mesenteries, and a continuous layer probably exists.

In closing, the general similarity between the ectoderm of the coral larva (practically the same in the adult *Manicina*) and the actinian ectoderm, as described by the Hertwigs, may be noticed. In particular, the two kinds of gland cells in the actinias are exactly represented in the coral. The Hertwigs suggested that possibly the granular gland cell was but a stage in the development of the mucus cell; but this appears not to be the case, as the two are distinguishable from the start, and have also a different distribution.

VI. MESENTERIES AND FILAMENTS FROM THE SECOND TO THE SIXTH PAIR.

Before proceeding to the detailed description of the reflection of ectoderm, which, as I conclude, leads to the formation of all the filaments except the first pair, it will be convenient to give an account of the order in which the mesenteries appear.

The first appearance of the second pair of mesenteries has already been described, Fig. 18. In a later stage, Fig. 27 (transverse section) this pair is complete at the level of the figure. At a lower level, just above the lip, Fig. 28, one of the pair, 3, is still complete, while the other, 4, is incomplete. The difference in growth between the two mesenteries of the second pair is an exception; they usually develop at the same rate. Below the œsophagus, Fig. 29, both mesenteries exist as slight ridges, which extend the length of the larva.

The third pair of mesenteries have appeared in Fig. 27. They remain insignificant during the swimming life of the larva. After the larva has become attached, the third pair is prominent; and the fourth pair is also found, in the position shown in Fig. 34 (a transverse section taken below the œsophagus — the primary mesenteries are supplied with large and coiled filaments). According to Lacaze Duthiers, the fourth pair appears between the first and second pairs. The Hertwigs suggested (?) on general grounds of symmetry that the order of appearance was as I have figured. As regards the fifth and sixth pairs, however, the old account of Lacaze Duthiers holds for *Manicina* as against the figures given by the Hertwigs for Adamsia (Taf. 1, f. 3). This is seen on referring to Fig. 39, a transverse section through the œsophagus of a stage with twelve mesenteries. The fifth and sixth pairs develop simultaneously on opposite sides of the primary mesenteries. In *Adamsia*, according to the Hertwigs, the two pairs of mesenteries appear on opposite sides of the long axis of the œsophagus, in the chambers between the first and second pairs.

Fig. 39 represents my oldest larval stage, and I was consequently not able to trace the development of the muscle plates and the rearrangement of the twelve primary mesenteries. According to the accepted account, the pairs 3 and 4, in Fig.

39, become the directive pairs, and on each side of the long axis of the œsophagus, 5 and 1 unite to form one pair, and 6 and 2 another pair.

In this connection it may be observed that after the larvæ became attached, the lumen of the œsophagus was decidedly bilateral in the living animal, and bore the relations to the mesenteries shown in Fig. 39. The shape of the lumen is, however, susceptible of great changes, and in many of the sections through attached larvæ the typical shape is not retained (Fig. 36), or the œsophagus is compressed in the (normally) long axis, and drawn out in the short (Fig. 45). In the swimming larva the small size of the mouth will not permit one to decide as to the shape of the œsophagus in the living animal. After examining a large number of sections I conclude that in stages as old as Fig. 27, the arrangements are as in the attached larva: the lumen is bilateral and has one of the first pair of mesenteries on each side of its long axis. In earlier stages, such as Figs. 7, 14, 18, I could not decide whether the œsophagus had acquired its ultimate shape.

We now come to the formation of filaments for the second and subsequent pairs of mesenteries. In Fig. 18 the reflected ectoderm which forms the œsophageal wall of the larger chamber extends horizontally from 1 to 2. The mesenteries of the second pair, 3 and 4, are extremely incomplete. In Fig. 27 these mesenteries are complete, and now the reflected ectoderm does not extend from 1 to 6, but is represented by the patch *R.E.* between 3 and 4. In sections of the same larva (Figs. 28 and 29, below the level of Fig. 27) a certain irregularity makes its appearance, which is connected with the formation of the third mesentery, and of which I shall speak later. In the typical larva of this stage the sections below Fig. 27, between it and the lip of the œsophagus, are precisely like Fig. 27. This means that the mesenteries 3 and 4 are both complete throughout the length of the œsophagus, and that the œsophageal wall of the chambers inclosed between 2 and 4, and 3 and 1 respectively, is endodermal. At the very lip of the œsophagus in some larvæ the œsophageal walls of these chambers are ectodermic. In a section just below the œsophagus it is found that the mesenteries 3 and 4 have short filaments. Further, the tract of ectoderm *R.E.* only extends upwards for about one-third the length of the œsophagus, while it will be remembered that in this stage (Fig. 18) the reflected ectoderm extends nearly the whole length of the œsophagus. Now what has taken place in the transition of the stage Fig. 18 into the stage Fig. 27? Plainly it is that the mesenteries 3 and 4, as they grew down and gradually became complete, carried along with them the reflected ectoderm, part of which came to lie along the mesenteries as short filaments, while the remainder was divided into three portions. Of these, the two lateral, which originally extended from 2 to 4 on the one side, and from 1 to 3 on the other (Fig. 27), were carried all the way down to the lip of the œsophagus, while the middle portion *R.E.* was not carried the whole way down.

A couple of longitudinal sections will further elucidate the series of changes which separate Fig. 18 from Fig. 27. The sections given in Fig. 25 were made from a larva at about the same stage as Fig. 27. The two mesenteries of the first pair had long filaments, and the mesenteries of the second pair were complete and equally advanced. The section *b* is a radial half-section through one of the second pair of mesenteries, say 4 in Fig. 27. The mesentery is complete, and to its edge clings a short filament. The other mesentery of the second pair, with its filament, is the exact counterpart of the one figured (in cutting the larva, radial sections of one mesentery and equally true transverse sections of the other were obtained). The precisely horizontal plane in which the filament of *b* lies, is probably due to the sudden expansion of the larva, on being killed, in the direction of the shorter transverse axis of the œsophagus (the transverse section would be elongated in a direction at right angles to the long axis of Fig. 27). The half-section *c* in Fig. 25 is reversed so as to complete the œsophageal lumen. It is the second section to one side of *b*, and *a* is the second or third on the other side. Comparing all these figures with Fig. 27, *b* is through mesentery 4, *a* is on the far side of 4, and consequently cuts the reflected ectoderm *R.E.*; *c* is on the near side of 4, and the ectoderm is not reflected round the free edge of the œsophagus.

Fig. 24 is a single longitudinal section from a stage slightly older than the one just described. On the right it is through one of the second pair of filaments, and on the left through an intermesenteric chamber. Referring the section to Fig. 27, the right half is through mesentery 4, and the left through the chamber opposite at about the point *x*.

Having now described the ordinary way in which the first and second pairs of mesenteries and filaments are formed, I will take up an exception, which has more bearing on the relationship between the Anthozoa and Scyphomedusæ. Figs. 30–33 are transverse sections, numbered from above down, of a larva in which the first pair of filaments extended about half the length of the body. The œsophagus throughout its vertical extent is apposed to the surface ectoderm over a wide tract, *a* to *b* in Fig. 30. On running through the series of sections it becomes evident that the tract *a–b* is not the meridian of a single mesentery, as it would be in a normal larva like Fig, 14, but is the space between two mesenteries. The first section below the œsophagus, Fig. 31, shows that a rather wide lobe of ectoderm is growing down, and also that between *a* and *b* this lobe has been forced apart from the body ectoderm. In Fig. 32 (two sections omitted between 31 and 32) a lobe of endoderm has grown in between *a* and *b*, and has thus given rise to two mesenteries, which are provided with a common filament. In the section below, Fig. 33, the lobe of endoderm is hollowed out, and the two mesenteries definitely established. In a section (not figured) below Fig. 33, the mesenteries *a* and *b* exist as separate ridges, and the common filament has split into its constituent parts, 1 and 3. The filament 3 extends a very short distance down, and the mesentery *b* only reaches the equator of the larva. The mesentery *a*, with its filament 1, is the fellow of 2, on the opposite side of Fig. 32. These two mesenteries belong to the first pair. I have assumed that *a* is the primary mesentery, since its filament is larger than that of 2.

Bearing in mind the normal development as illustrated in Figs. 12 and 14, the exceptional character of this larva is due to the fact that one of the second pair of mesenteries is formed at the same time and in the same manner as the mesenteries of the first pair. This aberrant member of the second pair, *b*, Fig. 30, etc., may be called the third mesentery. We may suppose that the œsophagus, applying itself to the body ectoderm along the line not only of the first *a*, but also of the third mesentery *b*, was unable to force down the endoderm in these lines without carrying down at the same time the endoderm between *a* and *b*. Thus came the condition shown in Figs. 30 and 31. When the time came for the mesenteries as such to be formed, the endoderm which had been pushed down between *a* and *b* was compelled to grow up again, becoming excavated so as to form the intermesenteric chamber. It is in this process that we see the endoderm in Figs. 32 and 33. The irregularity of the larva, it will be noticed, is confined to one side: the right side of the sections is normal, and doubtless the other member of the second pair of mesenteries would have developed in the usual way.

The larva just described was the only young specimen I observed, which exhibited this peculiar variation. I found a few older individuals, however, in which one of the filaments of the first pair was so intimately connected with one of the second pair, as to render it probable that the two were simultaneously formed from a common lobe in the manner shown in Figs. 30–33. The larva, Figs. 27–29, to which I have already referred several times, comes under this head. Though the section, Fig. 29, is an appreciable distance below the œsophagus, the filaments 1 and 3 are still united, and bear evidence of their common origin. The other mesentery of the second pair, 4 in Fig. 28, has itself been formed, and is gaining its filament, in the normal manner. The reflected ectoderm only extends from 2 to 3, and if the latter mesentery has been formed in the manner suggested, the ectoderm never was reflected between 3 and 1.

Returning to the normal development we have now to trace the origin of the filaments for the third pair of mesenteries. These filaments are derived from a lobe of ectoderm, which is reflected into the smaller of the two primary chambers. The reflection takes place after the larvæ have become attached. In a stage with twelve mesenteries, Fig. 39, the lobe is marked *x*. The section is taken at a level higher than that reached by the lobe belonging to the chamber *c* (marked *R.E.* in Fig. 27). In a section just above Fig. 39 the third pair of mesenteries bury themselves in the lobe *x*, much as 4 does in Fig. 28. In the uppermost sections, where the mesenteries are complete, *x* is not found. After a great many trials I succeeded in getting a radial section through one of this pair of mesenteries, which had forced down the reflected ectoderm so that the latter lay along its free edge as a tiny filament (Fig. 38, left half; the right half is through chamber *c*, Fig. 39). The lobe for the third pair of filaments is almost always present in larvæ with eight mesenteries: in Fig. 36, a section just above the lip, it is marked *c*. In this larva the mesenteries of the second pair are backward in development; they are not yet perfectly complete, though on one of them a very small filament is seen.

As the fourth pair of mesenteries continue to increase in size, the tract of ectoderm, which belongs to the chamber *c*, in Fig. 39, extends farther upwards. In Fig. 39 it reaches about the same level as in Fig. 27 (*R.E.*). In a slightly more advanced stage, Fig. 38 (right half), it extends nearly the whole length of the œsophagus; and in the series of transverse sections, Figs. 43–45, it likewise extends to nearly the uppermost limit of the chamber. The latter series is a very good one, as the polyp was killed in its natural shape. In life, when the young coral is expanded, there is a very distinct oral cone, indicated by the line *m–m* in Fig. 38. In dying, the oral surface is almost always retracted, and the median longitudinal section is then as in Figs. 37 and 38. The transverse section, Fig. 43, is taken through the line *x–y*, in Fig. 38. Figs. 44 and 45 lie above it. In the larva from which the series was taken, both the third and fourth pairs of mesenteries were very well developed below the level of *x–y*, but above this level they were not perceptible. Judging from all my other sections I should say that this rapid development of the mesenteries along the side-wall of the polyp, as contrasted with their backwardness in the upper œsophageal region, was exceptional. In the sections figured the first and second pairs of mesenteries are complete. The chambers *a* and *b*, together with *c*, represent the larger of the two primary chambers. The walls of *a* and *b* are endodermal except for a short distance above the œsophageal lip, but in *c* and in *d* (the smaller of the two primary chambers) the reflected ectoderm extends very far up. As the third pair of mesenteries lie in chamber *d*, the ectoderm of this chamber, as might be expected, extends farther up than in *c*, in which lie the fourth pair. In the ectoderm of *d* there are a few large nettle cells, a rare occurrence. At the upper limit of each tract of ectoderm, the overlapping of the layers, previously referred to, is shown. This overlapping of the layers, while uncommon, is noticed in a good many specimens. In Fig. 37 the left half of the section, through an intermesenteric chamber, exhibits this phenomenon. The right half of the section is through one of the second pair of mesenteries.

The fifth and sixth pairs of mesenteries appear simultaneously, but it is convenient to speak of one pair as the fifth and the other as the sixth. They are still very small in my oldest larval stage. The filaments for the fifth pair are probably formed from the lateral portions of the lobe *x*, Fig. 39, after it has been divided by the completion of the third pair of mesenteries. The filaments for the sixth pair, it seems, will be formed from the tracts of ectoderm, which belong to the chambers *a* and *b*, Fig. 39. These tracts, it will be remembered, were in most larvæ pushed completely back to the free edge of the œsophagus, where the second pair of mesenteries become complete. In stages with twelve mesenteries, however, such as Fig. 39, they have again appeared, though they usually extend but a very short distance above the lip. In a couple of larvæ as old as Fig. 39, they were unusually well developed, reaching as far up as the tract for the chamber *c*.

In summing up the facts of the reflection of ectoderm it will be convenient to refer to Fig. 39.

The ectoderm reflected into the larger of the two primary chambers is pushed down by the growth of the second pair of mesenteries. From it are formed the filaments for these mesenteries, while the remainder of the original tract splits into three divisions. The middle division, chamber *c*, is not pushed entirely to the edge of the œsophagus; later in life, when the fourth pair of mesenteries is well developed, this tract grows once more nearly to the upper limit of the œsophagus. The lateral divisions *a* and *b* are pushed to the edge, but after the sixth pair of mesenteries has appeared they begin to grow up again. When the mesenteries of the third pair are well advanced, the ectoderm is reflected into the smaller of the two primary chambers, and runs up the œsophageal wall nearly to the top of the chamber. The mesenteries, when they begin to grow down, carry a part of the ectoderm along their free edges as very slender filaments. The growth of the various tracts of reflected ectoderm is thus seen to follow in general the order of development of the mesenteries.

VII. ORIGIN OF THE FILAMENTS IN THE ADULT.

After studying the larval development it seems very sure that the filaments of the first twelve mesenteries are ectodermal. Further, I think the stage with twelve mesenteries holds the key to the condition in the adult. In this stage, Fig. 39, etc., there are complete (first and second pairs) and incomplete mesenteries (third pair), both provided with ectodermal filaments. Both kinds of mesenteries are exactly comparable with the two kinds in the adult, and if the incomplete mesenteries of the larva are successively supplied with filaments by the reflection and upward growth of the ectoderm, it seems probable that the incomplete mesenteries of the adult are supplied in the same manner.

The gap between my series of larval stages and the adult is partially bridged over by the transverse sections, Figs. 41 and 42. The young *Manicina* from which these sections were made was one-eighth inch diameter. I found a couple of about the same size on a piece of coral rock. In hardening these two specimens I was not fortunate, and they were consequently of no value for the study of such fine points as the reflection of ectoderm. Fig. 41 is through the œsophagus, and disregarding the skeleton, shows six pairs of complete and six pairs of incomplete mesenteries. The twelve complete mesenteries represent the mesenteries present in the larva, now rearranged in pairs and with simple muscle plates (only shown in the directive mesenteries). The incomplete mesenteries have appeared according to the general law governing the mesenteries above twelve.

Manicina remains a single polyp until it has reached a diameter of about one-third of an inch. In this condition it has all the characters of the adult, except those dependent on asexual multiplication. It is, moreover, not sexually mature. Such a coral has, disregarding local irregularities, twelve pairs of mesenteries of the first order (complete), twelve of the second order (incomplete), and twenty-four pairs of the third order (much more incomplete). Fig. 50 gives a median longitudinal section of the coral at this age. The polyp was in a state of complete contraction, the oral surface or peristome, *Pr*, pulled down, the mouth, *Mo*, widely open, and the tentacles, *T*, retracted. The section on the right is through a mesentery of the first order, on the left through one of the second order. The line 3 marks the position of the free edges of the tertiary mesenteries. The latter are not provided with filaments. On each side of the section, the mesentery is divided into a central and peripheral part (*R.P.*) by the calcareous theca, *Th.* (When the animal is expanded, the peristome is lifted high above the level of the skeleton. It then embraces the whole width of the animal, the tentacles forming a dense ring round its edge, while the mouth is narrowed to a slit-like opening.)

On the right side of Fig. 50 the epithelium of the œsophagus, Œ, is directly continuous with the filament 1, the mesentery being complete. On the left side the mesentery being incomplete, the œsophagus has a free edge. Now if my view is correct, not only the lining epithelium of the œsophagus is ectodermal, but the epithelium *x*, which forms the gastric covering of the œsophagus and peristome between the complete mesenteries, is likewise ectodermal: the ectoderm here, as in the larva, is reflected round the lip of the œsophagus, and extends upwards until it reaches the secondary mesentery, down which it courses as the filaments. Fig. 55 is a more highly magnified view of the lower part of the œsophagus, as shown in the left half of Fig. 50. The lining epithelium of this part of the œsophagus, the lower third, is composed of slender supporting cells. The upper two thirds contain large nettle cells, and in the region of the mouth mucus cells. The epithelium on the outer surface of the œsophagus, is for some distance (compare Fig. 55 with Fig. 50) exactly like the lining epithelium, except that it contains a few yellow cells. Then comes a region of vacuolated cells, which is followed by a very low epithelium made up of exceedingly small cells, the exact shape of which I could not determine. The low epithelium is continued up the œsophagus and over the peristome, and is continuous with the filaments on the secondary mesenteries. These filaments, though of large size at a lower level, gradually become very small as they approach their upper limit, and by this means run without any break into the low epithelium covering the peristome. The filaments on the third pair of mesenteries in the larva were likewise very small in the upper part of their course, though, to be sure, in my oldest larval stage they as yet only existed in this part.

The view that the gastric lining of the œsophagus and peristome is ectoderm can only be held by supposing the epithelium in question to have suffered a great histological change. (It is possible that a very careful histological examination of the epithelium, x, would show that it does not differ so much from the ectoderm as appears to be the case.) But though this tract of epithelium cannot be said to resemble the ectoderm, it differs quite as much from the undoubted endoderm. The endoderm of the adult, Figs. 51 and 52, is made up of large irregularly columnar cells, packed with "yellow cells," the vacuoles present in the larval endoderm being confined to special localities. The only apparent alternative to the view offered is that while the first twelve mesenteries are provided with ectodermal filaments, the filaments of all subsequent mesenteries are endoderm. Since the several orders of filaments in the adult differ only as regards size, and since even this difference is a transient one, owing to the constant transformation of incomplete into complete mesenteries during the growth of the coral, it seems improbable that such precisely similar organs should be formed by both layers.

On the other hand, E. B. Wilson (8) came to the conclusion that the dorsal pair of filaments in the Alcyonaria were ectodermal lobes, but that the remaining six filaments were purely endodermal. The two kinds of filaments in these polyps have, however, a very different histological structure, with which is associated a division of labor.

Von Heider (11) several years ago decided that the filaments of *Cerianthus* were ectodermal. He reached his decision by a histological study of the adult, and though this method is inconclusive, I am not surprised after studying myself some immature specimens of *Cerianthus*, that he came to this view. The Hertwigs in their classical work on the actiniæ pointed out that embryological deductions based on adult histology are not very reliable, and also brought forward as an objection to von Heider's view, the existence of filaments in the actiniæ generally on incomplete mesenteries.

VIII. HISTOLOGICAL STRUCTURE OF THE FILAMENTS.

The very young mesenteric filament is shown in cross-section in Fig. 17. In this larva, the first pair extend about half the length of the body. In Fig. 29, though the mesentery is elevated above the general endoderm, the filament retains its simple character. It is roughly hemispherical in section, and is separated from the mesentery by a thin sheet of supporting membrane. Besides supporting cells, there are present granular gland cells. In most larvæ in which the first pair of filaments reach the aboral end of the body, the filament is no longer separated from the mesentery by supporting lamella. Fig. 19 gives a surface view of such a larva, and Fig. 26, a cross-section of one of the long filaments. In the latter figure the sheet of supporting lamella, on which the filament formerly rested, has given place to an accumulation of jelly at the apex of the mesentery. Though the cells of the filament are practically continuous round this gelatinous axis with the cells of the mesentery, the line of demarcation is very evident on each side owing to the different histological characters of the endoderm and ectoderm cells. In the filament there are now numbers of large nettle cells, and the gland cells are far more numerous than in earlier stages. Nervous elements are very probably present, as there is a granular stratum in the deepest part of the filament. As is shown in Fig. 19, the filament increases in size towards its lower end. Near the close of the swimming life the first pair of filaments begin to get slightly curved and twisted in the lower part of their course. The young filament before its cells become continuous with those of the mesentery, is very loosely attached to the latter; in a number of cases I observed that the mesentery and filament had entirely separated from each other (Fig. 29, Mes. 3), owing, no doubt, to the contraction caused by the killing fluid.

Fig. 35 is through one of the first pair of filaments, and its mesentery, of an attached larva with eight mesenteries. In the attached larva these filaments pursue a straight course for a short distance below the œsophagus. In the lower part of their extent, they are curved and twisted as in the adult, and in this region sections like Fig. 34 are obtained. Fig. 35 is through the straight portion of the filament. On comparing this figure with Fig. 26 (magnified to the same degree) it is seen that the mesentery has become more elevated, and at the same time thinner; also, that where the endoderm cells end and the filament cells begin there has been a pinching in, which, added to the actual bulging out of the filament, has very distinctly worked off the latter from the mesentery. The bulging out of the filament is due to the lateral expansion of the axial jelly shown in Fig. 26. The expansion of the jelly has so taken place that the filament, Fig. 35, is divided into three portions: the main body to which are confined the nettle and gland cells; and two tracts, *v.l.*, which may be called the ventro-lateral tracts. The latter are composed exclusively of slender supporting cells. As in the swimming larva, the filament cells are sharply marked off from the cells of the mesentery. In spite of the twisted condition of the lower part of the filament, sections show that the structure is the same as in the upper part.

In the adult the upper portion of the filament on a complete mesentery is comparatively straight, but the main portion is twisted, Fig. 50. The filaments of the incomplete, are less twisted than those of the complete mesenteries. The filaments are attached their whole length to the mesenteries, there being no free acontium; they are, however, capable of extrusion both through the mouth and (though I could not find the apertures) through pores (cynclides) in the body wall.

Unlike the larval filament, that of the adult has a different structure at different levels. Figs. 52, 53, and 54 are sections through the different parts of a filament on a complete mesentery. Fig. 52 is through the upper third. The filament itself has almost exactly the shape shown in Fig. 35, but the mesentery is swollen out and forms two lateral lobes, *m.l.*, between which the filament rests. The ventro-lateral tracts are much better marked in the adult than in the larval filament. This is due to the continuation of the pinching in process which had already gone some distance in Fig. 35, and to the outgrowth of the mesenteric lobes, *m.l.* By these means the slender "waist" is produced, which indicates the separation of filament and mesentery.

The ventro-lateral tracts of the filament, both in the upper portion of its course, Fig. 52, and lower down, Figs. 53 and 54, are made up exclusively of supporting cells. The main body of the filament in Fig. 52 contains a large number of granular gland cells and numerous nettle cells. The mesenteric lobes are composed of cells which do not differ essentially from the rest of the endoderm; they are only much elongated and contain a number of very large vacuoles. The passage of the filament into the œsophageal epithelium is effected in the following manner. Immediately below the œsophagus, the "waist" in Fig. 52 becomes gradually wider until the ventro-lateral tracts no longer exist, and the filament cells are continuous with the mesentery cells round the horns, *h*, of the supporting lamella of the filament. At this level, the filament or œsophageal lobe is much flatter and wider than it is below (Fig. 52), and the supporting lamella of the filament is also nearly flat. The latter passes directly into the supporting lamella of the œsophagus, and the filament into the lining epithelium of the œsophagus.

Fig. 53 is through the middle third of the filament. The gland cells are absent in this region, but the nettle cells are very large and exceedingly abundant. The mesenterial lobes are not so well developed as in the region above.

The lower third of the filament, Fig. 54, contains neither nettle cells nor the typical gland cells. The body of the filament is here made up of very large granular cells, between which are scattered a few supporting cells. The granules are much more numerous in the peripheral than in the central halves of the large cells, and at the sides of the filament where the main body passes into the ventro-lateral tracts, they become gradually restricted to the peripheral ends of the cells. The granules are chemically different from those in the ordinary granular gland cell: they do not stain especially well with hæmatoxylin, but become dark brown with osmic acid. In a number of filaments these peculiar granular cells contained large, irregular concretions, which stained dark red with borax carmine, while the cell body stained but faintly. The mesenteric lobes in this region are slightly less pronounced than in the rest of the filament. In a transverse section through the filament of *Sagartia*, Von Heider (10) has figured the lateral parts of the simple filament (according to the Hertwigs, the section is through the acontium) as composed of just such large granular cells as I have described. The Hertwigs do not speak of these tracts.

From Fowler's brief description (15, II.) it would seem that the filaments of *Madrepora* are essentially like those of *Manicina.* The condition of the specimens, however, as the author states, did not permit a detailed study.

The filaments on the secondary are somewhat smaller than those on the primary mesenteries. The mesenteric lobes, too, are less pronounced, not reaching a development greater than is shown in Fig. 54. It has been mentioned that in the upper part of their course the secondary filaments become very small. Though the diminution in size is so great in this region, that it was impossible for me to make out the histological structure, I was able to trace the filament as a darkly staining and compact mass of tissue into the epithelium of the peristome. The filaments of the young coral, from which Figs. 41 and 42 were made, were like those of the adult, except that the mesenterial lobes were less developed.

I did not study the living filaments, but from the histology it is evident that the function of the ventro-lateral tracts is that of ciliated bands, while the digestive functions and nettle cells are distributed over the three portions of the main body of the filament. The mesenteric lobes I regard merely as a device to support the filament.

Before comparing the mesenteric filaments of *Manicina* with the actinian filament as described by the Hertwigs, I will give a brief account of the filaments of *Cerianthus,* this being the only actinia I have been able to study by way of comparison. In Nassau harbor the larval or free-swimming Cerianthus was common. All the individuals I obtained were at about the same stage of development. They were oval light brown bodies about one-fourth inch long, and had eight or nine very short, stubby tentacles. On sectioning the larvæ, I found they confirmed the theory advanced by the Hertwigs (*l.c.*) as to the mode of origin of the mesenteries. Fig. 49 is a section through the upper part of the œsophagus. The number of complete mesenteries is fifteen. At one end of the œsophagus is the ventral or directive pair of mesenteries, *D.M.* At the other or dorsal end are two incomplete mesenteries, 1 and 2, of which the former is the younger. The mesentery 3 becomes incomplete not far above the œsophageal lip, and 4 follows its example just above the lip. From these four mesenteries it may be gathered that each new mesentery appears along the dorsal meridian between the two last formed, and in such a way that the successive mesenteries come to lie on opposite sides of the dorso-ventral plane. The directive pair, *D.M.*, corresponds to the directive pair which the Hertwigs have figured (Taf. I., Fig. 8). These authors state, however, that this pair is the longest of all, extending to the anal pore. In the young specimens I have studied, this pair disappears some distance above the pore, and is exceeded in length by two or three mesenteries on each side of the dorso-ventral plane. Von Heider (11) made the discovery, which the Hertwigs confirmed, that in the adult there is a much shorter pair enclosed between the two directive mesenteries. This short pair only extends the length of the œsophagus. It must appear in stages later than Fig. 49, so that besides the formation of mesenteries which takes place dorsally, at least one pair is formed ventrally.

Filaments were found only on the complete mesenteries. Fig. 47 is from a section just below the œsophagus. The mesentery is composed of very large cells with immense vacuoles.

At the edge of the mesentery, just beneath the filament, the tissue is becoming more compact. This process has gone much farther in Fig. 48 (from the same mesentery at a lower level). The whole mesentery, as may be seen by comparing my figures with Hertwigs' Taf. VIII., gradually suffers this change as the animal becomes adult. In Fig. 47 the filament has a central body provided with gland and nettle cells, and two lateral ciliated tracts *m*, composed of supporting cells, which are gradually assuming the shape of distinct lobes owing to the subjacent growth of the jelly. The central body passes directly into the epithelium of the œsophagus, the lateral tracts becoming indistinguishable from the body of the filament just before the transition. This figure is but slightly different from the section of the adult filament given by the Hertwigs. At a lower level, Fig. 48, the ciliated tracts are no longer found. On many mesenteries the filament has almost no connection with the endoderm, as in the figure. In such figures as Fig. 48, it need hardly be said that violent contraction has had much to do with producing such complete separation of filament and mesentery; but this only shows how loose the connection is in early life. On other mesenteries the filament is continuous at its sides with the cells of the mesentery. None of the filaments in these young specimens of *Cerianthus* ran the whole length of the mesentery. Most of them stopped at about the equator of the body.

In the actinias, studied by the Hertwigs, the mesenterial filament in the upper part of its course is in section tri-lobed. There is a median secretory tract and two lateral ciliated tracts. The mesoderm extends into each lobe. On all the mesenteries the ciliated tracts are lost in the lower portion of the filament. On the incomplete mesenteries the median tract disappears towards the upper limit of the mesentery, the lateral ciliated bands remaining. On the complete mesenteries the median tract merely gets smaller towards the œsophageal end, but does not disappear.

The description I have given of the filaments of *Cerianthus* is, barring slight differences due to age, like the account the Hertwigs give for this actinia. From this description it is seen that the filament of *Cerianthus* corresponds in the main to a typical Hertwig filament, such as is on a complete mesentery. But the lateral lobes, *m*, Fig. 47, are very small even in the adult when compared with the lateral wings of the *Sagartia* filament (H., Taf. V., Fig. 10).

The filament of *Manicina* is a much simpler structure. It is not trifid, though the mesenteric lobes, *m.l.*, Fig. 52, give such an appearance to the edge of the mesentery. But on referring to Hertwig's figure of *Sagartia* (Taf. V., Fig. 10), it is evident that the mesenterial lobes of *Manicina* do not represent the ciliated bands of *Sagartia.* They are totally different histologically, and do not contain prolongations of the mesoderm. On the other hand, the ventro-lateral tracts of *Manicina* do correspond histologically with the ciliated bands in the Hertwig filament, and the glandular lobe of the latter is in general similar to the median stripe of the *Manicina* filament. As I take it, all three tracts of the Hertwig filament, taken together, are homologous with the simple filament of *Manicina.* They must all, therefore, be ectodermal: in the young *Cerianthus,* Fig. 47, the lateral lobes evidently belong to the median lobe, and are not modified parts of the mesentery; and since the median lobe at a lower level, Fig. 48, shows its independence of the mesentery, the conclusion seems to be that the whole filament is ectodermal. Though the filament of the adult coral is a much simpler form than the trifid filament, it would be difficult to derive the latter from the former, owing to the presence of mesenteric lobes in the coral. It is easy, however, to derive the trifid from the larval filament, Fig. 35. In this form the ciliated tracts, *v.l.*, and the median secretory tract, are already differentiated; to produce the trifid filament it is only necessary for these tracts to become separated by the division of the mesoderm into three lobes. By this division, while the median stripe gains but little, the ventro-lateral tracts are put in a position where it is possible for them to reach a high development.

The number of Actinozoa in which the mesenterial filaments have been carefully studied is very limited, but from the data at hand it seems probable that the ancestral filament, like the filament of the larval *Manicina*, was a simple undivided body, in which, however, the originally uniform ectoderm had become split up into three physiologically distinct tracts: a median tract, in which were concentrated the nettle and glandular elements, and which embraced most of the filament; and two lateral ciliated portions which were but slightly developed. The belief that the division of labor in the Zoanthorian filament dates very far back, is supported by the existence of a similar division of labor in the Alcyonaria. But in these polyps, as Wilson (8) has shown, the functions are not distributed over different parts of the same filament, but amongst the several filaments. The dorsal pair are ciliated bands, having no gland or nettle cells, while the remaining six filaments contain gland and nettle cells, but have no ciliated tracts.

IX. THE SKELETON.

Until the time of Von Koch's researches the skeleton of the Madreporaria was regarded as calcified mesoderm. The theca, or coral wall, according to this view, represented the supporting lamella of the lateral body wall of an actinia; and where, as in most corals, the theca was largely uncovered by animal substance, the explanation was that the ectoderm had atrophied. In 1879 Von Koch (12) showed that the theca is independent of the lateral body-wall, and projects into the cœlenteron of the polyp in such a way as to divide the cavity and mesenteries into central and peripheral parts. This conclusion, though not universally accepted, is, I think, now incontestable. Von Heider in 1882 (14) published the important observation that the skeleton is not only covered by supporting lamella and endoderm, but that between the calcareous matter and the supporting lamella is another layer of cells, to which was given the name of calycoblasts. Von Koch in 1883 (13) made the whole matter clear by showing that in the young *Asteroïdes* the skeleton is secreted by the ectoderm and is at first entirely outside the body. The ectoderm of the basal surface of the attached larva secretes a calcareous basal plate. Radial folds of the basal ectoderm then grow up between the mesenteries into the cavity of the polyp, lifting up, as they grow, the supporting lamella and endoderm. The cavity of the fold is filled with calcareous matter, which is the septum. The secreting ectoderm becomes the calycoblast layer of Von Heider. The origin of the basal plate and septa is thus clear enough, but Von Koch's account of the development of the theca is not satisfactory. As far as his observations went they appear to have confirmed his belief, gathered from a study of adult corals, that the theca is formed secondarily from the septa; the originally simple septa become bifurcate at their peripheral ends; the lateral processes of adjacent septa grow towards each other, pierce the mesentery, and, fusing, form the theca. Von Koch's account of the relation of the skeleton to the soft parts in the adult has recently been confirmed on a number of genera by Fowler (15) and Bourne (16), though as regards the extra-thecal part of the cœlenteron Fowler differs from Von Koch in the interpretation of his sections. From these papers it is also evident that the *Madreporaria* exhibit great variety in the details of the relation between the soft parts and skeleton. My own very incomplete observations on the skeleton of *Manicina* are for the most part a confirmation of Von Koch's statements.

In the newly attached larva, Fig. 37, the ectoderm of the basal surface is made up exclusively of supporting cells. The granular cells present at the aboral end of the swimming larva have all disappeared. Some time after attachment a small patch of calcareous matter is found on the basal surface, and sections through such larvæ, after the lime has been removed by acid, give figures like Fig. 38, though in many individuals the ectoderm was torn in freeing the larva from the bottom of the dish. In Fig. 38 the cells of the basal ectoderm radiate toward a common centre. There seems to be an effort on the part of the more peripheral cells to share in the secretion of the central patch of homogeneous substance shown in the figure. This homogeneous substance is the animal basis of the nascent basal plate. It exhibits no structure, but stains deeply with hæmatoxylin, and in its general appearance impresses one as a very much thickened cuticle. I was not able to trace the development of the skeleton any further.

The fully formed skeleton may very conveniently be studied in young polyps, which have not begun to multiply asexually. Ground sections of the skeleton are of some use, but with a little care the polyps may be decalcified so that the skeletal layer of tissue retains with great exactness the shape of the skeleton. Figs. 46, 50, and 56 are from young *Manicinas* about one-third inch in diameter. Fig. 46 is part of a transverse section through the line *a* in Fig. 50 (*oe. ec.* is the ectoderm of the peristome; *ec.* that of the lateral body wall). Were the section complete, it would show twelve primary, twelve secondary, and twenty-four tertiary pairs of mesenteries. At this level the secondary mesenteries are complete; a little lower down they are incomplete.

In going down through a series of sections, the tertiaries run out before the lip of the œsophagus is reached. In Fig. 50 the line 3 marks the free edge of a tertiary mesentery. The theca, *Th.*, divides the mesenteries and cœlenteron into peripheral and central portions. The septa, *S.*, are all entocœlic; *i.e.*, lie between the two mesenteries of one pair, and not between two adjacent pairs. The size of the septa varies with the rank of the mesenteries between which they lie. On the outer surface of the theca are the longitudinal ridges, *C.*, or costæ, which appear to be merely the peripheral prolongations of the septa. The edges of the septa are finely and regularly toothed. This is shown in the radial section, Fig. 56, which is taken through one of the coral septa. In Figs. 50 and 56 the relations of the columella, *Col.*, to the theca and septa are shown. In the former figure, through a mesentery on each side and consequently between two septa, a deep depression separates the columella from the theca. The primary mesenteries extend to the floor of the depression; the secondaries end some distance above it. The columella is circular in section, and the depression surrounds it as a trench. But the trench is not continuous, being completely divided in the radius of each primary septum, as is gathered from Fig. 56, which is taken through such a septum. In this figure the septum and columella are directly continuous with each other. The columella in reality is not solid, as it is drawn in the figure, but is spongy, being full of portions of the body cavity which it has cut off during its growth. Whether an originally simple and solid columella is formed as a central elevation of the basal plate, is an open question. But the subsequent growth of the columella takes place by the constant incorporation in it of the lower portions of the inner edges of the primary septa. The teeth on the edge of the septa, and the granulations found on their sides, sufficiently explain the spongy nature of the columella.

The skeleton inside the polyp is everywhere covered by the three layers of the body wall, of which the skeletogenous ectoderm or calycoblast layer is next the skeleton. In Fig. 46 and the radial sections these layers are not represented, but they are shown in Fig. 51, a more highly magnified portion of one of the peripheral entocœlic chambers of Fig. 46. The superficial ectoderm is marked *ec.*; the peripheral parts of the mesenteries *mes.* The calycoblast layer covering the costa, or, more exactly, the costal tooth, is as elsewhere a layer of flattened cells. The skeletal endoderm is likewise very flat, and markedly different from the endoderm of the body wall and mesenteries. In radial sections the calycoblast layer is found to be continuous with the superficial ectoderm round the edge of the extra-thecal part of the polyp, or *randplatte*, *R.P.* in Fig. 50.

That portion of the polyp, *R.P.*, that lies outside the theca, has been called by Von Heider the *randplatte*. It has been claimed (Moseley, 18; Fowler, 15) that this part of the polyp ought not to be regarded as normally on the outer surface of the skeleton; but that when the expanded polyp, which extends high above the skeleton, contracts, while most of the body is drawn into the interior of the theca, a portion is pulled down over the outer surface of the skeleton. However plausible this belief may be in the case of those adults in which the extra-thecal part of the polyp is confined to the upper edge of the theca, it is at once found to be untenable on examining a small number of young *Manicinae* of the size of Fig. 50. In the polyp, for instance, from which this section was made, the randplatte covered more than one-half of the lateral surface of the skeleton, and this was true both in the expanded and contracted condition of the animal. Further, in every dozen such young *Manicinas*, one or two asymmetrical ones will be found, in which, while the randplatte is confined to the upper half of the lateral surface on one side of the polyp, on the other side it covers the whole wall down to the surface of attachment. What puts the matter beyond dispute, in this genus at least, is that in the very young *Manicina*, Figs. 41 and 42, the whole skeleton is practically inside the polyp. I also found two or three older specimens (single polyps) in which the entire lateral surface of the skeleton was covered by the randplatte. One of these which I sectioned, was oval in transverse section, long axis about $\frac{2}{5}$ in.; short axis $\frac{1}{4}$ in. The skeleton had a flat surface of attachment, and was $\frac{1}{3}$ in. in height. The randplatte (on rather extra-thecal polyp) in this individual was unbroken, down to the piece of rock to which the coral was fastened; here its ectoderm turned in to form the calycoblast layer.

It appears, then, that up to a certain age, which varies much in individuals, the lateral surface of the skeleton is entirely covered by the polyp. The transformation of the originally large extra-thecal part of the polyp into the relatively small rand platte may possibly take place in many cases gradually, by the constant dying off of this part of the polyp at its free edge, and subsequent disappearance of the dead tissue. But in some instances this is not the case. I found a number of small single polyps in which I first thought the randplatte covered the entire lateral wall of the skeleton, but on looking again, I saw that a very definite line extended all round the lateral surface at about the level of the edge of the randplatte in Fig. 50. Above this line the soft parts looked perfectly healthy, but below it dull and sickly. On sectioning I found that above the line the randplatte was normal, but that the tissue below it was a membrane with scarcely a trace of cellular structure and made up for the most part of plant filaments. In some asymmetrical specimens the portion of the skeleton left uncovered by the randplatte was covered by a precisely similar membrane, which was marked off from the randplatte by a deep furrow. In all such specimens the ectoderm of the randplatte was continuous at the edge of the latter with the calycoblast layer. These peculiar membranes gave every indication of having been originally continuations of the randplatte; and I conclude that in the individuals possessing them, the extra-thecal part of the polyp had remained intact up to a certain time, but that then the whole lower portion of this part of the animal was cut off from the general gastric cavity. Deprived of its nutriment, this portion became membranous, and was infested by plant filaments. As the coral increases in size, the membranes are shed, leaving a large part of the theca bare. After the randplatte once becomes restricted to the upper part of the skeleton, there is no more shedding of large pieces of tissue. But as the skeleton is constantly growing in height, we have to suppose that the randplatte as constantly dies at its free edge, unless, indeed, we assume that the connection between the calycoblast layer and the skeleton is so slight that the randplatte is merely carried up with the growing skeleton.

In the young *Manicina*, Figs. 41, 42 ($\frac{1}{8}$ in. diam.), the skeleton is very immature, though the various parts of the adult skeleton can all be recognized. In this specimen there was a thin, flat, basal plate, uncovered at its periphery by the body wall. The skeleton above the plate was internal except at the points *a* and a′, where the lower edge of the extra-thecal part of the polyp was notched, so that at these points the skeleton was bare for a short distance above the basal plate. Fig. 41 is through the œsophagus, Fig. 42 is below, and strikes the apex of the columella. Though some of the septa are still independent at as low a level as Fig. 42, at a still lower level they all unite to form a theca, which on the right side of the directive mesenteries is very slightly developed, but on the left side is prominent. Two or three of the septa in the region where the theca is so slightly developed, exhibit the bifurcation of their peripheral ends which Lacaze Duthiers and Von Koch have described. In Fig. 42 indications of six primary septa are more or less evident, and in lower sections where the septa fuse with the columella they are easily distinguished. There are also six secondary septa to be made out in Fig. 42. These twelve septa, which are entocœlic, extend as high and higher than Fig. 41. Further, in Fig. 42 it is evident that twelve tertiary septa have started to develop, though only a few of them extend an appreciable distance above the theca. As only twelve pairs of mesenteries have been formed, the tertiary septa are temporarily exocœlic. Transverse and longitudinal sections through such a polyp as this show very clearly that the growth of the theca is continuous and from below upwards. Nowhere are two septa found which actually pierce a mesentery to form the theca, but everywhere the growing theca pushes the tissues of the mesenteries upwards. Where the theca is formed in such a manner as this, it is out of the question to believe, after Von Koch, that the radial cracks found in ground sections of the theca are due to the existence in these radii of the atrophied remains of the lower portions of the mesenteries.

The costæ in Figs. 41 and 42 are very feebly and irregularly developed. Each septum has, however, three or four teeth along its outer edge, and also a few on its inner edge. All the teeth on the outer edge of the septa open directly to the exterior over the side wall of the coral. In Fig. 41 the septum included between the near pair of directive mesenteries is cut just below the point at which it thus opens. Fig. 40 gives a more highly magnified view of the same septum cut at the level of its opening. In Fig. 42 a tooth has opened at *m*, and another at *n* is sectioned just beyond its opening. The apertures are of good size, and through them the external ectoderm is continuous with the calycoblast layer. This peculiarity of the teeth is no longer found in *Manicina* after asexual multiplication has begun, and only a few teeth open to the exterior in single polyps with the full complement of septa. In one such polyp, however, all the teeth opened in this way. From this it would seem that the connection of the calycoblast layer with the surface ectoderm at these points is a characteristic of youth which is gradually lost. It is possible that this peculiarity may have been acquired in order to bind the little polyp and its simple skeleton firmly together.

X. ORIGIN OF THE ANTHOZOA.

As is well known, the reigning view as to the origin of the Anthozoa is that advanced by Claus and Haeckel, according to which the Anthozoa are descended from hydropolyps with gastric ridges. This hypothesis, which considers the distinguishing feature of the Anthozoa (and Scyphomedusæ) to be the possession of tænioles, or endodermal ridges (mesenteric ridges), has recently been attacked by Professor Götte in a very interesting paper (17) on the development of the Scyphomedusæ (Aurelia). The author conclusively proves the Anthozoan nature of the Scyphostoma larva, showing it to possess four complete mesenteries and an ectodermal œsophagus. Unfortunately, no observations were made on the origin of the mesenterial filaments, which in all probability are ectodermal lobes. Regarding, then, the Scyphomedusæ as an offshoot from the older Anthozoan stem, Götte argues that the manner in which the mesenteries and intermesenterial chambers are formed in the larva of the former, is directly opposed to the old view of the hydroid origin of the Anthozoa. The mesenteries and chambers are formed in the following manner: the planula is bilateral, and the permanent layers are formed before the invagination of the œsophagus takes place. The latter is invaginated in such a shape that in the shorter transverse axis of the larva the endoderm is pushed down, while in the other transverse axis two endoderm sacs are formed. The woodcut, Fig. 1, is a transverse section of this stage, through the œsophagus, and Fig. 2 is a longitudinal section through the shorter transverse axis. In a subsequent stage,

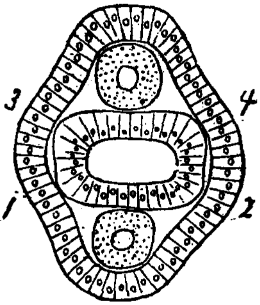

Fig. 1

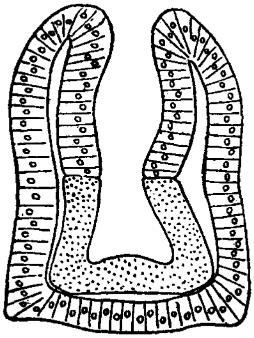

Fig. 2

Ectoderm represented as made of columnar cells. Endoderm is dotted. Supporting lamella left untouched. After Götte, Pl. II., Figs. 20 and 24.

two endoderm sacs grow up from the cœlenteron in the shorter axis, and the œsophagus is then surrounded by four sacs. The sacs are the intermesenteric chambers, and their partition walls form the mesenteries. Götte concludes that in this development there is no stage which corresponds to the hypothetical hydropolyp ancestor. The young Scyphostoma itself, which has hitherto been regarded as a hydropolyp with tænioles, is in reality an Anthozoan with four complete mesenteries; and the development previous to the Scyphostoma does not pass through a hydroid stage, but, on the contrary, jumps directly from a hollow planula to the larva provided with two (later four) endodermal sacs. This larva is called the Scyphula, and from *Kowalevsky's* account of the development of *Cerianthus* (4), Götte believes it to be common to both the Scyphomedusæ and Anthozoa, and consequently an ancestral form. In *Cerianthus* according to the abstract given by Hoffman and Schwalbe of Kowalevsky's paper, the œsophageal invagination does push down the endoderm along two opposite meridians; but though the abstract is not definite on this point, the implication is that the meridians are those of future mesenteries. If this is so, *Cerianthus* agrees essentially with *Manicina*, and not with *Aurelia.*

The ancestral Scyphula form was derived, according to Götte, directly from the hollow planula, the invagination of the œsophagus *necessitating* the simultaneous formation of endoderm sacs. The infra-œsophageal mesenteric ridges, from this point of view, are not of any phylogenetic importance, and have nothing to do with the endoderm ridges of Tubularian or Siphonophore polyps; they have come into existence merely as the after-result of the formation of endodermal sacs. This theory contains in itself an obvious difficulty: the sudden and direct transformation of such a simple form as the planula into such a complex form as the Scyphula. What could have caused this complex group of changes, Götte does not suggest. But aside from this objection it seems clear that the development of *Aurelia* is a highly modified form of the development of *Manicina,* and the manner in which this peculiarly symmetrical modification was brought about is suggested by the variations shown in Figs. 30–33.

If Fig. 30 is compared with the woodcut Fig. 1, it is seen that as far as the left halves of the sections are concerned, they are identical in all essential respects. In each the œsophagus is opposed to the surface ectoderm along the meridians of two adjacent mesenteries (*a* and *b*, 1 and 3), and also over the intervening tract. In a later stage an endoderm lobe grows up between *a* and *b* in Fig. 30, and between 1 and 3 in the woodcut, and in each this lobe becomes an intermesenteric chamber. If, now, in the larva, Figs. 30–33, the right side had followed the example of the left, that is, if the second and fourth mesenteries had been formed in the same manner as the first and third (*a* and *b*), there would have resulted an exact counterpart of the condition in the *Aurelia* larva.

The four mesenteries of Scyphostoma would thus seem to correspond to the first and second pairs of mesenteries in *Manicina*. We may suppose that in the primitive Scyphostoma the mesenteries were usually formed in the gradual way which is normal in *Manicina*, but that the Scyphostoma had inherited from the parent stock (probably Anthozoa with a large number of mesenteries) a tendency towards the variation illustrated in Figs. 30–33, and that this variation gained ground and finally became the normal process. There is, of course, an alternative to this hypothesis, namely, to regard the variation found in *Manicina* as a case of partial reversion to the ancestral condition as presented by *Aurelia*. But the derivation of the Anthozoa from such an ancestor as the young Scyphostoma (or Scyphula with four endoderm lobes) is beset with the greatest difficulties; for instance, the formation of the first before the second mesentery, and the very general occurrence of a primary tentacle in actinia larvæ and in the Scyphostoma itself. Moreover, the Scyphula larva has not been found in any Anthozoa, unless, indeed, the case of *Cerianthus* be really, as Professor Götte seems to have considered it, similar to *Aurelia*.

Having shown that it is possible to derive the so-called Scyphula larva from the larva of *Manicina*, and that it is consequently in all probability an instance of secondarily acquired symmetry, I consider Götte's objection, based on the existence of this larva, to the hydropolyp ancestry of the Anthozoa, as no longer valid. The question whether or not the Anthozoa are descended from hydropolyps must be argued out on the ground of some more primitive Anthozoan development, such as that of *Manicina.* And here it is at once seen that, contrary to Götte's idea, the invagination of the œsophagus does not necessitate the formation of endodermal sacs. In Figs. 5 and 7 the œsophagus is already formed, but is still surrounded on all sides by endoderm. The apposition of the œsophagus to the surface ectoderm along the lines of the first and second mesenteries takes place later; and though, since this process occurs in the Scyphomedusæ as well as the Zoantharia, it must date very far back. I am inclined to believe it was secondarily acquired and was not a peculiarity of the primitive Anthozoa. This belief is supported by the entire absence of the process in the Alcyonaria (Wilson, 3). The explanation of the process is possibly connected with the early development of the first pair of filaments.

BALTIMORE, March 25, 1888.

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DESCRIPTION OF THE FIGURES.

In the larvæ, the supporting membrane is represented as a heavy black line; the jelly, where present, as light brown. In the adult, and in the complete section of *Cerianthus*, the supporting substance is uncolored. All the sections were drawn with the camera. Zeiss lenses are referred to, and the figures are reduced to one-half the size of the original drawings.

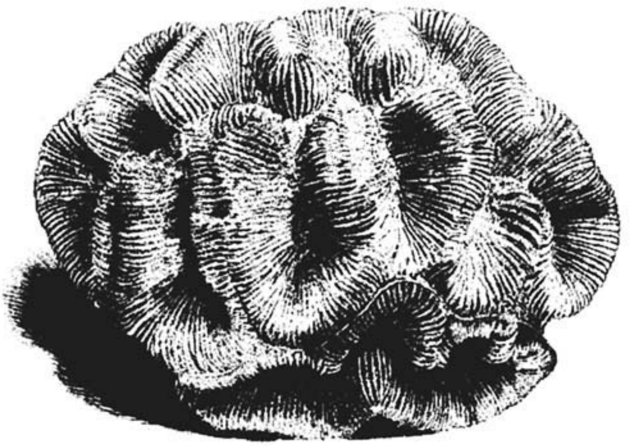
The following letters have been used uniformly in the figures: —

c.b.	Calycoblast Layer.
C.	Costa.
Col.	Columella.
D.M.	Directive Mesenteries.
ec.	Ectoderm.
en.	Endoderm.
Mo.	Mouth.
Mes.	Mesentery.
m.l.	Mesenterial Lobes.
Oe.	Œsophagus.
Pr.	Peristome.
R.P.	Randplatte or Extra-thecal Part of Polyp.
S.	Septum.
T.	Tentacle.
Th.	Theca.
v.l.	Ventro-lateral Ciliated Tracts.

DESCRIPTION OF PLATE I.

FIG. A. Corallum of a Manicina colony, viewed from above. Natural size.

FIG. B. Side view of same, to show the pedicel. The randplatte extends but a short distance below the rim of the theca; its lower limit is marked by a slight accumulation of irregular laminæ.



A. Hoen & Co. Lithocaustic, Baltimore.

DESCRIPTION OF PLATE II.

FIG. 1. Section through a blastosphere. C, 4.

FIG. 2. Section through delaminating blastosphere. C, 4.

FIG. 3. Part of another blastosphere such as Fig. 2. D, 4.

FIG. 4. Median long. sec. through a solid planula with commencing œsophagus. C, 4.

FIG. 5. Long. sec. through a larva in which the permanent layers are forming. C, 4.

FIG. 6. Long. sec. of slightly older stage. Position of œsophagus is eccentric. C, 4.

FIG. 7. Trans. sec., through œsophagus, of larva at about the stage of Fig. 5. The formation of the permanent layers is not so far advanced as in the latter figure. D, 4.

FIG. 8. Long. sec. through a larva in which the œsophagus has opened centrally. D, 4.

FIG. 9. Trans. sec. through a larva in which the œsophagus is still more eccentric than in Fig. 8. The section is through line *a* in Fig. 8. D, 4.

FIG. 10. Trans. sec. of same larva at lower level, through line *b* in Fig. 8. D, 4.

DESCRIPTION OF PLATE III.

FIG. 11. Trans. sec., through lowest part of œsophagus, of a larva in which the œsophagus along its whole length is apposed to the surface ectoderm. D, 4.

FIG. 12. Long. sec. of larva at about the same stage as Fig. 11 in the plane of the first two mesenteries. D, 4.

FIG. 12′. Median long. sec. of a larva, in which the œsophagus is applied to the surface ectoderm along the lines of the first and second mesenteries. An older stage than Fig. 12. D, 4.

FIG. 13. A section to one side of Fig. 12, through future intermesenteric chambers. D, 4.

FIGS. 14, 15, 16, 17. Series of transverse sections, numbered from above down (Fig. 14 is through the œsophagus), from a larva in which the first pair of filaments and the first mesenteric ridge are present. Along the line of mesentery 2, the œsophagus is still applied to the surface ectoderm. D, 4.

FIGS. 18, 18 *a*. Trans. sec., through œsophagus, of a larva with two complete mesenteries and a pair of filaments. Fig. 18 *a* is the upper of the two. D, 4.

FIG. 19. Surface view of balsam preparation. The larva has two long, and one (possibly two) short filaments. C, 2.

DESCRIPTION OF PLATE IV.

FIGS. 20, 21, 22, 23. Series of long. sec. from a stage somewhat younger than Fig. 18. Fig. 20 is through the first pair of mesenteries and filaments; Fig. 23 is through the line *a*, *b* in Fig. 18; and the other sections fall between. C, 4.

FIG. 24. Long. sec. through a larva such as Fig. 19; on the right, through one of second pair of filaments, on the left through an intermesenteric chamber. D, 4.

FIG. 25. From a larva with two long and two very short filaments, *a*, *b*, *c*, are three half-sections from the same side of the larva. *b* is through one of second pair of mesenteries with its filament; *a* and *b* are on opposite sides of this mesentery. D, 4.

FIG. 26. Trans. sec. through one of primary pair of filaments and mesenteries of a stage like Fig. 19. F, 4.

FIGS. 27, 28, 29. Series of trans. sec. from a larva like Fig. 19. Fig. 27 is through the œsophagus, 28 is just above the lip, and 29 is below the œsophagus. The sections are very slightly oblique. The third pair of mesenteries exist as longitudinal ridges of the supporting lamella. *R.E.* is the reflected ectoderm. D, 4.

DESCRIPTION OF PLATE V.

FIGS. 30, 31, 32, 33. Series of trans. sec., numbered from above down, from a larva with two pretty long (half the length of larva) and one very short filament. The first and third filaments have been formed from a common lobe, and the third mesentery (*b*) has been formed at the same time and in the same way as the first (*a*). D, 4.

FIG. 34. Trans. sec., below œsophagus, of attached larva with eight mesenteries. B, 4.

FIG. 35. Trans. sec. through upper part of one of the primary filaments of an attached larva. The large clear cells are nettle cells. F, 4.

FIG. 36. Trans. sec., through œsophagus, of attached larva with eight mesenteries. The second pair of mesenteries is not quite complete, and consequently at this level (just above the lip) the reflected ectoderm is found all round the œsophagus. B, 4.

FIG. 37. Long. sec. through attached larva; on the right through one of second pair ot mesenteries, on the left through an intermesenteric chamber. C, 2.

FIG. 38. Long. sec. through attached larva in which the basal plate has appeared; on the left through one of third pair of mesenteries with its filament, on the right through an intermesenteric chamber. The line *m, m* indicates the outline of the polyp when expanded. C, 2.

FIG. 39. Trans. sec., through œsophagus, of attached larva with twelve mesenteries. B, 4.

FIG. 40. A more highly magnified view of one of the septa of Fig. 41 (that lying in the near "directive" chamber), sectioned at the level of its opening. *c.b.* is the calycoblast layer.

DESCRIPTION OF PLATE VI.

FIG. 41. Trans. sec. through œsophagus of young Manicina, ¼ in. diam. *D.M.*, the directive mesenteries. X, 60.

FIG. 42. Section of same specimen, below œsophagus. Skeleton is bare at *a* and *a'*. The tip of the columella lies in the cœlenteron. X, 68.

FIGS. 43, 44, 45. Series of trans. sec., numbered from below upwards, through the oval cone of a larva like Fig. 38. Fig. 43 is through the line *x*, *y* in Fig. 38. Only the first two pairs of mesenteries extend into the uppermost part of the cœlenteron. The overlapping of the reflected ectoderm and endoderm is well shown. D, 4.

FIG. 46. Part of a trans. sec. of adult single polyp, through line *a* in Fig. 50. The ectoderm of the peristome is marked *oe.ec.*; that of the lateral body wall, *ec*. X, 30.

FIG. 47. Trans. sec. of filament and mesentery of a larval *Cerianthus*. Level of section is just below the œsophagus. *m* is the commencing ciliated band (flimmerstreif). F, 2.

FIG. 48. Section of same filament lower down. The violent contraction has caused the halves of the mesentery to spring apart, leaving the coagulated supporting lamella partially free. F, 2.

FIG. 49. Trans. sec., through œsophagus, of a larval *Cerianthus*. *D.M.*, the (larval) directive mesenteries. The numbers 1, 2, 3, 4, mark the four youngest mesenteries, in the order of their age, 1 being the youngest. X, 60.

DESCRIPTION OF PLATE VII.

FIG. 50. Median long. sec. through an adult single polyp; on the right through a primary, on the left through a secondary mesentery. The line 3 marks the position of the free edge of a tertiary mesentery. The surface of attachment was irregular, but the corallum extended only a very short distance below the limit of the skeleton in the figure. X, 30.

FIG. 51. One of the extra-thecal entocœlic chambers of Fig. 49 more highly magnified. *Mes.* is the peripheral portion of a mesentery.

FIGS. 52, 53, 54. Trans. sec. of an adult primary filament. Fig. 52 is through the upper, 53 through the middle, and 54 through the lower portion. The large clear cells in Fig. 53 are nettle cells. D, 4.

FIG. 55. A more highly magnified figure of the lower portion of the œsophagus, as shown in the left half of Fig. 50. *Oe.ec.* is the lining epithelium of the œsophagus.

FIG. 56. One-half of a median long. sec. of an adult single polyp. The section is through one of the primary septa. X, 30.