Contributions on the Morphology of the Actinozoa: V. The Mesenterial Filaments in Zoanthus sociatus (Ellis)

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CONTRIBUTIONS ON THE MORPHOLOGY OF THE ACTINOZOA.

V. THE MESENTERIAL FILAMENTS IN ZOANTHUS SOCIATUS (ELLIS).

J. PLAYFAIR McMURRICH.

SEVERAL years ago I began a study of the mesenterial filaments of *Zoanthus sociatus* (Ellis), taking this form as a representative of the order Zoantheae, and intending, eventually, to extend my observations to other species and other groups. Various matters have, in the mean time, presented more pressing claims for attention, and I have so far been unable to carry out my original plan. I have, however, been able to study with considerable thoroughness the filaments of the adult *Z. sociatus*, and have also secured some data as to their development in bud embryos. I have not been successful in obtaining egg embryos of this species, but have observed certain interesting peculiarities in the development of the filaments in some zoanthid larvae whose parentage could not be determined; some of these I collected myself, while others I owe to the kindness of Mr. Alexander Agassiz, who obtained them by the surface net in West Indian waters.

It has seemed to me advisable, notwithstanding the imperfections of my material, to place my observations on record; the more so that it seems improbable that I shall be able to carry out my original plan of a thorough study of the filaments of the Anthozoa both from the histological and the embryological side.

I. HISTORICAL.

Before considering the literature which refers especially to the filaments of the Zoanthidae, a brief review of the literature of the hexactinian filaments seems advisable, since it is in this group that the filaments have been most thoroughly studied.

Of the structures usually grouped together as parts of a mesenterial filament, the acontia, which are extruded from the body by the Sagartiadae, were naturally the first observed, having been described by Dicquemare in 1775, and, according to Contarini, by Gesner as far back as 1558. The first description of the filament proper of which I am aware was by Spix (**'09**),[1] but from his time onward frequent references to them occur. The older authors knew only that portion of the filament which we now term the *glandular streak* (Nesseldrüsenstreif), and they regarded this as a coiled tube occupying the free edge of the mesentery. The supposed tubular character of this structure led it to be considered either as a reproductive organ or a reproductive duct, a view to which Teale (**'37**) was the first to take exception. He, believing with Rapp (**'29**) that testes did not occur in the Actiniae, and that the ova developed without fertilization, and were rather "germ granules" or "gemmiferous bodies" than true ova, and recognizing that the filaments were not oviducts, suggested that they might be analogous to the salivary, pancreatic, and hepatic follicles of higher animals. Erdl (**'42**), by the discovery of testes, disproved the opinions of Teale and Rapp with regard to the organs of reproduction, but he, too, suggested a possibly hepatic function for the filaments.

The underlying idea of these suggestions of Teale and Erdl that the filaments were concerned in the digestive processes gained in popularity as new observations were added, while at the same time their direct homology with liver, pancreas, or salivary glands became more improbable. Without reviewing the various theories as to their function at greater length, it may

[1] I have not been able to consult the paper of Spix and know it only by a quotation given by Teale (**'37**).

be stated that their participation in the digestive processes seems to be now generally accepted, chiefly owing to the observations of Krukenberg ('**80**), and Metschnikoff ('**80**), and, more recently, of Willem ('**93**).

The earliest recognition of a difference in the structure of the upper and lower portions of the filaments was by Hollard ('**51**), who, however, merely noted its existence. A more careful description of the upper part of the filament was given by Haime ('**54**), who not only recognized the acontia and the glandular streaks, but speaks of the upper part as "gros cordons," each of which has attached to its sides "un feston très régulier et muni de cils puissants." Thorell ('**58**) also recognized the same three portions, terming the acontia "capsule cords," the glandular streaks "mesenterial threads," and the ciliated bands, on account of their proximity to the reproductive organs, "ovary cords."

Rathke, in 1840, had observed that the acontia of *Metridium dianthus* (*Act. plumosa*) were solid structures and not hollow, as had usually been supposed; and, a year later, Leuckart ('**41**) advanced the idea that the mesenterial filaments were also solid. Some later authors, such as Haime and Thorell, adhered to the earlier ideas; but Gosse ('**60**) described them as cords and named them craspeda, failing, however, to recognize the ciliated bands.

The first careful study of the filaments by modern methods was made by von Heider ('**77**). He confirmed Leuckart's observations as to their solidity, showing that the central axis of the filament was really the expanded edge of the connective tissue (mesogloea) of the mesentery. He also figured the trilobed condition of the upper part of the filament, but failed to perceive the peculiar nature of the epithelium of the lateral lobes, each of which according to his idea "das für die Mesenterialfilamente charakteristische Epithel trug." He seems, indeed, to have regarded the lobes merely as coils of the glandular portions of the filaments.

Finally, in 1879, the brothers Hertwig gave a very thorough account of the structure of the hexactinian filaments, and practically nothing has been since added to our knowledge of them.

The Hertwigs showed that they are solid structures and that two portions are recognizable (three in the Sagartiadae which possess acontia). The upper portion consists of two wing-like lamellae attached to the edge of the mesentery, which, in consequence, presented a somewhat trilobed condition in transverse section. The two lateral lobes are characterized by the epithelium of their outer surfaces being composed of long and very narrow cells, each of which bears a single cilium. These cells vary somewhat in length at regular intervals, so that longitudinal sections show the lobes to have a wavy contour. No glandular or nematocyst cells occur in this portion of the filament, which the Hertwigs termed the *Flimmerstreif*.

The lower portion consists of a more or less coiled cylindrical cord attached throughout its entire length to the edge of the mesentery. Its epithelium consists of gland cells, nematoblasts, supporting cells (Stützzellen), and sensory cells, the nerve fibers from these last forming a plexus between the bases of the other cells. This portion was termed the *Nesseldrüsenstreif*. In its upper part it is an almost straight cord, and in perfect mesenteries is continuous with the central lobe of the ciliated bands, and through this with the stomatodaeal ectoderm; in imperfect mesenteries, however, there is no such continuity with the ectoderm, the glandular streaks gradually fading out above, and, the central lobe of the ciliated bands being wanting, the lateral lobes are separated by a depression lined by ordinary endoderm cells. It would seem from this that the central lobe of the ciliated bands is in reality the upper part of the glandular streak.

The arrangement just described may be regarded as the typical one for the hexactinian filaments, though certain departures from it have been observed. Thus in the Madreporaria the ciliated bands have not yet been observed, and they are also absent in certain Actiniaria, such as Protanthea and Gonactinia (Carlgren, '93) and Corynactis, Ricordea and Rhodactis (Duerden, '98).[1]

[1] I may state that I can confirm Duerden's observation as to the absence of the ciliated bands in the last two forms.

So far, however, as the majority of the Hexactiniae are concerned both parts occur.

In the Zoantheae the ciliated bands are, as a rule, the most striking portions of the filaments, and, consequently, have received more attention than the glandular streaks. The earliest writer on the filaments of the Zoantheae, Lesueur ('17), describes, however, both portions in *Zoanthus solanderi* and in *Palythoa* (*Corticifera*) *glareola*. He described white filaments bordering the edges of the mesenteries and noted that above, attached to the base of the stomach, there were "thick white arcuated organs, striated in annulations, folded on each other and divided through their whole length by a small canal." He thought that the ciliated bands, or, as he called them, the arcuated organs, might "be considered as performing the functions of the liver."

Dana ('46) described the glandular streaks in *P. caesia* as spermatic cords and noted that "above the spermatic cords there is attached to each larger lamella, immediately below the stomach, a pair of flat branchia-like organs." Verrill, who observed these same structures in 1869, agreed with Dana in regarding them as branchiae, and they were again briefly described by Andres in 1877. None of these authors, however, seemed to regard the "branchia-like" or "arcuated" organs as parts of the mesenterial filaments, nor did Andres nor Verrill perceive their identity with the ciliated bands of the Hexactiniae which had been described by Haime and Thorell. This was left for R. Hertwig ('82), who described them as portions of the mesenterial filaments of his *Z. danae* (?) and pointed out that it is quite erroneous to consider them as structures peculiar to the Zoantheae.

Erdmann ('85) described both the glandular streaks and the ciliated bands, adding, however, nothing to our knowledge of their structure; and Koch ('86) failed to find mesenterial filaments in the forms which he studied, and maintained that they were not present, at least in the same form as in other actinians. Three years later I described ('89) the two portions of the filaments of *Z. flos-marinus*, and, in addition, noted that the cells covering the surfaces of the mesenteries for some distance outwards from the glandular portions of the filaments were much higher than the general endoderm, and were loaded with green granules and fragments of sponge spicules. I suggested that this region of the endoderm was essentially digestive in function, an opinion which has since been confirmed experimentally by Willem ('93) for the Hexactiniae.

Haddon and Shackleton ('91 and '91a) confirmed my observations on other zoanthids and pointed out that slight variations in the form of the ciliated lobes occurred in certain forms, such as *P. axinellae.* Finally, von Heider ('95), in his description of *Z. chierchiae*, entered somewhat fully into the structure of its mesenterial filaments. He found in the ciliated bands what he regarded as a distinct area intervening between the central lobe and the ciliated portions of the lateral wings, and characterized by possessing numerous gland cells. He terms it the glandular swelling and attributes to it a digestive function. He also observed the heightened epithelium lateral to the glandular portions of the filaments which had been described by Haddon and Shackleton, and myself, but objects to its interpretation as a digestive area, believing it to be the region in which the reproductive cells are to develop, none of the specimens which he examined possessing these cells.

II. DESCRIPTIVE.

1. *The Ciliated Bands.*

To correctly interpret a series of transverse sections of an adult Zoanthus it is necessary to understand the course of the free edge of the mesentery. For this purpose I made a wax reconstruction of the upper part of one of the perfect mesenteries of *Z. sociatus*, together with the portion of the stomatodaeum to which the mesentery was attached. From this it is evident that the lower edge of the stomatodaeum is bent back upon itself, as represented in the diagram (Fig. 1), and that its ectoderm becomes continuous with the epithelium of the large ciliated bands. From the reflected stomatodaeum the free edge of the mesentery, with the filament, extends outwards and then arches downwards. Consequently, in transverse sections through the column the filament will be cut practically longitudinally above (Fig. 1, *DD*), then somewhat obliquely, and below transversely (Fig. 1, *AA*).

I have represented in Figs. 2–4 sections through the ciliated bands at approximately the levels indicated in Fig. 1 by *AA*, *BB*, *CC*, and *DD*. In Fig. 2 two mesenteries are shown, and the section probably not having been perfectly transverse and the amount of contraction not having been quite the same in each mesentery, the filaments are cut at different levels, *2A* approximately at the level indicated by *AA* in Fig. 1, and *2B* at the level indicated by *BB*. In *2A* the filament is cut almost transversely. The free edge of the mesentery is occupied by

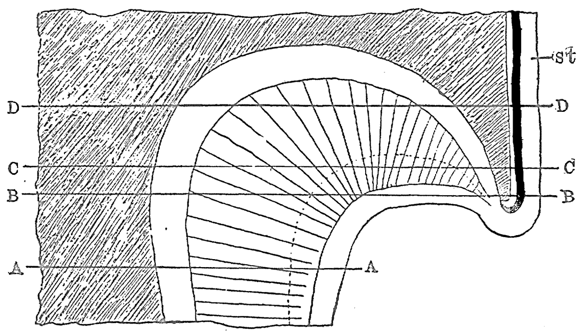

FIG. 1.—Diagram to show the relations of the ciliated bands. *st* = stomatodaeum; *AA* and *BB* = levels of sections shown in Fig. 2; *CC* = level of Fig. 3; *DD* = level of Fig. 4.

a tolerably high epithelium which contains numerous clear gland cells, probably mucous in character; the free edge of the mesogloea is somewhat expanded to support this epithelium, and, resting upon it, is a layer of very fine longitudinal muscle fibers. Probably a layer of nerve fibers is also present, but I could not be sure of it. From each side of the base of the expanded edge of the mesogloea a strong wing-like lamella arises, lined on the surface next the mesentery by endodermal cells similar to those of the surface of the mesentery; on the surface turned away from the mesentery, however, the epithelium is of a different nature. Nearest the free edge of the mesentery it consists of cells, for the most part resembling ordinary supporting cells (Stützzellen), with an occasional gland cell, containing numerous deeply staining granules, interposed. Towards the free edge of the lamella, however, the cells are very slender, so that the nuclei seem closely packed, and are provided with rather long cilia; no gland cells are to be seen in this region. On one lamella of Fig. *2A* these cells form a continuous layer occupying the greater part of the surface, at the attached edge appearing to dip under the less specialized epithelium. On the other lamella they are arranged in groups, separated by patches of less specialized epithelium, beneath which some of the groups, indeed, appear to lie. This latter arrangement is, however, merely an apparent one, and due partly to the contraction of the tissues and partly to the obliquity of the section of this lamella; all the groups are really at the surface in an expanded filament. The arrangement in groups, however, is a normal characteristic whose significance will be more readily understood from longitudinal sections, and the difference on the two sides of Fig. *2A* is due to a slight difference in the plane on which the section passes through the two lamellae, one of which is probably slightly curved.

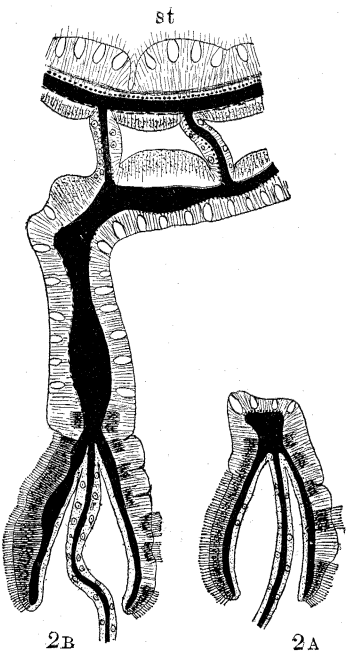

FIG. 2. *A* and *B*. — *2A* is a section of the ciliated band at the level indicated in Fig. 1 by *AA*. *2B* is at the level indicated in Fig. 1 by *BB*.

In *2B* a section higher up, at the level indicated by *BB* in Fig. 1, is figured. It cuts the median portion of the filament longitudinally and shows clearly its histological continuity, and, it may be said, its histological identity with the stomatodaeal ectoderm. The structure of the epithelium of the lamella is the same as in *2A*.

In Fig. 3 the section no longer cuts the median portion of the filament, but takes the wing twice nearly transversely and the intermediate portion, near the line of attachment of the wings to the edge of the mesentery, practically longitudinally. It is at the level indicated in Fig. 1 by *CC*, and the edge of the region of attachment of the wings to the edge of the mesentery being indicated in this figure by the dotted line. In this section one sees the ciliated areas dividing the less specialized, or, as it may be termed, the *intermediate* epithelium, into a number of bands, a depression between each of these leading down to

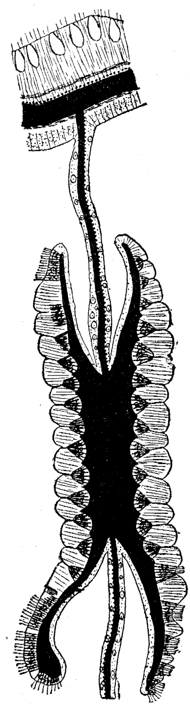

FIG. 3. — Section of the ciliated band at the level indicated in Fig. 1 by *CC*.

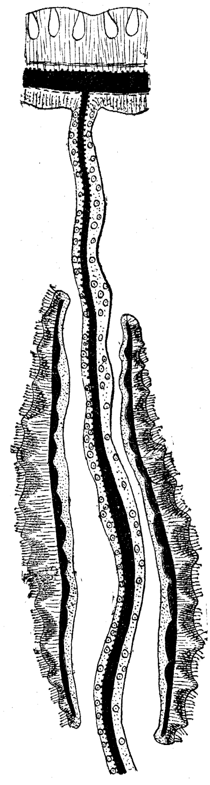

Fig. 4. — Section through the ciliated bands and a mesentery at the level indicated by *DD* in Fig. 1.

a group of ciliated cells, it being plainly evident that these latter do not reach the surface merely owing to the state of contraction of the tissues.

In Fig. 4 the section passes along the line indicated by *DD* in Fig. 1; that is, above the line of attachment of the lamellae to the mesentery. The intermediate portion of the ciliated band is again cut longitudinally and the marginal portion obliquely. The arrangement of the ciliated cells in bands is clearly seen, the bands being much wider in comparison with the bands of intermediate tissue than in the last section, indications, indeed, of their continuity being shown by the short but narrow and closely packed cells which line the surface of each intervening ridge. Finally, it may be stated, in a section still higher up one finds a perfect continuity of the bands of ciliated cells, the section cutting the marginal ciliated cells longitudinally.

The general structure just described is essentially that described by previous authors, and more especially by von Heider ('95). My interpretation of the various parts differs, however, somewhat from that given by von Heider. He recognizes the intermediate epithelium, but regards it as an endodermal layer separating the marginal ciliated ectoderm from the median lobe of the filament, which he identifies with the glandular streak of the hexactinian filament. I shall return to a discussion of the nature of the epithelium of the median lobe later; in the mean time I may point out what seems to me a fundamental error in von Heider's interpretation. He regards the entire intermediate region of the wings as digestive in function, terming it the "Drüsenwulst," and identifying it with the endodermal areas of the glandular streaks which Willem ('93) has shown to be digestive.

As a matter of fact, there are two very different kinds of epithelium in this intermediate region; (1) that lining the furrows which run across it, and (2) that occupying the intervals between the furrows. The former is exactly like the epithelium found at the free margins of the lamellae, and is, indeed, continuous with this. In other words, the ciliated epithelium, which forms a continuous streak near the free edge of each lamella, sends inwards almost to the free edge of the mesentery a number of prolongations which line the bottom of depressions on the surface of the lamella. Each of these prolongations is separated from its neighbors by a non-ciliated band (at least, I have not been able to detect cilia in my preparations) of epithelium. It is this arrangement of the ciliated cells in transverse streaks which produces the characteristic transversely striated appearance of the lamellae noted by nearly all observers, and it is interesting to note that Thorell in 1858, with his usual accuracy, described the arrangement of the ciliated cells in transverse streaks in the ciliated bands of *Metridium dianthus.*

The intermediate area cannot then be regarded as consisting wholly of endoderm, since it is generally admitted that the ciliated cells are ectodermal. Is then the intermediate epithelium endodermal and digestive? This is a question difficult to answer, but it may be said that the epithelium is certainly continuous with the stomatodaeal ectoderm above, and not with the endoderm. I do not find it essentially glandular in *Z. sociatus;* indeed, it contains relatively few gland cells in comparison with the epithelium of the median lobe. Those which do occur, however, are very different from the usual stomatodaeal glands with clear contents, since they stain deeply and are packed with granules. It is possible that such glands are digestive in function; they are especially abundant, as will be seen later, in the glandular streak of the filament, but they also occur here and there in the stomatodaeal ectoderm, and their occurrence in the intermediate epithelium cannot be accepted as evidence of its endodermal nature. From the evidence at my disposal, I am inclined to regard the intermediate epithelium as being ectodermal, as is the rest of the ciliated band epithelium, and think it erroneous to homologize it with the digestive, or rather ingestive, area described by Willem, which is unquestionably endodermal. I think, however, that intracellular digestion does occur in this epithelium, as I have seen imbedded in it particles which were neither zoöxanthellae nor normal constituents of the tissue, but which may have been ingested food particles.

2. *The Glandular Streak.*

Following a series of sections downwards below the level indicated in Fig. 2*A*, one finds the lamellae of the ciliated bands extending downwards for some distance, but they finally disappear, the median lobe of the filament alone persisting. The general appearance of the glandular streak has been described and figured frequently, and reference may be made to the figures given by von Heider ('95), Haddon and Shackleton ('91), and myself ('89). The epithelium of this part of the filament forms a rounded or crescentric layer resting upon a somewhat *T*-shaped enlargement of the edge of the mesogloea. The tips of the crescent extend to about the tips of the transverse limb of the *T*, the outer surface of the limb being covered by a very different kind of epithelium, generally admitted to be endodermal. The general surface of the mesogloea of the mesentery immediately external to the attachment of the *T*-shaped enlargement is covered by a thick endodermal epithelium, which, traced outwards, gradually diminishes in thickness to pass into the ordinary epithelium of the mesentery.

In *Z. flos-marinus* I found ('89) in this thickened epithelium numerous foreign bodies, and suggested that it was a special region for intracellular digestion. Haddon and Shackleton ('91a) have described the thickening in *Z. macgillivrayi*, and von Heider in *Z. chierchiae*, — the latter, however, taking exception to my interpretation of its function, believing it to be the area in which the reproductive elements will develop. This idea is readily disproved by the examination of specimens in which the gonads are developed. For instance, I have preparations of *Z. nymphaeus* which show the thickened endoderm very distinctly crowded with foreign bodies, and, quite externally to this, in the region where the endoderm has assumed its usual low form, the sexual cells are found. On the other hand, my interpretation is confirmed by Willem ('95), for it is in exactly the region of the thickening that he finds an abundant ingestion of carmine particles in the Hexactiniae, these forms also presenting thickenings of the endoderm, usually less pronounced than in the zoanthids, immediately external to the glandular streaks of the mesenterial filaments.

It is very generally believed that the epithelium of the middle lobe of the ciliated bands is in direct continuity with the epithelium of the glandular streak; indeed, it has generally been regarded as the upper part of the glandular streak. It appeared that there was a marked difference in *Z. sociatus* between this median epithelium and that of the glandular streak, and to test the accuracy of this appearance I endeavored to obtain a longitudinal section of the filament which would cut the epithelium of the median lobe above and the glandular streak below. After many trials I obtained a series, from three successive sections of which it was easy to reconstruct a median section through the filament. Such a reconstruction is represented in Fig. 5, somewhat diagrammatically.

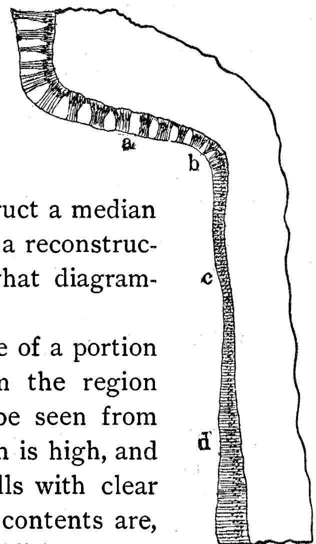

FIG. 5. — Reconstruction from three sections of a longitudinal section through the stomatodaeum, the median lobe of the ciliated band and a glandular streak of *Z. sociatus*. *a–d* = the levels from which Figs. 6–9 are taken.

In Fig. 6 is shown the appearance of a portion of the stomatodaeal ectoderm from the region indicated in Fig. 5 by *a*. It will be seen from this that the epithelium in this region is high, and that it contains numerous gland cells with clear contents ; gland cells with granular contents are, on the contrary, rather rare. In addition, some darkly staining, slender, probably sensory cells occur, the rest of the tissue being composed of ciliated cells which stain only moderately, and are probably supportive cells. As I have already stated, the median epithelium of the ciliated bands is continuous with this above, and is histologically identical with it. Tracing the section downwards, however, it will be found that the median epithelium gradually becomes lower, and, at a certain region, it changes somewhat abruptly its histological character.

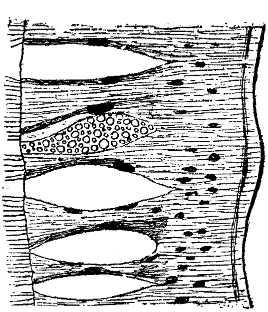

FIG. 6. — Portion of Fig. 5 about the region marked *a*, more highly magnified.

Fig. 7 represents a portion of the epithelium at the region where the change takes place (*b* in Fig. 5). The upper part of the portion figured is essentially the same as the stomatodaeal ectoderm, but in its lower part there appear cells which stain somewhat darker than the ordinary supporting cells and have large oval nuclei situated about the middle of their length. At the same time the large mucous gland cells disappear. Lower still (at *c* in Fig. 5) the change is complete and an entirely new form of epithelium occurs (Fig. 8). In this the cells are still lower; they contain large oval nuclei arranged in about two or three layers at the middle part of the epithelium, and there is apparently an entire absence of gland cells. I could not distinguish cilia in this region in my preparations, but am not prepared to say that they do not exist.

Following this stretch of tissue downwards, it is found to change again to form the epithelium of the glandular streak

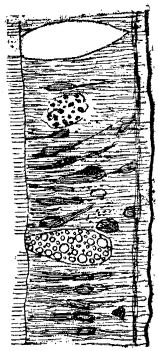

Fig. 7. — Portion of Fig. 5, about the region *b*, more highly magnified.

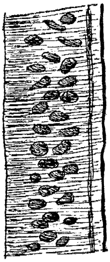

Fig. 8. — Portion of Fig. 5, about the region marked *c*, more highly magnified.

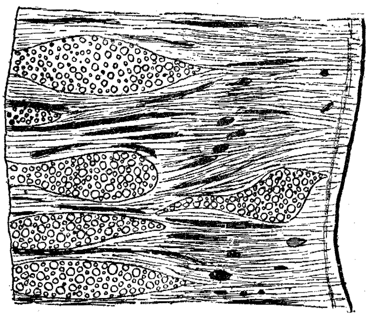

Fig. 9. — Portion of Fig. 5, about the region marked *d*, more highly magnified.

(Fig. 9). This is very high again, higher even than that of the stomatodaeum. It consists, like the latter, of supporting, sensory, and gland cells, but the gland cells are all of the kind with granular contents. I have found no nematocysts in the glandular streak of *Z. sociatus*, but their absence is by no means peculiar to that form.

It is clear then that in *Z. sociatus* there is neither a histological continuity nor a histological identity of the upper part of the median streak of the filament with the lower or glandular streak proper. The upper part is merely a continuation downwards of the stomatodaeal ectoderm, and this gives place to a low epithelium destitute of gland cells and of a generally indifferent character, below which the characteristic epithelium of the glandular streak comes into view. It seems to me from these results that one is not justified in assuming, as has so frequently been done, that the glandular streak epithelium is a prolongation of the stomatodaeal ectoderm. What I have just described, taken in conjunction with the observations of E. B. Wilson (**'84**) on the development of the filaments in the Alcyonaria, and with what I have found (**'91**) as to their development in the Hexactiniae, seems to me rather to point to a complete distinction between the two kinds of epithelium, and I regard the structure of the adult filament of *Z. sociatus* as confirmatory of the conclusions obtained from embryological studies, that the ciliated bands of the filaments are ectodermal in origin, while the glandular streak proper is an endodermal structure.

III. The Development of the Filaments in Egg Embryos.

The material at my disposal for the study of the embryonic development of the filaments was not sufficient for an exhaustive study of the subject. The youngest larvae already possessed twelve mesenteries arranged in the manner described by van Beneden (**'90**) and myself (**'91a**). On none of the mesenteries were there any indications of the ciliated bands, but, on the other hand, the glandular streaks were plainly indicated on the perfect mesenteries as an epithelium occupying the free edge of the mesentery and composed of cells with closely set, elongated, and deeply staining nuclei, very different from those of the general endoderm of the mesenteries. But what is more interesting, on the lower part of the free edge of each of the imperfect mesenteries a similar, but smaller, patch of epithelium was plainly visible. In Fig. 10 is given a representation of a part of a section through the lower portion of the column of one of these youngest larvae. Owing to its base having been somewhat depressed by contraction, this has been cut towards the central part of the section. Transverse sections of four mesenteries are shown; the two larger mesenteries are one of the macrodirectives (III), and one of those which I have taken for the first formed (I), and the two smaller are those indicated in a previous paper ('91a, Pl. IX, Fig. 6), as V and VI.

The larger mesenteries, when traced upwards, are seen to become attached to the stomatodaeum, while the smaller ones are imperfect. The epithelium which represents the glandular streak seems to be continuous above with the ectoderm of the stomatodaeum in the cases of the perfect mesenteries, though close examination shows some slight differences in the two epithelia. In the cases of the imperfect mesenteries such a continuity is out of the question, and there is not the slightest indication of a band of ectoderm extending up the outer wall of the stomatodaeum, across the under surface of the disc and thence down the free edge of the mesentery, by which a connection between the glandular streak and the stomatodaeum might be accomplished. The glandular streak epithelium can be traced upwards upon the imperfect mesenteries to a level a little above the lower edge of the stomatodaeum, where it fades out, the free edges of the mesenteries being occupied from that point upwards by cells of exactly the same nature as those covering their surfaces. That there may have been in an earlier stage some continuity between the stomatodaeal ectoderm and the glandular streaks of the imperfect mesenteries is possible; in my youngest embryos there are, however, no signs of any such connection.

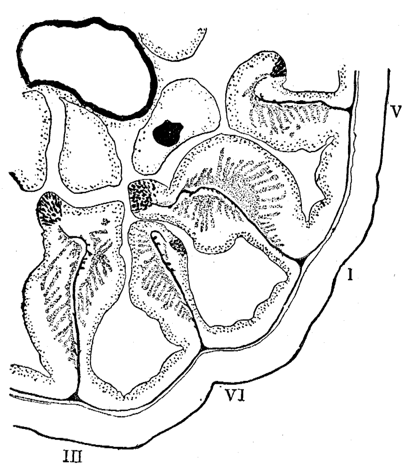

Fig. 10. — Transverse section through a portion of the column of a young zoanthid larva.

In the adult condition mesenteries V and VI have no filaments (VI has in macrocnemic forms), and one might expect that older embryos would show a disappearance or diminution of the filaments of those mesenteries. In Fig. 11 is represented a part of a section through an older larva, in which the number of the mesenteries still remains at twelve. The filaments, however, have assumed an appearance much more like those of the adult, and the histological differentiation of their epithelium is quite pronounced. The mesenteries figured are the same as those shown in Fig. 10, but of the opposite side of the body. It will be seen that in mesentery VI all traces of the glandular streak have vanished, but in mesentery V the streak is still persistent, and indeed has undergone a progressive development, just as those of the perfect mesenteries. That this is not because the larva is the young of a macrocnemic species is

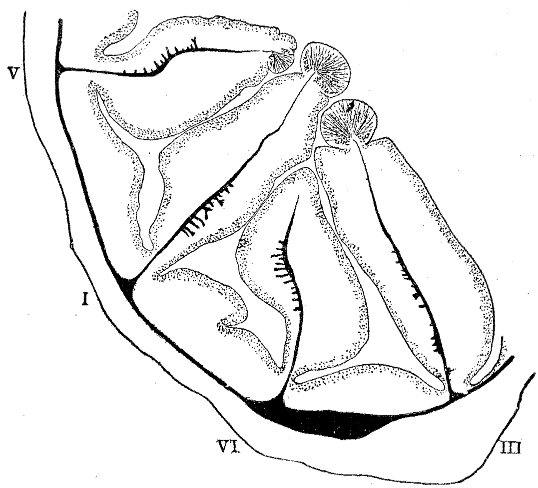

Fig. 11. — Transverse section through a portion of the column of a zoanthid embryo somewhat older than that from which Fig. 10 is taken.

shown by the fact that it is not mesentery VI, the additional perfect mesentery, in these species, which has retained its filament, but mesentery V. Probably later stages would show a disappearance of the filament of this mesentery also, but the point which is of concern is the fact of the development of filaments on these imperfect mesenteries whose epithelium is, so far as can be ascertained, at no point in contact with ectoderm.[1]

[1] Attention may be called to the fact that the discovery of filaments in these mesenteries serves to emphasize the correctness of the conclusion as to the order of the appearance of the mesenteries in the Zoantheae which has been stated by Boveri (**'89**) and myself (**'91a**), and I may add that indications of filaments in the microdirectives can also be distinguished, though they are much less evident than those of V and VI, possibly on account of an earlier degeneration.

IV. THE DEVELOPMENT OF THE FILAMENTS IN BUDS.

The time relations of the ciliated bands and glandular streaks in buds is just the reverse of what obtains in egg embryos; that is to say, the ciliated bands are the first to develop, the glandular streaks appearing later.

In a bud of *Z. sociatus* 2 mm. in length the stomatodaeum is already formed, and on the edges of the perfect mesenteries, immediately below the lower margin of the stomatodaeum, the ciliated bands can be seen presenting practically the same appearance as in adult polyps. Following a band downwards, it is found to disappear below and no trace of a glandular streak can be found, and no enlargement of the endoderm just external to the free edge of the mesentery. Indeed, there is nothing to distinguish a perfect mesentery from an imperfect one below the level of the stomatodaeum, except greater width. The free edges of both mesenteries is occupied by cells indistinguishable from ordinary endoderm except by their apparently somewhat smaller size.

The glandular streak begins to develop, however, soon after this stage, since in a bud but little older they were readily recognizable, and the ectoderm just external to them had become relatively high and was packed with foreign bodies; in buds 3.5 mm. in length all the parts of the filament occurring in the adult were present.

It is interesting to note that in the buds of Alcyonaria the same acceleration in the development of the ciliated bands has been observed by E. B. Wilson (**'84**), the glandular streaks in the egg embryos of these forms developing before the ciliated bands, as in zoanthids.

V. CONCLUSION.

I have shown above (1) that in adult polyps of *Z. sociatus* there is no histological continuity between the glandular streaks and the ciliated bands; (2) that in egg embryos the glandular streaks develop before the ciliated bands make their appearance; (3) that in the same embryos the streaks make their appearance on mesenteries that are not connected in any way apparently with the ectoderm, and (4) that in bud embryos the ciliated bands appear before the glandular streaks.

It seems to me from these facts that the ciliated bands must be regarded as being ontogenetically distinct from the glandular streaks. The two have been very generally regarded as different parts of the same structure, but this idea is, I think, untenable.

If they be recognized as distinct structures, there are no *a priori* reasons for regarding both as products of the same germ layer. The question of the origin of the filaments, whether from the ectoderm or from the endoderm, is one that has been frequently discussed, and with very varying answers. The majority of authors have regarded both parts as ectodermal or as endodermal, E. B. Wilson having been the first, from his studies on the Alcyonaria, to point out the probability of the development of the ciliated bands in these forms from the ectoderm and that of the glandular streaks from the endoderm. In my studies on the development of the hexactinians ('91), I reached the same conclusion, and the evidence presented above seems to point to a similar story in the zoanthids.

However, there is a more fundamental consideration at the base of all questions as to ectodermal and endodermal origin in the Coelentera. Is there sufficient fixity of the germ layers in these forms, whether the layers be regarded from the morphological or the physiological standpoint, to warrant the importance which has generally been attached to them? The germ layers have evolved; like other structures, they have had a phylogeny, and it may be remarked that just as in other structures we find discrepancies between the phylogenetic and ontogenetic development, so too we may expect and undoubtedly do find discrepancies between the ontogeny and the phylogeny of the germ layers. It has generally been accepted that the Coelentera represent a stage in the phylogeny of the germ layers, two of them being fully differentiated; indeed, Huxley's homology of the coelenterate ectoderm and endoderm with the epiblast and hypoblast of the embryologists may be regarded as one of the foundation stones of the germ-layer theory. But, after all, can we directly homologize the embryological and coelenterate layers? Are the coelenterate layers morphologically differentiated? It seems to me that they are not; every kind of cell, glandular, muscular, sensory, ganglionic, and even nematoblastic, which we find in the ectoderm, occurs also in the endoderm. The Coelentera represent a stage in the evolution of the diploblastic condition, rather than the completion of that condition, and we are assuming too much when we make a direct homology of their ectoderm and endoderm with the epiblast and hypoblast of, let us say, a vertebrate embryo.

I have spoken of only two layers in the Coelentera, omitting the mesogloea. This term, now generally accepted for the intermediate layer of the Coelentera, is sufficient reason for so doing, since it implies a lack of homology of the intermediate layer with the mesoderm of higher types. It seems to me, and I have so expressed myself elsewhere, that, if we are to seek for a homologue of the coelenterate mesogloea in higher forms, we must look for it in the limiting membrane which occurs just below the ectoderm. Indeed, a comparison of the mesogloea with the limiting membrane of certain polyclades is exceedingly instructive.

If, then, we regard the Coelentera as presenting merely an approximation to a diploblastic condition, the distinction between an ectodermal and an endodermal origin of any of their parts becomes relatively of little moment. And, furthermore, we need not be surprised to find that structures which in certain antimeres develop from one so-called germ layer, may arise from the other in other antimeres. This may be the case with the glandular streaks, and both those who have spoken in favor of their ectodermal origin and those who have maintained that they were endodermal may have right on their side. The observations of Goette ('93) and Miss Hyde ('94) have given reasons for believing that, in the Scyphomedusae, while the first pair of radial chambers is endodermal, the second pair is ectodermal in origin. If such variation occurs in this group in connection with such fundamental structures, surely we may meet with variations in the origin of the glandular streaks in the Anthozoa. H. V. Wilson may be quite correct in maintaining an ectodermal origin for the glandular streaks of the first four mesenteries of *Manicina* ('88), and altogether wrong when he extends this origin to the streaks of the later formed mesenteries.

I would conclude, from my own observations, that the ciliated bands are probably in all cases ectodermal, and that, in some mesenteries at least, the glandular streaks are endodermal; yet I am prepared to accept as correct the ectodermal origin of the glandular streaks in other mesenteries. It is to be understood that I use the terms "ectodermal" and "endodermal" here merely for convenience and not as expressing a definite homology.

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