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## CONTRIBUTIONS ON THE MORPHOLOGY OF THE ACTINOZOA.

### I. THE STRUCTURE OF *CERIANTHUS AMERICANUS*.

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THE genus *Cerianthus* was established in 1829 by Delle Chiaje for the Mediterranean form which we now know as *C. membranaceus*, it having been originally described by Spallanzani as *Tubularia membranacea*. Until 1854, however, no thorough study of the internal structure was made, but in that year appeared the excellent memoir of Haime ('54). In this it is shown that each "loge" has communicating with it two tentacles, one belonging to the marginal, the other to the oral group. Haime also described the arrangement of the mesenteries, showing that two mesenteries, the cavity between them forming a continuation of the "fossette gastrique" (siphonoglyphe), extend the entire length of the body to the terminal pore, while the rest stop at a short distance below the internal opening of the stomatodæum, and are unpaired, although they are alternately slightly unequal in length and prominence. Haime described, too, the hermaphroditism of this species, and gave an incomplete account of some stages in its development. His account of the histology was, however, by no means exhaustive, though admirable, when the facilities for such work at that time are taken into consideration.

For twenty-five years nothing further was done towards the

elucidation of any members of the genus *Cerianthus*, but in 1879 two papers of importance appeared. The brothers Hertwig ('79) in their studies on the nervous system of the Actiniaria, examined histologically *C. membranaceus* and *C. solitarius*, and added much to our knowledge of the minute anatomy of these forms, discovering the nervous tissue, describing the arrangement of the muscle-cells correctly, and showing the similarity of all the tissues to those of the other groups of Actiniaria. As regards the general structure, however, they made no advance upon what had been done by Haime, not even correcting some of the errors into which that author had fallen.

The other paper of 1879 was by von Heider, who treated *C. membranaceus* in as thorough a manner as he had previously done *Sagartia troglodytes*. Where the Hertwigs are lacking, von Heider excels, giving a more correct account of the anatomical features of the species than Haime had done, but his treatment of the histology is in some points not so complete. As regards the anatomy, he showed that the pair of elongated mesenteries are not the most ventral, but that between them is a pair reaching the wall of the siphonoglyphe, but terminating a very short distance below the margin of the groove. These are the ventral directives. He also extended Haime's discovery as to the alternating inequality in length of the mesenteries, by showing that as a rule there is an alteration of gonophoric and non-gonophoric mesenteries, and accordingly divided the mesenteries into three groups; namely, (1) Filament septa, which are non-gonophoric; (2) Genital septa; and (3) Continuous septa, which are represented only by the single pair which reaches the terminal pore. Von Heider describes the Filament septa as giving rise to the acontia, while the Genital septa are provided with mesenterial filaments (craspeda, Gosse). The Hertwigs, in a supplement to their description, after confirming several of von Heider's results, criticise this differentiation of the filaments in the two groups of mesenteries, stating that "in der Beschaffenheit der Mesenterialfilamente zwischen beiden kein Unterschied vorhanden ist." It will be seen that, so far as the structure of the filaments is concerned, this is true also for *C. Americanus*, though there is a slight difference in the arrangement of the different parts of the filament.

In 1880 a paper by Jourdan ('80) appeared, written, however,

before the publication of the contributions of the Hertwigs and of von Heider. It adds nothing to Haime's description of the general structure, and falls much behind the Hertwigs' contribution in the treatment of the histology.

In 1888 a paper by C. Vogt ('88) was published, in which was confirmed the supposition of the Hertwigs that new mesenteries are formed in *Cerianthus* solely at the dorsal surface, in the region which corresponds in other orders of Actiniaria to the intra-mesenterial space bounded by the dorsal directives. Vogt also calls attention to the unpaired tentacle corresponding to the ventral intra-mesenterial space, which had previously been observed by Haime in *Cerianthus* and by A. Agassiz ('62) in *Arachnactis*, and demonstrated the close relationship existing between these two genera.

Later in the same year, H. V. Wilson ('88) added to Vogt's observations by showing a similar method of formation of new mesenteries in a free-swimming larva of an unidentified species of *Cerianthus* obtained at Nassau, Bahama Islands, W.I.

In the following year Fischer ('89)<sup>1</sup> again called attention to the unpaired ventral tentacle, and to the bilateral symmetry of *C. membranaceus*.

Up to this time no accounts of the internal structure of any other species of *Cerianthus* had been given. The Hertwigs state that they studied *C. solitarius*, but make no special statements concerning its general structure. In 1889, however, Danielssen ('89) published an account of the structure of a Norwegian *Cerianthus*, which he termed *C. borealis*,<sup>2</sup> and which presents many important variations from the structure of *C. membranaceus*. The principal anatomical peculiarities are the small number of mesenteries, sixteen only, the occurrence of either ova or spermatozoa only in any individual, and the difference in the arrangement of the mesenteries in the males and females, all the mesenteries in the latter extending to the terminal pore, except the ventral directives, which stop a short distance above it, while in the males the arrangement is much more similar to what is found in *C. membranaceus*.

<sup>1</sup> The original paper I have not seen; my knowledge of its contents is derived from the abstract in the Journal of the Royal Microscopical Society, December, 1889.

<sup>2</sup> It seems probable that this form, which Danielssen holds to be distinct from *C. Lloydii*, is not the same as Verrill's *C. borealis*, described in 1873. In this case Verrill's application of the name has the priority, as Danielssen's description was not published until 1877.

*CERIANTHUS AMERICANUS*, L. AGASSIZ.

The earliest mention of this form is by L. Agassiz ('59), who states that it was found by H. James Clark, in 1852, at Charleston, S.C., where it lives in tubes sunk in the mud-flats of the harbor. It is referred to the genus *Cerianthus*, but no specific name is given. Agassiz observed the terminal pore, which he terms the anus, and states that the upper parts of the mesenteries bear female reproductive organs, and the lower parts male organs.

The specific name is stated by Verrill ('64) to have been bestowed in manuscript by Agassiz, and Verrill gives the first full description of the species, from drawings made for Agassiz by his artist, Burkhardt, and from alcoholic specimens in the Museum of Comparative Zoölogy at Harvard College.

In a subsequent paper Verrill ('72) records its occurrence on the coast of North Carolina, where it was collected by Dr. Yarrow, and where it had previously been found by Stimpson, but adds nothing to the description given in 1864.

Among the "Challenger" material R. Hertwig ('82) found a single specimen of a *Cerianthus* obtained in thirteen fathoms in the mouth of the Rio de la Plata. He identifies it with *C. Americanus*, but unwilling to mutilate the single specimen, did not investigate it anatomically.

Finally I added ('87) a few points to the general description, but gave no account of the internal anatomy and histology which have never hitherto been examined.

## I. EXTERNAL FEATURES.

The specimens of *C. Americanus* which I studied were found at Beaufort, N.C., where the Summer Station of the Johns Hopkins University was located in 1885. In the shallow sounds there the bottom is largely very dark mud, sometimes with a superficial coating of sand. Large areas of such mud are uncovered at low tide, forming what are termed the mud-flats, and it is on these flats that *Cerianthus* is found, usually just below the average low-tide mark. It lives in cylindrical burrows extending, usually at an angle, downwards for some distance, how far I was not able to determine. Like other members of

the genus it secretes a case, open at both ends, and composed of hardened mucus and nematocysts. Animals removed from the case and kept in an aquarium rapidly secrete for themselves a new habitation, which, however, is naturally thinner than the original one and of a lighter color, being almost white, while normally the tube is dark gray, due to staining by the black mud with which it is in contact. The inner surface is purplish gray, being tinged by the pigment of the animal.

The largest specimen I obtained measured about 20 cm. in length, with a diameter at the middle of 1.5–2 cm., and at the disc of 1.8–2.5 cm. The outer tentacles measured 3.4 cm., while the oral series measured 1–1.2 cm. These measurements fall very short of those given by Verrill, who states that the largest specimens in expansion measure 60–70 cm. in length, with a diameter at the disc of nearly 4 cm. and at the middle of the column of 2.5 cm. My preserved specimens measure 5.5–6 cm. in length, and about 1.5 cm. in diameter.

The color of the column is some shade of brown (Pl. VI., Figs. 1 and 2), varying from pale chocolate-brown to deep purplish brown. The upper part is always darker than the lower, and in some cases the column is marked with longitudinal lines of a lighter shade than the ground color. The marginal tentacles are of a paler brown than the column, except the outermost, which are purplish blue. The oral tentacles in all the specimens I observed were pure white; Verrill, on the other hand, describes them as being darker than the marginal ones, and marked with white longitudinal lines. In the Beaufort specimens, however, the tentacles of both series are unmarked by lines, spots, or annulations. The disc is yellow with white lines crossing it radially.

The column is cylindrical and smooth, tapering gradually towards the posterior extremity, which is rounded, and bears a small terminal pore. The marginal tentacles vary somewhat in number. Verrill states that they are 125 or more, but in the Beaufort specimens they did not amount to 100, varying, according to the counts made, from 89 to 94 (95?). We know from the observations of Vogt and Fischer that there is always an odd number, the unpaired tentacle corresponding to the space bounded by the ventral directives. The absolute number of the tentacles perhaps increases throughout the entire life of the animal, and

the discrepancy between the number found in the Beaufort specimens and that given by Verrill is probably in accord with the smaller size of my specimens. A tentacle of the oral series corresponds to and is opposite each marginal tentacle, and both series seem to be arranged in three cycles, not four, as I stated in my previous paper, but I was not able to ascertain the relations of the various cycles in the two series. The accounts given by von Heider ('79) and Fischer ('89) of these relations in *C. membranaceus* differ materially. The number of cycles, however, does not have the same significance here that it has in the Hexactiniæ, and the arrangement of the tentacles in cycles is no doubt, as von Heider suggests, altogether mechanical, and due to crowding, and accordingly their relation in the marginal and oral series, and the number of the cycles in which they are arranged, may vary.

## 2. INTERNAL STRUCTURE.

On laying open a specimen of *C. Americanus* by a longitudinal incision, the appearance presented is that indicated in Figure 1, Pl. VII., in which, however, the disc and tentacles have been omitted. In the upper part one sees the stomatodæum with a well-marked longitudinal groove — the siphonoglyphe. By close examination it may be seen to be finely grooved longitudinally, each groove corresponding to a mesentery; a few transverse grooves may usually be seen, but they are more or less irregular, and are no doubt due to contraction. Its lower margin is usually reflected, so that a transverse section in this region gives the appearance represented in Figure 3.

The mesenteries are arranged on a very different plan for what has been described for *C. membranaceus* and *C. borealis*, Danl. On first laying open a specimen of *C. Americanus*, one sees that more than one pair of mesenteries reach the posterior extremity of the body, and yet all do not extend so far. In the specimen figured twenty-three well-developed mesenteries are present. The total number of mesenteries is really ninety-two, as will be seen later, but of these only twenty-three pass more than half-way down the column, and it is to the arrangement of these that I wish first to direct the attention. Extending the entire length of the body from the region of the siphonoglyphe is a pair of mesenteries corre-

sponding to the similar pair in *C. membranaceus*, which von Heider terms the Continuous septa. Between these, and in reality constituting the ventral directives, is a pair, as in *C. membranaceus*, which are very short, and hardly extend below the level of the lower opening of the stomatodæum. Next to the ventral continuous mesenteries on either side comes a mesentery which only extends a short distance beyond the middle of the column. Dorsal to it come three continuous mesenteries, the middle one of which, however, hardly reaches the extremity of the body. Then follow two extending slightly beyond the middle of the column, and similar in length therefore to the one immediately succeeding the ventral continuous mesenteries: and succeeding these is a single continuous mesentery. So far the symmetry has been perfect, and I have found the arrangement here described to hold in another specimen which I studied. Unfortunately, the third specimen I had for investigation was not favorable for the examination of the mesenteries.

The succeeding mesenteries passing dorsally on either side vary from the regular arrangement. They are more recent in date of formation than those towards the ventral line, and may not yet have reached their final development, or may remain in this somewhat immature condition. On one side, dorsal to the continuous mesentery last mentioned, there is another similar to it, but on the other side occurs one belonging to what may be termed the second grade, reaching only to about the middle of the column. Occupying the dorsal region are four mesenteries, all of the second grade, two alternate ones, however, being slightly longer than the other two. Upon what is the left side of the figure a mesentery, also of the second grade, was detached in making the longitudinal incision, and was omitted from the drawing. The last mesentery of the second grade on the left side is the youngest of those of the first two grades, being nearest the median dorsal line.

I have denoted the mesenteries so far described according to their length as the first and second grades, the latter being the shorter ones which extend only about half-way down the column. In the figure (Fig. 1) these mesenteries are the only ones represented for the most part, but three (3) still smaller than those of the second grade are indicated. In reality, the mesenteries of this third grade alternate with those of the first and

second grade, and there are consequently twenty-three of them. These third-grade mesenteries extend only a short distance below the internal opening of the stomatodæum, not more than a centimetre, and usually less than that. Like the longer ones, they are perfect in their upper part.

Figure 2, Pl. VII., is a semi-diagrammatic representation of the mesenteries of the various grades, and it will be seen from this that there is still a fourth grade of mesenteries, shorter than any that have hitherto been described, and alternating with the mesenteries of the other three grades. There are, therefore, forty-six of them, and altogether in all the grades, accordingly, there are ninety-two mesenteries, one more than the number of tentacles, marginal or oral, of which I counted ninety-one. These fourth-grade mesenteries hardly reach below the lower opening of the stomatodæum, and are not readily seen in a preserved specimen, being usually overlapped by the adjoining mesenteries, and further concealed by the tangled mass of acontia which arise from the edges of the mesenteries just below the stomatodæum. The ventral directive mesenteries, as already mentioned, belong to the fourth grade.

Figures 3, 4, and 5 show some interesting features in the relations of the mesenteries of the four grades. They are transverse sections of the ventral region of the column in its upper part. Figure 3 passes through the stomatodæum shortly above its lower extremity, cutting its reflected portion. The ventral siphonoglyphe (*sz*) is readily made out, the ectoderm lining it not being thrown into folds as it is elsewhere. The ventral directives (*D*) are still in connection with the stomatodæum, but the other mesenteries have separated from it. Sections a little higher up show that all the mesenteries are perfect; but the ventral directives retain their connection with the stomatodæum throughout a greater portion of its length than do the others. The mesentery (1) immediately adjoining the directives is one of the ventral continuous mesenteries, which at this level are narrow, as are all the mesenteries immediately below the point where they lose connection with the stomatodæum. Succeeding it comes a mesentery of the fourth grade (4), and following this one of the third grade (3), both of the same width as the ventral continuous mesentery. The mesenterial filaments of these three have the same structure, being



somewhat bilobed, constricted by a well-marked "neck," and evidently comparable with the "Flimmerstreifen" of the mesenterial filaments of the Hexactiniæ. The section has not cut all the mesenteries at the same relative level, so that those furthest from the ventral median line show features which are to be found in 1, 4, and 3, a little farther down. The mesentery (4') which succeeds 3 is again of the fourth grade. It is much wider than those nearer the middle line, and its mesenterial filament is quite different, appearing simply as a small rounded knob at the free edge of the mesentery not separated distinctly from the endoderm by a neck, and corresponding to the "Nesseldrüsenstreif" of the Hexactiniæ. A few sections higher up this mesentery, and the other mesenteries of the fourth grade represented (4'' and 4'''), which resemble it in width and structure, are exactly similar in all points to 4. The three mesenteries which alternate with 4', 4'', and 4''' are of the second (2), third (3'), and first (1') grades, and exactly resemble 1.

Figure 4 is a section nearly 2 mm. below that just described. The ventral directives, only one of which is figured (*D*), have practically disappeared, being indicated simply by a slight elevation of the mesogloea. The mesenteries of the first, third, and second grades nearest the middle line (1, 3, and 2) are broader than they were higher up, but still retain the same kind of filaments they possessed there. The more external (dorsal) mesenteries are much wider, and, in fact, have now reached their final width, and ova have begun to appear in their mesogloea. Their mesenterial filaments have not been represented, but they are still of the same nature as they were higher up. The mesenteries of the fourth grade (4, 4', 4'', and 4''') have lost all trace of their mesenterial filaments, and have become very narrow.

Figure 5 is from a region about 1.5 mm. below the preceding figure. The mesenteries of the fourth grade have now disappeared, being represented, like the ventral directives, only by slight projections of the mesogloea. The mesenteries of the first three grades still persist; all are gonophoric, but all have lost their mesenterial filaments.

Still further down, in a section taken about 1 cm. lower, the mesenteries of the third grade (3 and 3') would have dis-

appeared, and in a section slightly below the middle of the column only the mesenteries of the first grade would be found.

In a section a little higher up than the third (Fig. 5) of those figured, on the gonophoric mesenteries, just before the mesenterial filaments die out, a very small portion of the "Nesseldrüsenstreif" can be seen. It is histologically like the same portion in the mesenteries of the fourth grade, but does not reach anything like the development it has upon these latter mesenteries, being of very small extent, and somewhat apt to be overlooked.

It will be seen from what has been said that the mesenteries of the fourth grade are noticeably different from those of the other three grades with which they alternate. They are much shorter; they never bear reproductive elements; and they possess both the "Flimmerstreifen" and the "Nesseldrüsenstreif" of the mesenterial filaments well developed. On the other hand, the mesenteries of the first three grades are all gonophoric, and their filaments consist almost entirely of the "Flimmerstreifen," the "Nesseldrüsenstreif" being very short.

*C. membranaceus* has been found to be hermaphrodite by all who make statements on this point, the ova and spermatozoa being both present upon all the gonophoric mesenteries. *C. borealis*, Danl. is, according to its describer, bisexual, and *C. Americanus* agrees with it. Agassiz, as already noted, states that this last form is hermaphrodite, the ova occurring in the upper part of the mesenteries, and the spermatozoa lower down; but this is certainly not the case in the three specimens I had for study. All were females, ova only occurring in the gonophoric mesenteries, and sections taken at varying distances down the column to within 2 mm. of the posterior extremity show no trace of spermatozoa.

Of course it is possible that *C. Americanus* may be dichogamous, as Lacaze-Duthiers ('72) believes the Hexactiniæ to be. In all the Actinians which I have examined, amounting to over fifty species, with the exception of certain Zoanthææ, which are known to be hermaphrodite, I have never found any trace of dichogamy or hermaphroditism. If dichogamy occurred as a rule, one would expect to find occasionally, at any rate, some traces of spermatozoa associated with ova, or of ova with sper-

matozoa ; but this, so far as I know, never occurs in any of the Hexactinians. I believe, therefore, that *C. Americanus* is really bisexual, and not dichogamous.

### 3. HISTOLOGY.

The maceration of fresh tissues gives the most satisfactory results as to the structure of the histological elements in the Actiniaria. This method I was unable to employ, and the maceration of preserved specimens gave as usual unsatisfactory results. Nearly all the facts I have to present have been derived from the study of sections, and are therefore somewhat fragmentary. They suffice, however, to show a very close similarity in the histology of *C. Americanus* to that of *C. membranaceus*, as described by the Hertwigs ('79), von Heider ('79), and Jourdan ('80), and, on the other hand, considerable differences from what Danielssen ('89) has described for *C. borealis*, Danl.

#### (a) *Tentacles and Disc.*

The ectoderm in these parts is covered by a very distinct cuticle, which shows a dotted appearance, produced probably by the existence of perforations for the passage of the cilia. The outer portion contains numerous nematocysts which stain deeply with borax-carminé and are cylindrical or slightly curved with the filament spirally coiled. They resemble those described by von Heider and Haime in the same situations. Two kinds of gland cells are present ; one resembles goblet cells, and are by far the most abundant, the other kind occurring only sparingly, and being of the structure figured by the Hertwigs (Pl. VIII., Fig. 15, *d*) and by Jourdan (Pl. XII., Fig. 85, *g*). I could not observe that the latter kind were more numerous in the oral tentacles than in the marginal as Jourdan describes, the histological structure of both series of tentacles being identical. In the disc, however, they do seem to be more abundant than in the tentacles. In sections which were slightly torn I could perceive indications of the presence of "Stützzellen" and sensory cells, but maceration preparations are necessary for their proper study.

Below the epithelial layer to which these structures belong comes the nerve layer. In the tentacles the nerve fibrils are

few and not readily distinguishable; but in the disc they are much more distinct, and form a well-marked band in sections (Pl. VII., Fig. 6, *n*). This difference in the development of the nerve tract is in correlation with the development of the longitudinal muscles in the two regions. Occasional nuclei can be distinguished in the nerve region, which are probably the nuclei of ganglion cells; they are no larger, however, than the nuclei of the cells of the epithelial layer. They appear to be more numerous in the disc than in the tentacles.

The longitudinal muscles have the same development as in *C. membranaceus*. In the tentacles they cover slight elevations of the mesogloea, and are arranged in a single layer; in the more contracted tentacles they appear to form two layers, the fibrils of the upper layer alternating with those of the lower, but they never show so extensive a development as that figured by Jourdan (Pl. XII., Fig. 83). On the disc, however (Fig. 6, *lm.*), they are arranged on both sides of delicate lamellæ of the mesogloea, which are arranged "like the leaves of a book," the entire muscle having a thickness of a 0.032 mm. I could find in the oral tentacles no trace of the ectodermal circular muscles described by Jourdan from maceration preparations.

The mesogloea is homogeneous and destitute of cells. Its ectodermal surface in the disc is raised into thin lamellæ for the support of the longitudinal muscle fibres. These lamellæ do not terminate immediately below the nervous layer, however, but branch, and send branching fibres up through this layer (Fig. 6, *pm.*). This is very clearly seen in some of my preparations, especially some which were stained with eosin. One is reminded by this arrangement of what R. Hertwig ('88) has described as occurring in *Ilyanthopsis longifilis*.

The endoderm is destitute of Zoöxanthellæ. Its cells give rise at their bases to muscle fibres, which, as usual, are arranged circularly. Occasional gland cells are seen, but I did not find them so numerous as the Hertwigs figure them in *C. membranaceus*; they are of one kind only, namely, the granular club-shaped kind.

#### (b) *The Column Wall.*

The ectoderm of this portion of the body is characterized by the great abundance of large nematocysts, with an irregularly

coiled thread, similar to those originally described by Haime. They are especially abundant in the upper part of the column, and occur throughout the entire thickness of the epithelial layer down to the nerve layer. In the lower part of the epithelium, however, they are principally represented by highly refractive globules of various sizes, some perfectly homogeneous, others split with irregular portions of various sizes; these globules I judge to be developing nematocysts on account of their behavior to various staining reagents, which is exactly like that shown by the fully developed cysts. They have been described and similarly identified by Jourdan. A second form of nematocyst is also present, chiefly in the outer portions of epithelium. It is much smaller than the large *Cnidæ glomiferæ* (Gosse), and is cylindrical, measuring  $28\ \mu$  in length, and  $5\ \mu$  in breadth. It is well differentiated by both gold and saffranin staining, taking with the former a faint pinkish tinge, and with the latter a bright orange. It is clear, the spiral portion of the filament not being visible, while the "Axen-körper" (Möbius) is very readily seen. A few nematocysts resembling those found in the tentacles and disc also occur. Undoubtedly too much stress has been laid upon slight differences in shape, in distinguishing different forms of nematocysts. Haime certainly erred in this respect, and von Heider also, though to a less degree. The two forms described by the latter from the tentacles differ only in size, and are probably the same, and it does not appear to me to be necessary to distinguish between the two forms of *Cnidæ glomiferæ* he describes from the column wall. Probably the second form I have described above is identical with von Heider's form *d* from the column epithelium.

The epithelium is covered on its free surface by a cuticle. Gland cells are very abundant, and are of the same kinds as were found on the disc.

The nerve layer consists of a very strong band of fibres, which lies immediately above the muscle band. It is traversed at right angles by fine processes, both from the epithelial cells and from the mesogloæal lamellæ which support the muscle fibres. A few nuclei are to be seen lying among the nerve fibres, but they are very few and small, resembling those found in the nerve layer of the disc. They are probably gan-

glion cells, but there is certainly no such development of ganglion cells as Danielssen describes as occurring in his *C. borealis*.

This description agrees essentially with that of the Hertwigs. It is well known, however, that von Heider's observations differ somewhat from those of the Hertwigs. He describes as occurring in the lower part of the epithelial layer an "Interbasalnetz" of fibres, formed by the anastomosis of fine branching processes of the epithelial cells. In the meshes of the network are fine, sharply outlined points, which are supposed to be cross-sections of delicate fibrils. These fibrils are nervous, and send branches upwards to the epithelial cells, and downwards to the mesogloea. The Hertwigs, in discussing in an appendix von Heider's results, identify this "Interbasalsubstanz" with their nerve band. This, however, is a mistake. In all sections taken from one of my specimens I get an appearance similar to that shown in the Hertwigs' Pl. VIII., Fig. 11; in all the sections taken from another specimen, I get von Heider's "Interbasalnetz." Why there is this difference in the two specimens I cannot say. It may be due to a difference in the amount of contraction. The nerve band in those preparations which show the "Interbasalnetz" is plainly visible, lying between the muscle layer and the network, and corresponding therefore with the fibrillar layer which von Heider describes as appertaining to the "mesoderm," which is shown in his Pl. V., Fig. 35, *f*. It is this fibrillar layer then, and not the "Interbasalnetz," which is the nerve band. It is possible that the "Interbasalnetz" appearance may be produced by the great contraction of the mesogloea and of its processes, which extend up into the epithelial layer. This idea is strengthened by the fact that gland cells and nematocysts are of very frequent occurrence in the network, — a fact that shows that it belongs to the epithelial layer.

The longitudinal musculature of the column is as usual well developed. For some distance below the margin it is no higher than the musculature of the disc, but lower down it increases in size, reaching its greatest height about the middle of the column, where it is many times higher than on the disc. This height it retains almost unaltered to within at least 2 mm. of the posterior extremity, except along the dorsal median line, where it is throughout low as in *C. membranaceus*. It has essentially

the same structure as in the disc, except that the fibres near the base of the lamellæ are much smaller in diameter than those which cover the greater portion of their surface. I have not been able to discover the slightest trace of circular muscles intermingled with the longitudinal, as Danielssen describes in *C. borealis*, Danl.

The mesogloea presents the same structure here as on the disc. The muscle lamellæ are prolonged at their free edges into numerous fine branching processes, which traverse the nerve layer, and pass up into the epithelial region of the ectoderm. Continuations of the epithelial cells also traverse the nerve layer, and pass down between the muscle lamellæ, and are perhaps nervous, or partly nervous, and partly the basal portions of the "Stützzellen." A circular musculature is present on the inner surface of the mesogloea.

(c) *The Stomatodæum.*

As already stated, the surface of the stomatodæum is raised into numerous longitudinal folds, each of which corresponds to an interval between two mesenteries (Fig. 7). The ectodermal surface of the mesogloea is raised into slight ridges corresponding to the folds of the ectoderm, and is provided with short lamellæ supporting the longitudinal muscle fibres, which have a much smaller diameter in this region than elsewhere. The delicate branching processes from the mesogloal lamellæ are very evident (Fig. 7), especially those which arise from the muscle processes covering the ridges. They can be traced for some distance up into the ectodermal epithelium, forming supports for its cells.

The epithelial and nerve layers have the same structure and histological characters as in *C. membranaceus*. Circular muscles occur in the endoderm.

(d) *The Mesenteries.*

The disc in *Cerianthus* being funnel-shaped, a section made transversely through the column wall in its uppermost part will cut the disc tangentially (though slightly obliquely to its thickness) and the marginal angles of the mesenteries obliquely; that is to say, the section of the mesenteries shows their actual thickness, but it is at an angle to both their length and breadth.

In such sections the mesenteries present a very different structure from what is found lower down.

The endoderm in such a section (Fig. 8) resembles very closely in structure that of the column wall, but lower down, in sections which pass through the column wall and the stomatodæum, it is much lower, very granular, and without any trace of cell outlines. In the gonophoric region (Fig. 9) it again becomes high, higher even than in the uppermost region. The protoplasm of the cells is crowded towards their free extremities, which take the carmine stain, and in this region the nuclei are most abundant; towards the mesoglœa, however, the cells form a network (Fig. 10), the meshes of which are mainly occupied by a substance which does not stain. Slight traces of a granular substance are also present, and in some regions there are large numbers of apparently homogeneous spherical bodies (Fig. 10), which do stain somewhat deeply, and which vary considerably in size. It is possible that they may be nuclei, but I am rather inclined to think from their homogeneity and varying size that they are food particles. They occur also in the endoderm of other regions.

It is possible that the network is formed by branching and anastomosing processes of mesoglœa, but such an origin for it could not be made out. If it should be of this nature, it would be in accord to a certain extent with what Danielssen has described in his *C. borealis*. Delicate lamellæ having a wavy outline project from the mesoglœa of the mesenteries into the epithelium: upon their surface are arranged both longitudinal and transverse muscle fibres. No such arrangement occurs in *C. Americanus*, nor apparently in *C. membranaceus* and *solitarius*, but, as stated, the network, if mesoglœal, might be regarded as representing it. The granular substance which lies along the fibres composing the network no doubt corresponds to the muscle fibres described by Danielssen, these, like the pinnate lamellæ, being "äusserst dünne." Maceration preparations of *C. Americanus* failed to show the presence of muscle fibres in the meshes of the network. In the endoderm of the mesenteries, as elsewhere, no Zoöxanthellæ are present.

In the sections which pass through the disc and column wall, the endodermal musculature of the mesenteries is very clearly seen (Fig. 8). The muscle fibres form a single flat layer on



both surfaces of the mesogloea, and in the sections are cut more or less obliquely, some being cut almost transversely, and others more longitudinally. From the way they run, however, it is clear that they are really transverse, and their apparent oblique, or even longitudinal direction, is due to the manner in which the mesentery is prolonged up into the angle formed by the column wall and the funnel-shaped disc. Lower down they are not so apparent, and in transverse sections of a mesentery in the gonophoric region they cannot be made out with certainty, although maceration preparations show their presence. This arrangement of the muscles agrees with what the Hertwigs have described for *C. membranaceus*.

The mesogloea is differently developed in different regions. It is thinnest in the stomatodæal region, and somewhat thicker in the gonophoric region, being in both these parts almost homogeneous, and without any cells in its substance. In the uppermost angle of the mesenteries it is much thicker than elsewhere (Fig. 8), and contains cavities, reminding one of the cavities found in the mesenteries of the Zoantheæ, except that the contents are not cellular as in that group, but consist of a granular substance which does not stain at all with borax carmine.

As stated above, all my specimens were female. The ova are large, and are imbedded in the mesogloea of the mesenteries, as is well shown in the preparation figured (Fig. 9), where the mesogloéal investment has separated from the ovum at one point. The nucleus is large, and is always eccentric, usually projecting very noticeably beyond the general surface of the ovum, which is packed with densely staining yolk granules. One large nucleolus is always present, but the rest of the nuclear substance in all my preparations is apparently broken down, the nucleus appearing as an irregularly shaped space with well-marked walls, containing the large nucleolus and a few granules.

The histological details of the mesenterial filaments I hope to describe fully in a future paper.

I have not been able to find any mesenterial stomata in *C. Americanus*.

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## EXPLANATION OF PLATES VI. AND VII.

## PLATE VI.

FIGS. 1 and 2. *Cerianthus Americanus*, Ag.—Fig. 1, natural size; Fig. 2, reduced one-third.

## PLATE VII.

FIG. 1. View of specimen laid open by a longitudinal incision passing near the mid-dorsal line. *si* = siphonoglyphe, *ac* = acontia, *st* = stomatodæum, 3 = mesentery of third grade.

FIG. 2. Semi-diagrammatic, showing the relations of the mesenteries of the different grades. 3 = mesentery of third grade, 4 = mesentery of fourth grade.

FIG. 3. Section through ventral portion of column, just above the lower end of the stomatodæum. *D* = ventral directive mesenteries, 1 and 1' = mesenteries of the first grade, 2 = mesentery of the second grade, 3 and 3' = mesenteries of the third grade, 4, 4', 4'', and 4''' = mesenteries of the fourth grade.

FIG. 4. Section through ventral portion of column wall, about 2 mm. below Fig. 3.

FIG. 5. Section through ventral portion of column wall, about 1.5 mm. below Fig. 4.

FIG. 6. Portion of tangential section of disc. *cm* = circular muscles, *mg* = mesogloea, *lm* = longitudinal muscles, *n* = nerve layer, *pm* = process of mesogloea. (Zeiss obj. J, oc. 2.)

FIG. 7. Transverse section of stomatodæum (Zeiss obj. J, oc. 2).

FIG. 8. Section of mesentery in the angle formed by the meeting of the disc and column wall (Zeiss obj. J, oc. 2).

FIG. 9. Transverse section of mesentery in the gonophoric region, with ovum (Zeiss obj. D, oc. 2).

FIG. 10. Portion of Fig. 9, more highly magnified to show the network. *mg* = mesogloea, *f* = food particle (?). (Zeiss obj. J, oc. 2.)



