

XXIII. — *NUDICLAVA MONOCANTHI*, THE
TYPE OF A NEW GENUS OF HYDROIDS
PARASITIC ON FISH.

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While examining some tow net material collected in 1897 from the Andaman Sea by the naturalist of the R.I.M. Survey Ship "Investigator," my attention was arrested by a small fish, to the side of which was attached a curious lobulated growth. The fish (plate xvi, fig. 1), which measured only 18 mm. in length, was one of a number of specimens belonging to the species *Monocanthus tomentosus*, recently recorded by Johnstone from Indian seas for the first time (1). A portion of this growth was detached, stained and mounted. On examining the specimen microscopically, the following details were noticed (fig. 2) :—

- (1) The most conspicuous feature was the presence of a large number of elongated club-shaped bodies, much resembling the contracted hydranths of *Clava* or *Coryne*, but entirely devoid of tentacles.
- (2) At the base of these bodies, usually one to each, were a number of small globular objects. These, from the type of their structure and contents, were at once recognised to be closed gonophores or sporosacs.
- (3) These structures arise from a basal plate, which is attached to the skin of the fish. This plate consists of a labyrinthine system of irregular spaces and tubules.

As a result of this preliminary examination, the growth was recognised to be most probably a hydroid colony of new type. Other small portions were detached and mounted, others again were cut into serial sections. Although the amount of material was very limited, and its state of preservation none of the best, yet it was found possible to elucidate the principal features of its structure. The material being so limited in quantity, in order to obtain sections of the male gonophore, it was found necessary to carry out the following procedure : A small portion of the growth was lightly stained and mounted *in toto* ; as this showed some good examples of the male gonophore, and no further material was available, the slide on which the specimen was mounted was placed upright in xylol. After a few hours the cover-glass became detached by its own weight, leaving the specimen adhering to the slide : the specimen itself soon after fell away from the slide. After

soaking it freely in fresh xylol for about six hours it was imbedded in paraffin and cut into sections. Sections so obtained seemed quite as good as others, treated in the usual way. Owing to the heat of Calcutta, high-melting paraffin had to be employed in making these sections. Portions of the colony were placed in paraffin of 55° C. melting point for half an hour ; this interval of time was found to be long enough for complete penetration.

The Hydranth—

Each hydranth is a club-shaped body measuring about .75 mm. in length in the contracted state. In internal structure it differs remarkably from other hydroid colonies, but it seems difficult to arrive at any other conclusion than that the form in question is a hydranth and part of a hydroid colony. It resembles the genus *Protohydra* (2) and the parasitic *Hydrichthys mirus* (3) in that it is entirely devoid of tentacles or any trace thereof ; but apart from this, the internal structure, as seen in sections, shows some most unusual features.

The ectoderm is relatively thin and, owing perhaps to want of proper fixation, does not show much structure. The appearance it presents in section is that of a somewhat irregular layer of protoplasm, containing a single series of nuclei (plate xvii, figs. 1 and 4). This layer is easily distinguished from the mass of endoderm cells, which show peculiar structural features. Careful search failed to demonstrate the presence of nematocysts in this ectoderm.

The endoderm is, in these contracted specimens, very much lobulated, so that the central cavity, which can be clearly made out both in optical and actual section, usually takes a sinuous course. The opening of the central cavity at the distal end of the hydranth can be clearly seen, and there is usually a slight external depression at its site. The endoderm cells, which make up the bulk of the hydranth, are of a peculiar structure : they are ovoid or spherical and have well-defined outlines. After staining with hæmatoxylin a nucleus cannot be demonstrated in them, but each cell contains a large number of small spherical granules, arranged round the periphery with great regularity. These granules take the stain exactly like nuclei, and they are probably composed of chromatin and perform the functions of nuclei. These large cells do not actually line the central cavity, but are separated therefrom by a pavement epithelium—a single delicate layer of flat cells in which nuclei are easily demonstrable. This epithelium not only lines the central cavity but is continued outwards through the mass of the spherical cells and joins the peripheral ectoderm. Where it lines the central cavity, this epithelium is composed of one layer of cells, but where it passes out to join the ectoderm it is, like a mesentery, composed of two layers. This is clearly seen on examining favourable sections under a $\frac{1}{12}$ -inch objective (fig. 4). As shown in figs. 1 to 3, the endoderm of the hydranth is divided by this epithelium into two separate parts,

The bilateral symmetry thus established is further emphasized by the presence of what appears to be a strand of muscle-fibres which occupies the central axis of each half. These fibrous strands are clearly seen in both longitudinal and transverse sections. They commence below, in the very base of the hydranth, which is largely made up of them, and pass upwards through the spherical cells of the endoderm nearly to its apex. Throughout their length they distribute fibres among the peripheral endoderm cells in the manner shown in figs. 3 and 4. Under a $\frac{1}{12}$ -inch objective longitudinal sections of these structures show a fibrillated appearance which is well defined, and the individual fibres can be seen distributed between the spherical endoderm cells. These fibrils do not show nuclei. There can be little doubt that they have a muscular function.

The simple arrangement shown in the transverse section (fig. 1) in which the hydranth is divided into two separate halves, each of which contains a muscle-strand, was found in the proximal part of every individual examined in section, but in their distal parts the number of these "mesenteries" is increased. Some sections show three, others four or more. Figure 2 is of a somewhat oblique section showing four such mesenteries. At the base of the hydranth the specialised endoderm ceases abruptly in a sharply-defined line, which can be readily seen in optical section (pl. xvi, fig. 4). The central cavity is continued below into a tube of small dimensions composed of somewhat delicate cells. This tube, which usually has the form of a dice-box, its calibre being smallest in the middle of its length (fig. 4), opens into a long straight tube with thick walls composed of regular columnar cells. The other end of this straight tube opens into one of the irregular endodermal spaces of the cœnosarc.

The Basal Plate or Cœnosarc—

The basal plate is so closely attached to the skin of the fish that on removing a portion of it an outer layer of the fish's skin is often detached with it. In structure the plate is not the same throughout its whole extent. As a whole it is very like the attachment plate or cœnosarc of *Hydractinea* (4), but without the strong chitinous element so characteristic of that genus. Throughout most of its extent it is composed of two layers of ectoderm widely separated by irregular tubules and spaces with endodermal walls which communicate with one another freely and form a complex labyrinthine structure. The outer layer of ectoderm does not everywhere pass over this endodermal labyrinth in a smooth and unbroken fashion, but dips down between the layers of endoderm in places, and occasionally the cuticle is carried along with the ectoderm into the same situation. Although most of the cœnosarc has this complex structure, parts of it show the more primitive type consisting of an open meshwork of irregular trabeculæ, each of which is a tube composed of two layers—ectoderm and endoderm with an external cuticle.

Considerable difficulty was experienced in interpreting the structure of the basal plate, for although the histological detail was fairly well preserved, there was little or no difference in the appearance of the endodermal and ectodermal layers; both varied in thickness, to a great extent, in different parts. Figure 5 (pl. xvii), which was drawn with the camera lucida from a favourable section, shows the principal features in the structure of the cœnosarc. It will be noticed that the cuticle is relatively very thin, in some parts of the colony it is hardly recognisable.

Gonophores—

The colony shows both male and female gonophores. With hardly an exception, one gonophore is situated at the base of each hydranth. Careful examination shows, however, that the endodermal layers of the gonophores are not directly connected with the endodermal canal at the base of the hydranth, but spring from the irregular endodermal spaces of the neighbouring cœnosarc. This is shown in pl. xvi, fig. 4. The gonophores are of the closed type known as sporosacs. They show no traces of tentacles, radial canals or ectodermal invagination.

The female gonophore was only studied in optical section, but as its structure was much simpler than that of the male ones, a comprehensible plan of the structure can be made out after study by this means alone. Figure 5 shows the principal features of the structure of these organs. They are spherical bodies, measuring .17 mm. in diameter, and are each attached to the cœnosarc near the base of a hydranth. Their endodermal contents, which arise from the cœnosarc and not from the special endodermal canal of the neighbouring hydranth, split into two layers on entering the gonophore. The outer of these layers forms an uninterrupted sheet, closely applied to the ectoderm; the inner forms a spadix of characteristic shape. This spadix, the walls of which are, by invagination, composed of a double layer of endoderm, forms a globular body separated by a considerable space from the wall of the sporosac. There is an opening in one side of the spadix due to the invagination, so that in longitudinal sections it forms a characteristic C-shaped figure. Developing ova can be seen between the layers of the spadix: in at least two cases ova of larger size than the others can be clearly seen in the canal of the neck of the spadix. Perhaps this is a preliminary position before the ovum passes into the central cup-like hollow. When the surface of a large ovum is examined under a high power of the microscope, it shows a delicate hexagonal pattern, caused by the approximated ends of the long columnar cells of the spadix pressing on it. Ova more advanced than the one shown in fig. 5 were not found.

The male Gonophores—

While the part of the colony seen in fig. 3 showed female gonophores chiefly, other parts showed the male form. This is of about the same size as the female gonophore, but is shaped like a

pointed fir cone; it is more opaque than the female one, and consequently can only be properly studied in serial sections. Figures 6 to 8 show three of a series of such sections. The endodermal contents are more complex than those of the female form and do not seem quite the same in every case, but like that form there is a spadix which shows a more or less C-shaped figure in longitudinal section. No male gonophore was met with in a ripe condition; they mostly contained spermatoblasts.

Theoretical considerations—

In spite of the anomalous structure of the hydranth, this genus should, I think, find a place among the gymnoblastic hydroids, and a comparison with two hydroid genera, *Hydrichthys mirus* and *Stylactis minoi*, which are also parasitic on fish, leads to some interesting conclusions.

Stylactis minoi was described by Alcock in 1892 (5) and has been since found several times in Indian seas, always attached to the skin of the small rock perch *Minous inermis*. It is a typical hydroid in every way.

The peculiar form *Hydrichthys mirus* discovered in 1887 by Fewkes growing to the carangoid fish *Seriola zonata* at Newport, U.S.A., cannot be called a typical hydroid. It resembles the present genus very closely in some respects, in others it differs widely from it. *Hydrichthys* is described as follows by its discoverer:—

“The base of attachment to the fish is a flat, thin plate with ramifying tubes, by means of which the colony is fastened to the fish, and upon it separate clusters of sexual bodies (gonosomes) and filiform structures (hydranths?) are united together.”

The author compares this basal plate to that of *Hydractinea*, without the chitinous projections, and it is obviously very like that of the genus described here. *Hydrichthys*, however, has long arborescent gonosomes to which medusæ in all stages of development are attached. The fish, with its parasite, was kept alive in an aquarium and “thousands of these medusæ were raised.” The medusæ swim freely, and each has four tentacles. The generative organs are therefore totally different from those of the new genus, in which these organs are represented by a few closed sporosacs, sessile on the basal plate. Turning now to the hydranth, the comparison between the two forms is of such interest that it seems well to quote Fewkes’s account *in extenso*, especially as the nature of the hydranth of *Hydrichthys* is regarded somewhat doubtfully by that author:—

“In addition to the botryoidal clusters of gonosomes there also arise from the basal plate by which the colony is fastened to the fish, long, flask-shaped bodies, recalling in their external form the tasters of the Siphonophores. These bodies, like the gonosomes, arise from the upper walls of the basal plate of tubes attached to the body of the fish. Like the gonosomes they are numerous in the hydroid colony. The filiform bodies are elongated flask-shaped

structures, of about uniform size throughout, arising from different points of attachment at the base from the gonosomes. They are, like the gonosomes, destitute of appendages, but they probably have an opening at the free extremity. The walls of the filiform bodies are composed of an outer thin and an inner thickened layer. There is a cavity within. The walls are dotted with pigment spots, which are especially numerous around the free extremity. In one of these filiform bodies there is a spherical mass, which resembles half-digested food. It is doubtful whether this mass is food. The free end of the filiform bodies is sometimes trumpet-shaped, but ordinarily rounded, the opening being concealed by the contraction of the lips. The bodies of the filiform structures move backwards and forwards on their attachments, and are sometimes spirally coiled in a single turn. They recall in general appearance the spiral zooids of *Hydractinia* and the tasters of *Siphonophora*, but, unlike either of these structures, have an orifice at their free end. They are thought to have close likenesses to the 'central polyp' of *Velella*."

The difficulty of interpreting the nature of the flask-shaped bodies of *Hydrichthys*, becomes lessened in the light of the new genus *Nudiclava*; and the present writer is strongly of the opinion that the flask-shaped bodies of the former and the club-shaped bodies of the latter are both hydranths devoid of tentacles. Furthermore, that it is by means of these hydranths that the colonies obtain their food. In his description of *Hydrichthys*, the author expresses the following view of its mode of nutrition, a view expressed, necessarily at that time, somewhat doubtfully:—

"The absence of tentacles, or organs the function of which is the capture of food, would seem to deprive *Hydrichthys* of those means of capturing and drawing food to the mouth which are almost universal among fixed hydroids. Possibly in its parasitic life the hydroid obtains its sustenance from the fish on the sides of which it lives."

The close resemblances in the structure of the two forms now under comparison make it most probable that, whatever the mode of nutrition, it is of a similar nature in both cases. It seems from the following observations, that the genus *Nudiclava* does not obtain sustenance from the fish to which it is attached. It was previously mentioned that on removing a portion of the colony, an outer layer of the fish's skin was removed with it. Part of this was separated from the hydroid and examined microscopically; it was found to be quite intact; there was no sign of perforation by any radical organs. In the absence of any such special organs, it does not seem likely that the fish would be so accommodating as to diffuse nutriment, uncompelled, through its own skin into the tissues of the hydroid.

How, then, do these colonies obtain their food? The assumption is made here, that *Hydrichthys* and *Nudiclava* obtain nutriment in the same way. The absence of tentacles in these

parasitic hydroids deprives them of the power of catching their prey in the manner common to all other hydroids. Their mode of life is identical in both cases. Both were found adhering like a tuft to the skin of small fishes which were caught near the surface of the sea. Judging from Fewkes's well-executed illustration of the fish with its parasite, the superficial appearance of both would be very similar.

From the relatively large size of the hydranths of *Nudiclava* it is difficult to suppose that they are degenerate bodies of little functional value to the colony. The peculiar features of the endoderm of *Nudiclava*, the well-developed muscle strands, and the special pavement epithelium lining the central cavity, suggest that the methods by which these hydranths obtain food is as follows:—

It is supposed that in their natural state, they assume, by expansion of the mouth, the shape of a wide-spreading funnel (pl. xvi, fig. 2). As the host speeds through the surface waters, the small members of the plankton, such as copepod nauplii, etc., must come within the grasp of these funnel-shaped mouths. The well-developed muscles, situated in the endoderm, which are peculiar to the genus, point to a special power of rapid and forceable retraction, an act which would be very necessary when anything comes within the grasp of the funnel. The special pavement epithelium is perhaps developed as a protection and covering to the endodermal cells which would otherwise be exposed to the water, when the mouth is gaping widely.

We can illustrate the possible efficiency of this mode of food-capture thus: It is not unlikely that the hydranth, which measures .75 mm. in length when completely contracted, could expand its mouth into a circle .5 mm. in diameter. The hydranths in the colony, which number about 50, would together present an area of about 10 square mm., which is at least as great as that of the gaping mouth of the fish host itself.

In the case of *Hydrichthys*, the hydranths, from their size, must also be considered important members in the colony. And there is some evidence in Fewkes's account that it obtains its food in this manner. Thus we read above, that the free or oral ends of the filiform bodies of this genus are sometimes trumpet-shaped, and one of these bodies contained a mass resembling food. *Hydrichthys* was kept alive in an aquarium for some time, but it would have been impracticable to examine the colony without catching the fish, a procedure which would cause at least partial contraction of the parasite: consequently it would be very difficult to observe the state of the oral apertures in their expanded condition, and the fact that some few were observed to be trumpet-shaped, makes it most likely that all would possess, in their expanded condition, a wide funnel-shaped mouth.

Let us pass now to a consideration of the third genus of hydroids which is found on fish. The case of *Stylactis minoi* on the fish *Minous inermis* is quite different from that of the others. The hydranth has a well-developed circle of long

tentacles and a hypostome, and clearly catches its food like other hydroids. The hydrophyton is in the form of a creeping stolon which may almost entirely cover the fish. These differences point to a different mode of life from the other parasitic forms. An explanation of these differences seems to be found in the different nature of the fish. *Minous inermis* has been found many times in the Bay of Bengal in company with such teleostean genera as *Uranoscopus*, *Platycephalus*, *Lophius*, *Pterois*, which are essentially bottom fish: whereas the fish hosts of the other two genera under discussion were both captured in the tow net. The extent to which the Minous is coated with the hydroid growth, caused its discoverer to hold the opinion that the hydroid must benefit the fish by concealing it to some extent. On this assumption, we can imagine the Minous remaining still for considerable periods of time during which the *Stylactis* could pursue its vocation of catching prey, in the fashion of other hydroids which are attached to rocks.

We see, therefore, that whereas the modes of life of *Hydrichthys* and *Nudiclava* seem essentially similar, they both differ considerably in this respect from *Stylactis minoi*: although all three forms appear to be hydroids parasitic on small teleostean fish.

Affinities—

Comparison with other more normal hydroid types has not led to any definite conclusions as to which particular type this new genus may have been derived from. It undoubtedly resembles the abnormal genus *Hydrichthys* in some ways, in the structure of the basal plate and the absence of tentacles, and in its mode of life generally. Here the similarity stops, and the two genera are separated by the great differences in the gonophores, and in the internal structure of the hydranth, which in *Hydrichthys* is quite of the usual hydroid type. The conclusion arrived at is that the similarities have been acquired in adaptation to the circumstances of the peculiar life which are alike in both cases; while the differences are due to the fact that the ancestors of both forms which took to this parasitic life were essentially different, especially as regards the nature of the gonophores. The genus *Nudiclava* has, however become more specialised than *Hydrichthys*, as the result of this mode of life.

Stylactis minoi presents a third example of a hydroid, which has scarcely been modified at all by its association with a fish. Being attached to the skin of a sluggish rock-haunting species, it is capable of obtaining food in the same manner as most other hydroids. Consequently its structure has not been modified.

Definition of the genus—

The hydrophyton is a compact plate-like structure composed of an irregular labyrinthine cœnosarc with very poorly developed perisarc.

The hydranths are claviform when contracted, and totally devoid of tentacles ; their cavities are lined by a special layer of pavement epithelium, and they contain well-developed muscle-fibres among the endoderm.

The gonophores are closed sporosacs, without radial canals, tentacles, or ectodermal invaginations.

The species is parasitic on the skin of a surface-swimming fish.

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