ON TWO SPECIES OF HYDRACTINIA LIVING IN SYMBIOSIS WITH A HERMIT CRAB

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TWENTY-THREE FIGURES

Two species of Hydractinia have been known among us for many years, which, though very different in external appearance, have the same habit of living always in symbiosis with a hermit crab, Eupagurus constans Stimpson, and of forming "shells" of their own entirely composed of a chitinous framework, so that in most specimens there is apparently no basis of gastropod shell, as is the case in most other known species of Hydractinia. The skeleton of one of the species is totally devoid of spines and its substance is very thin and papery, while that of the other is richly armed with large spines, which are conical when small but irregular in shape and branching when large. The latter species has recently been described by Stechow from the Doflein collection and identified by him with the Hydractinia sodalis of Stimpson[2] who in his description of Eupagurus constans, men-

[1] After writing the above I received a valuable letter from Dr. Stechow, to whom I had written concerning this hydroid, giving some further information in regard to its literature. According to him the hydroid and the hermit-crab are treated on pp. 218–220 of the paper entitled, "Report on the Crustacea collected by the North Pacific Exploring Expedition, 1853–1856," by W. Stimpson, recently published in vol. 49 of the Smithsonian Miscellaneous Collection, 1907, the discovery of the paper being due to Miss Rathbun. According to Dr. Stechow the description in the text and the good figure reproduced in pl. 24 leave no doubt that Stimpson had before him the Hydractinia with large spines. For supplying me with this valuable information my best thanks are due to Dr. Stechow.

[2] Stechow: '07, p. 192; *same*: '09, p. 21.

tioned a species of Hydractinia living in symbiosis with it.[3] Since Stimpson's paper is not accessible to me I have no basis on which to form my own opinion, but if, as Stechow says, Stimpson devoted only two lines to the characterization of his Hydractinia sodalis, it is very doubtful whether it was precise enough to enable one to decide which of the two species mentioned at the beginning of this paper was before him. Since, however, it is not desirable to introduce unnecessary confusions into zoölogical nomenclature, which threatens to become formidable, I prefer to accept Stechow's identification. The other species is, in my opinion, new, and I propose the name of Hydractinia spiralis for it. These two species are the subjects of this paper, and it is but fitting that I should dedicate it to the memory of the lamented Dr. Brooks, since it was from him that I received my first advanced instruction in hydroid morphology.

1. HYDRACTINIA SODALIS STIMPSON

The skeletons of this species are rather common and sold in a dry state at Enoshima and other places, where they are known as "Igaguri-gai," or "chestnut burr shell." I have been told that when Prof. E. S. Morse was here he was interested in these "shells," and was aware that there was always a gastropod shell in the apex. Aside from Stimpson, whose reference to this species has been above mentioned, Inaba is the only author who to my knowledge has described the animal. Owing, however, to the difficult conditions under which he had to work, he regarded it doubtfully as a species of Podocoryne. His description is as follows:[4]

36. Podocoryne sp.? (Figs. 103, 104, 105.)

Trophosome.—The chitin of the hydrorhiza is very strong and bears at places chitinous spines with branches. Hydranths large, growing out in numbers from a hydrorhizal substratum; there are two forms of hydranths, one large, the larger ones 5 mm. high and 1 mm. across, with about 30 filiform tentacles arranged in a single row

[3] Stimpson: '58, p. 225. [4] Inaba: '92, p. 96.

near the mouth; the other as long as the former but very slender, with over 60 filiform tentacles arranged in several rows around the mouth.

Gonosome—Unknown.

Locality—Between Misaki and Jogashima;[5] covering shells containing hermit crabs. It was collected by Mr. I. Shishido in April, 1889; but there are no reproductive bodies. It cannot therefore, be decided whether it belongs to Podocoryne or Hydractinia; but there are two forms of hydranths, and the species has been referred provisionally to Podocoryne on the assumption that the larger polyps are nutritive and the smaller ones give rise to the reproductive bodies. The two forms of hydranths are comparatively large.

The figures accompanying the description leave no doubt that it refers to the species before us, although the entire form of the colony is not reproduced. It is, however, but natural that Inaba's description has not been recognized by western students of hydroids, since it was published in the Japanese language. Therefore Stechow's recent descriptions are practically the first adequate ones accessible to general students. They, but especially the full description of '09, are, as a whole, sufficiently accurate and generally accessible, so that I shall confine myself to one or two remarks and the addition of a few details not mentioned in his descriptions.

First as to its occurrence. It appears to be common in several parts of the Bay of Tokyo and of Sagami, and according to Stimpson it occurs as far north as Hakodate. Stechow,[6] gives its bathymetrical range as 7-180 m. (4–100 fathoms), and for six of the specimens collected by Haberer it is stated with a query that they were found on the beach—"Strand?" The specimens collected by myself are all from the Bay of Tokyo, off the small village of Kanazawa, where they can be easily obtained by collecting with the hand trawls commonly used by the fishermen of this part. They are from shallow waters, about 16 meters or so, and I have also picked up living specimens on the beach, where they were evidently washed up with the hermit crab still alive and occupying the skeletal shell.

[5] A small island off the town of Misaki. [6] *Loc. cit.*: '09, p. 24.

As to the relation between the gastropod shell and the chitinous skeleton of the hydroid, Stechow thinks that the former is dissolved by the latter. In his full paper he says,[7] "Bei unserer Form breitet sich die druchweg chitinöse, nicht kalkige, hell—bis dunkelbraune Skelettschicht krustenförmig über die Schneckenschale aus, die sie offenbar sehr schnell auflöst. Ich fand nirgends, nicht einmal bei jungen Kolonien, auch nur Spuren von Kalk, weder in den Stacheln noch in der eigentlichen Schale." This is, as already suggested, a mistake. It is true that in most cases the larger part of the "shell" is composed entirely of the chitinous skeleton of the hydroid, but if one breaks open its apex a small gastropod shell, Columbella[8] or other genera is invariably found retaining its natural surface intact. It may therefore be inferred that the hydroid colony starts on the surface of a gastropod shell probably already inhabited by Eupagurus constans, and that after covering up the whole surface of the shell it grows out beyond its mouth. The hermit crab also growing hand in hand with the hydroid colony, and having no need of migrating into a new and larger shell to accomodate its growing body, there is thus established a permanent symbiosis between the two animals. That this is the case is proved by specimens occasionally met with, in which the hydroid apparently started on a comparatively large shell and has not succeeded in coveringup its whole surface but has left a part still more or less exposed. Such a one is shown in fig. 2, in which the shell is a species of Buccinidæ, and in which the exposed part is seen to have many small circular holes. That these are, however, not due to the action of the hydroids is very clear from the fact that they are most numerous where the hydroid colony is still very thin. In view of the destructive action of Hydractinia echinata (in this case in symbiosis with a Pagurus) on the shell which it covers, as was observed by Carter,[9] it is nevertheless not impossible that our hydroid may have a certain action on the substance of the shell, although such is not apparent in

[7] *Ibid*: '09, p. 22.

[8] For the determination of the shells mentioned in this paper I am indebted to my friend, Prof. T. Iwakawa of the Imperial Household Museum.

[9] Carter: '73, p. 2.

any of the specimens examined by me. There is no doubt that the chitinous spines of the hydroid have no relation to the spines of the gastropod shell, since the latter are usually absent. Again, if, as Stechow supposes, the entire colony is developed on the surface of a gastropod shell which is then dissolved away, the skeleton of the hydroid ought to form an exact cast of the shell; but that the former may depart widely from any form of gastropod shell may be seen on examining a few specimens of the hydroid. This point is also shown very well in the photographic reproductions of Stechow,[10] in which several degrees of spiral winding are manifest.

The outer surface of the hydroid, which is chestnut brown in color, is sculptured by numerous fine, irregular, elongated, anastomosing ridges and furrows, which are especially apparent on the surface of the spines, but are completely hidden from view where the surface is covered by a thick layer of coenosarc. Their appearance and arrangement vary so in different specimens that a general description can hardly be given, the anastomoses in particular being so numerous in some cases that a fine reticulated appearance is brought about. The inner surface of the hydroid shell is perfectly smooth, being lined by a very thin subcontinuous chitinous lamella which would come in direct contact with the body of the hermit crab. The thickness of the chitinous shell may amount to more than 1 mm., the spines being left out of account. In the body of the shell the chitin is comparatively soft, and there is no difficulty in preparing thin free-hand sections with ordinary razors. In such a section carried across the whole thickness of the shell, it is seen to consist of a dense spongework, exactly as in Solanderia (Dendrocoryne, Ceratella, Dehitella, Spongocladium, Chitina) (fig. 3). Toward the outer surface the meshes are larger, the trabeculæ are stouter and darker in color, and are seen to form projections and indentations corresponding to the ridges and furrows on the surface. The meshes become smaller and rounder at a short distance from the outer surface and remain nearly constant inwards. The inner surface

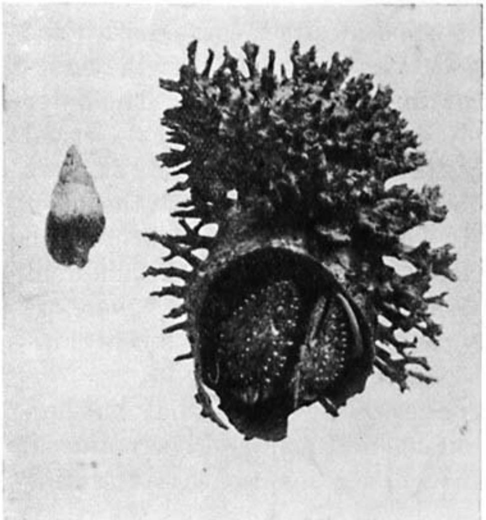
[10] *Loc. cit.*: '09 pl. 1.

is lined by a subcontinuous thin layer of chitin which stains deeply with haematoxylin. In favorable places the trabeculæ are seen to consist of superposed lamellæ around an axial substance.

The spines, which form a characteristic feature of this species, are very numerous and of various sizes and shapes from simple, short, rounded conical projections to large, stout branching, antler, like spines nearly 2 cm. in height and 1 cm. or more between the tips of the outermost branches. The inner structure is essentially the same as in the body of the chitinous shell, with the difference that in the spines the meshes are largely elongated and are arranged with their long axes parallel to the length of the spines, so that in a longitudinal section, such as is reproduced in fig. 4, it is common to see long tubular cavities, especially in the axial parts. The formation of the chitinous trabeculæ from concentric layers around an axial substance is especially clear in sections of the spines, the axial substance being sometimes very conspicuous by its opacity. Stechow mentions in cross-sections of the spines "zwei deutlich geschlossene Röhre mit etwas dickerer Wandung," which he considers as possibly the first formed part of the spine,[11] but according to my observations they are constant neither in number nor occurrence.

As to the mutual relation of the chitinous skeleton and the soft parts, it may be said that it is in general similar to what obtains in Solanderia;[12] that is to say, each mesh is filled with ectoderm and endoderm, the latter forming, in sections, a well stained core with a small central lumen, surrounded by tall, somewhat vacuolated cells of the ectoderm which is in direct contact with the surrounding chitin. Where two meshes communicate with each other the ectoderm is seen to be directly continuous. Colcutt[13] says that in Hydractinia echinata the meshes of the deeper part of a colony are filled with degenerating coenosarcal masses; but in the present species the deepest meshes are filled with coenosarc which is in no way different from that of the upper part. It has already been mentioned that the meshes of the deepest layer are closed by a thin, deeply staining chitinous membrane,

[11] *Ibid*: '09, p. 22. [12] Goto: '97 [13] Colcutt: '98, p. 85.



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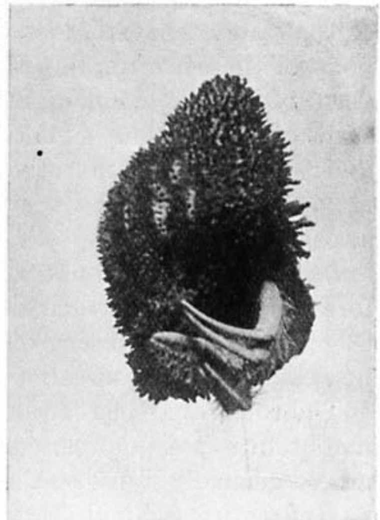

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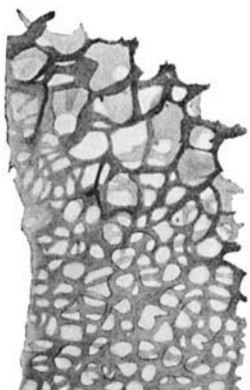

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HYDRACTINIA SODALIS

Fig. 1 A colony without polyps, with the enclosed gastropod shell (Columbella sp.) on one side. Nat. size.

Fig. 2 A colony without polyps on a gastropod shell of one of the Buccinidae. Nat. size.

Fig. 3 Transverse section of the chitinous skeleton at right angles to the mouth of the shell. 60 diam. The upper side is the outer.

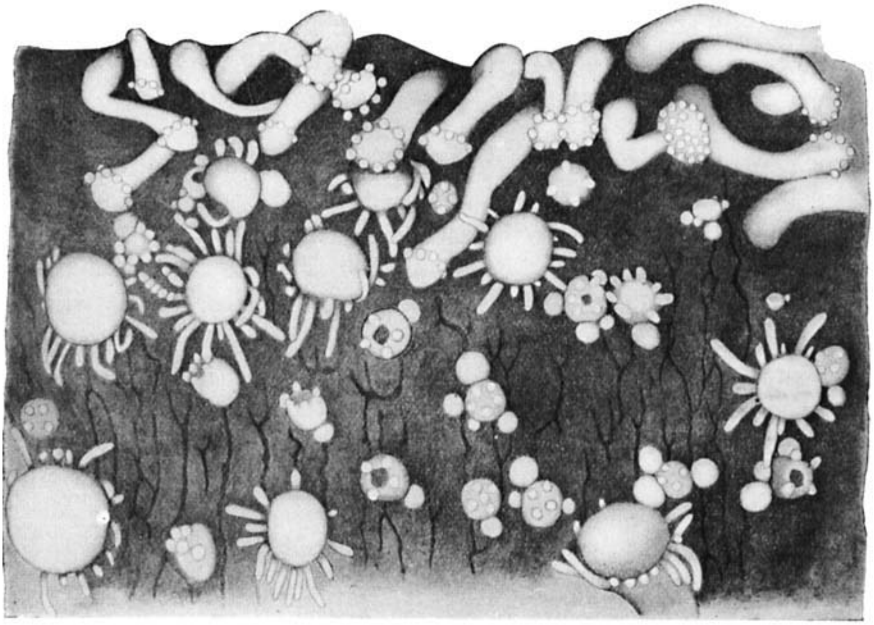
Fig. 4 Longitudinal section of spine, axial part. 60 diam.

so that the coenosarc does not come in direct contact with the body of the hermit crab. It goes without saying that the endoderm of the whole colony is continuous throughout. The outer surface of the colony is entirely covered over by an ectodermal layer, which is comparatively thick in the superficial furrows already mentioned and very thin on the ridges, so that the latter appear as if directly exposed. In this superficial layer of ectoderm are seen numerous endodermal tubes, from which the different forms of polyps take their rise. The entire colony may therefore be regarded as consisting of two sets of sponge-works, the chitinous and the coenosarcal.

The colonies are, so far as I have observed, unisexual; but hermaphrodite gonophores, containing both ova and spermatozoa, are occasionally found. A similar case is mentioned by Bunting in Hydractinia echinata.[14]

The individuals of a colony are composed of the following forms: (*a*) gasterozoöids, (*b*) dactylozoöids, (*c*) blastostyles, (figs. 5 and 6). The gasterozoöids again occur in three apparently different forms. Two of these were noticed by Inaba and regarded by him as gasterozoöids and blastostylesres, pectively; but a comparison of a large number of these polyps has convinced me that they are simply different conditions of one and the same form. By far the larger number of polyps are long and slender, the tentacles very numerous and arranged in several whorls, the hypostome very prominent, hemi-ellipsoidal in form and with a small mouth in the center (fig. 7). In sections the endoderm of the tentacles is seen to be separated from that of the gastric cavity by septa of supporting lamella. These gasterozoöids are very numerous and are found all over the colony, on the general surface as well as on the spines (fig. 5). In most of the specimens they are especially abundant on the large spines on the lower surface of the colony i.e., that side on which the colony would slide along when the hermit crab moves on. Sometimes they form such thick tufts on the spines that the latter are well nigh hidden from view. The

[14] *Loc. cit.*: '94, pl. 9, fig. 7.



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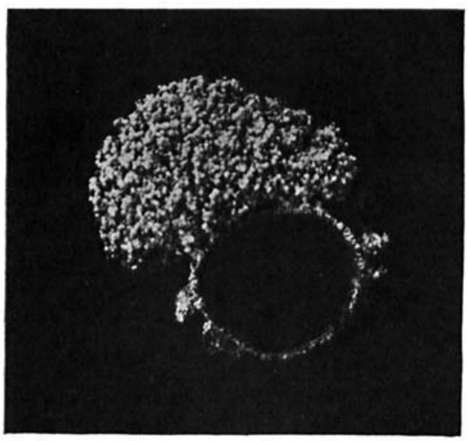

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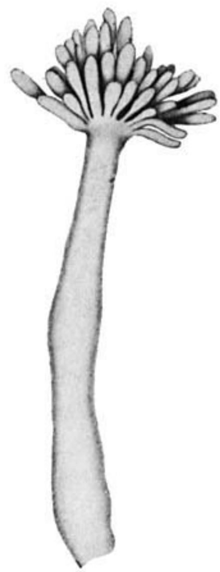

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HYDRACTINIA SODALIS

Fig. 5 A colony with polyps. Nat. size.

Fig. 6 Surface view of a portion of a colony adjoining the mouth of shell; spiral zooids, young nutritive zooids and blastostyles. 30 diam.

Fig. 7 Nutritive polyp. 30 diam.

second form of gasterozoöids is also found anywhere on the colony without any regular arrangement, but generally they are far less numerous than the first form. They are thick and comparatively short, the hypostome is large and prominent, the mouth is widely open, and the tentacles are arranged strictly in a single whorl and usually less contracted than in the first form (fig. 8). At a glance these appear to be essentially different from the first form and were so regarded by Inaba, the different arrangement of the tentacles being especially noticeable; but close observations have shown that they are connected by all degrees of intermediate stages with the first form. In fact the polyps of the second form are those that have gorged themselves with prey. It is true that in none of my sections of these polyps have I been able to recognize the nature of the prey, but the gastric cavity was filled with a half digested material. It is rather hard to understand how the different arrangements of the tentacles pass so smoothly into each other, but when we take into account the great elasticity of the body wall such a feat is not impossible. The third group of gasterozoöids includes young ones without a mouth and with a single whorl of tentacles. These are especially numerous near the mouth of the chitinous shell (fig. 6).

The dactylozoöids are long and slender, and, when numerous, form a thick zone along the mouth of the hydroid shell (fig. 5); their number appears to vary a great deal in the different colonies, only a few being found here and there in some. They are usually situated close to the margin of the chitinous shell but are sometimes found also on the inner surface at a short distance from the mouth. The individual polyps are subject to some variation. Stechow[15] describes them as having a mouth, and with nearly the whole hypostome bearing short tentacles. I find that the form and number of these tentacles are subject to great variation. Thus, in the portion of a colony reproduced in fig. 6, most of the spiral zoöids are seen to be provided with only a single row of tentacles which are so exceedingly short as to appear like so many simple knobs, but one of them has many tentacles which are

[15] *Loc. cit.*: '09, p. 22.

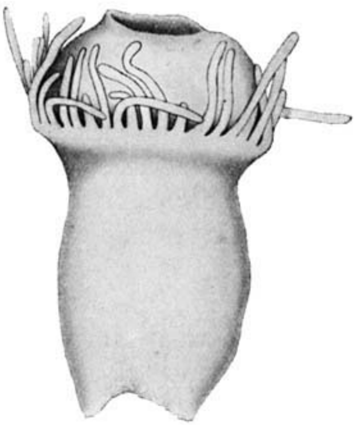
arranged in several rows and cover nearly the entire surface of the hypostome. Now, in some other places and colonies spiral zoöids, of the latter form are much more numerous, and the tentacles are frequently longer. Again, there are sometimes found near these spiral zoöids true gasterozoöids which are much more slender than their fellows and with shorter tentacles, forming in fact a transition to the true spiral zoöids. The latter have the gastric cavity well developed, but in no case have I been able to find the mouth, although the above observations would not justify one in entirely denying its presence, the more so as there are all degrees of transitional forms.

The blastostyles are found in large numbers on many of my specimens, fig. 9, which were all collected in the first part of the month of April, both on the general surface of the chitinous shell and on the spines. They appear, however, to be absent from the apical part of the spines. They are considerably smaller than the other polyps (figs. 6, 9), fusiform in shape, with a small but variable number of short tentacles without any definite arrangement, and with an inconspicuous hypostome destitute of a mouth. They are, as already mentioned, generally unisexual, but occasionally hermaphrodite ones occur. For instance, among 51 blastostyles taken at random from three colonies, viz., 13 from colony *a* (all ♀), 20 from colony b (mostly ♀) and 18 from colony c (all ♂), there was only one hermaphrodite gonophore (from colony *b*). The gonophores appear to arise from a somewhat narrowly defined zone about midway along the length of the blastostyle (fig. 9). The female gonophores are spherical, the male ellipsoidal, but the elongation in the latter is so slight that the difference is noticeable only in sections passing through the long axis of the gonophore. When there are many gonophores on a blastostyle they are arranged roughly in a circle, although some of them may be superposed. In the following will be given an account of the development of the gonophores as made out from a complete series of stages. My results differ from those of previous observers working on Hydractinia echinata.

Female gonophores

I have never been able to find ova outside the blastostyles, but in the neighborhood of very young gonophore buds which are simple outpocketings of the body-wall they are fairly numerous in the endoderm. I have not been able to make out satisfactorily whether they are formed by division of a single endoderm cells or by their bodily transformation, but my observations so far incline me to the latter alternative. On this point Smallwood[16] has come to the same conclusion in H. echinata. Fig. 10 represents a young female gonophore bud, a simple protuberance of the body-wall of the blastostyle, its cavity filled up by endoderm cell which do not show any distinct epithelial arrangement, and containing several ova in the spacious interstitial cavities. Several ova are also found in the endoderm of the blastostyle in the immediate neighborhood of the bud. Generally speaking, the ova in the latter position are younger than those in the bud, although exceptions are not rare, of which one instance is seen in fig. 10. The young ova are very conspicuous in sections by their size, the deeply staining granular protoplasm and large vesicular nucleus containing a nucleolus and a diffuse, faintly staining chromatin network. They are generally irregular in shape, but whether this is to be ascribed to an active movement on their part or is due to a mere passive adaptation to the shape of the spaces in which they lie cannot be determined. It is at least not necessary as Goette ('07) maintains, to assume an active amœboid movement to explain the passing of the young ova into the gonophore buds. At a slightly later stage (fig. 11) in which the bud is solid, is seen the beginning of the bell nucleus, or as Goette[17] prefers to call it "Innenectoderm," or "Parectoderm." This is formed by the proliferation of the cells at or near the apex of the bud, in consequence of which the supporting lamella is pushed inward. Thus a fold of the latter is formed, which is continuous all around the bud, the bell nucleus soon becoming more or less cap-shaped and an endodermal lamella forming. Previous observers[18] have either not mentioned or denied

[16] Smallwood: '09, p. 210. [17] Goette: '07, p. 78.



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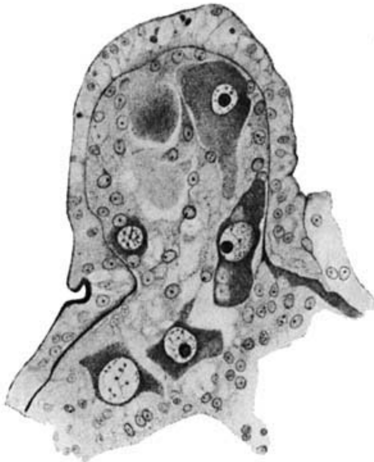

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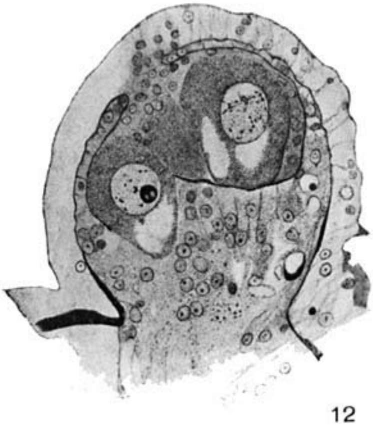

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HYDRACTINIA SODALIS

Fig. 8 Nutritive polyp. 30 diam. Fig. 9 Blastostyle. 45 diam.
Figs. 10-13 Developmental stages of the female gonophores. 370 diam.

the existence of the endoderm lamella in Hydractinia echinata, but there cannot be the least doubt of its presence in the species we are considering[19] On a close examination of the figures reproduced by Bunting[20] there is hardly any doubt that the parts marked *bn* in figs. 6, 10, 11, 12, 13 are endoderm lamellæ, although, strangely enough, nothing is said about them either in the text or in the explanation of figures. The lettering would suggest that she probably regarded them as parts of the bell-nucleus. Bunting and Goette must have missed the important stages. It must be remarked, however, that the endodermal lamellæ are never more than one cell layer thick and no trace of canals is ever developed. In the stage represented in fig. 11 the ova still lie entirely in the endoderm, although some of them are in close contact with the supporting lamella. In a somewhat later stage, represented in fig. 12, the endodermal lamella is very distinct; nearly all the egg cells have passed out of the endoderm into the inner ectoderm and one is seen to be just passing through the supporting lamella, causing a big temporary hole in it. With the passing out of the egg cells from the endoderm of the bud a cavity becomes apparent in the latter, the endoderm cells assume an epithelial arrangement, and the lumen of the bud becomes continuous with the gastric cavity of the blastostyle. The cells of the inner ectoderm have become scattered between the egg cells and between these and the supporting lamella; but they are as yet comparatively few. Another point that deserves notice in this stage is the eccentric position of the opening by which the outer ectoderm communicates with the inner. This condition occurs frequently, although it is not invariable, and the same can be found in many gonophore buds of a much younger age. At the stage represented in fig. 13 the gonophore has grown much larger, the endodermal lamella has become thinner, the spadix

[18] Bunting: '94, Colcutt: '98, Goette: '07.

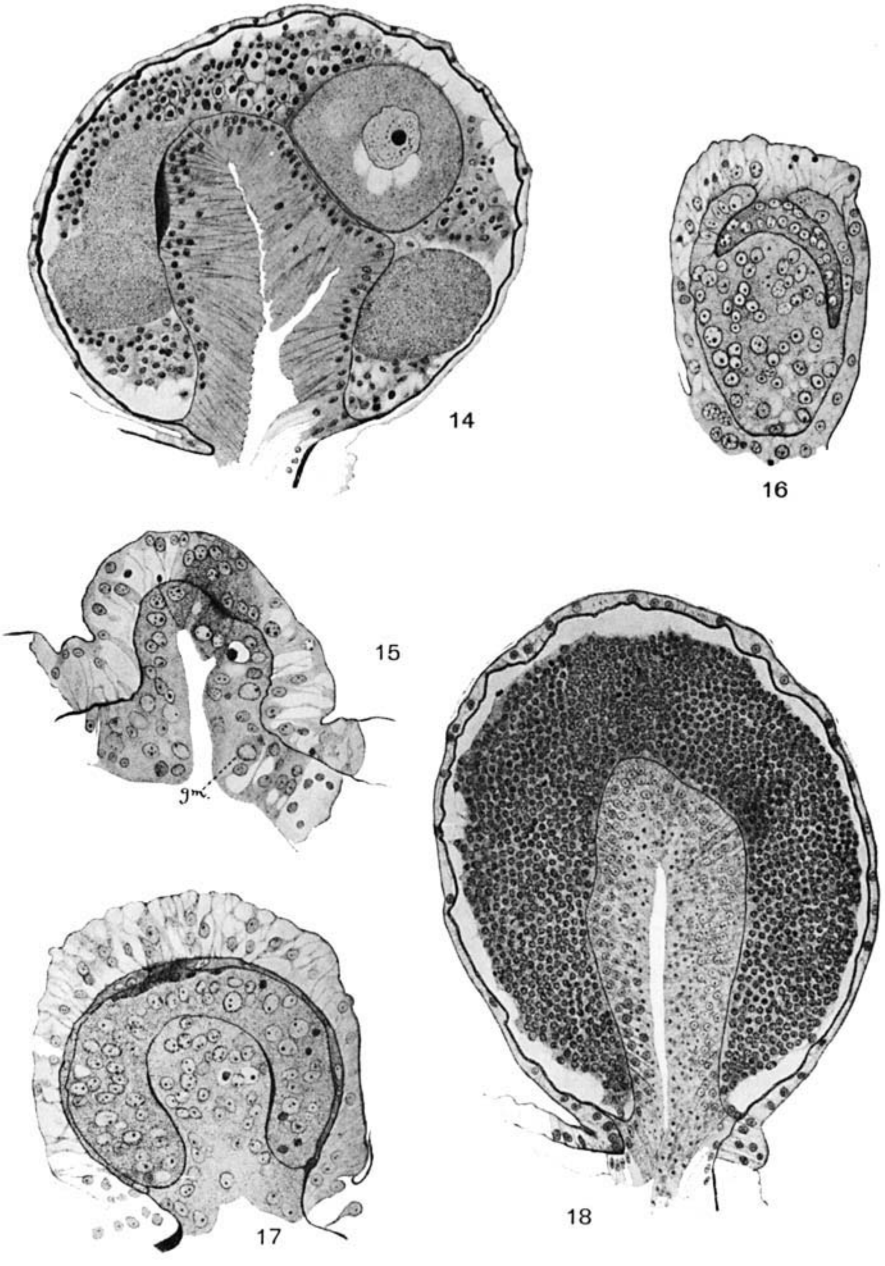
[19] It appears to me that Agassiz ('60 and '62, pl. 16) shows in his fig. 8 the presence of the endoderm lamella, marking it b[1] and calling it the "inner wall of the medusa." The figs. of Allman ('71, p. 32, and pl. 15, fig. 6) are not clear enough to enable one to say anything definite on this point.

[20] Bunting: '94, pl. 18.

has become distinctly elevated; the opening by which the inner ectoderm communicates with the outer is also eccentric in position but has become smaller, and shows signs of being closed up, as may be inferred from the presence of a deeply staining substance similar to that of the supporting lamella which spans the space lying between the edges of the endodermal lamella. The cells of the inner ectoderm are not very numerous, and their nuclei can be clearly distinguished between the egg cells. The young ova that are sometimes found in the endoderm of the blastostyle close to the base of the gonophore bud at this stage are probably reserved for the next bud. In the final stage here reproduced (fig. 14) in which some of the ova are nearly ripe, the gonophore is nearly spherical, the spadix is very conspicuous and may sometimes show a tendency to branch and grow outward between the egg cells. The endodermal lamella has become exceedingly thin and the nuclei contained in it are recognizable with extreme difficulty, so that at such an advanced stage the presence of an endodermal lamella can hardly be made out. The failure on the part of previous observers to recognize the existence of the endodermal lamella in Hydractinia echinata is probably due to the fact that it becomes exceedingly thin at a very early stage. The opening at or near the top of the gonophore by which the inner and the outer ectoderm communicate with each other is probably never closed entirely; for in a nearly ripe female gonophore examined to settle this point, there was found an opening at the place in question which ran through two sections (each $=7.5\ \mu$). The opening occupied the centre of a septum consisting entirely of the supporting lamella, the first formation of which was seen in a previous stage (fig. 13). Another fact that must be noted in this stage is the great increase in number of the cells of the inner ectoderm and their different appearance. So far these cells had a naked protoplasm, but now most of them have developed a distinct cell wall, and by mutual pressure have assumed a polyhedral form. The few cells which are still seen in fig. 14 to be destitute of a membrane probably develop it later. Frequently the egg cells are separated from one another by wide spaces completely filled with these cells, which thus almost deserve the name of "follicle cells" (Nährzellen of Weismann '83). In the gonophore represented in fig. 14, one of the ova has a very distinct layer of ectosarc, hence it was probably ripe. I have never observed a cell layer on the inner side of the endodermal lamella, although such is suggested in certain stages of the male gonophore (vide infra).

Male gonophores

As already stated, the male gonophores are generally found in a different colony from that of the female, although hermaphrodite gonophores are occasionally found. The position and mode of origin of the male gonophores are in no essential way different from those of the female. In fig. 15 is reproduced a very young bud. It contains a lumen which is a direct continuation of the gastric cavity of the blastostyle, and numerous mitotic divisions are taking place at the apex both in the ectoderm and endoderm, but especially in the latter. The cell proliferations in the ectoderm give rise to the rudiment of the inner ectoderm, which is seen to be a darkly stained mass of cells with granular protoplasm and without any distinct cell boundaries. In the section here reproduced it has just slightly pushed the supporting lamella inward. The divisions in the endoderm give rise to the germ cells. These are mostly formed near the apex of the bud, but some appear to migrate into it ready formed from the adjoining endoderm. One such case is shown in fig. 15 (*gm.*) In the next stage here reproduced (fig. 16) the inner ectoderm has been formed and is seen to form a cap-shaped mass of cells communicating with the outer ectoderm by a comparatively small opening, which is bounded on all sides by the apical margin of the endodermal lamella. The position of this opening is mostly apical but it may be shifted considerably to one side, as in the female gonophores. The cell proliferation in the endoderm has become so intense as to greatly obscure the internal cavity, although this appears to be always present more or less. In my opinion, the germ cells are still all in the endoderm in the section reproduced in fig. 16, so that all the nuclei contained in the cap-shaped mass above mentioned



HYDRACTINIA SODALIS

Fig. 14 A nearly ripe female gonophore. 230 diam.
Figs. 15-17 Developmental stages of the male gonophore. 370 diam.
Fig. 18 A nearly ripe male gonophore. 230 diam.

are truly ectodermal in nature. The germ cells are very numerous in the endoderm, although it is hard at this stage to distinguish them individually from cells that remain definitively endodermal. They are however characterized by large vesicular nuclei. The gonophore grows larger, the inner ectoderm spreads out more and more, the germ cells passing through the supporting lamella come to lie in the inner ectoderm, and the endoderm rises up in the center of the bud to form the spadix, until the stage represented in fig. 17 is reached. A very conspicuous feature of this stage is the inner ectoderm. This forms a conspicuous deeply staining mass in and around the original opening by which it communicated with the outer ectoderm. In the section here reproduced the opening has been largely filled by a membranous septum of supporting lamella. Numerous small nuclei are scattered between the germ cells, staining more deeply and diffusely than the latter, and doubtless belong to the cells of the inner ectoderm. A similar layer of the inner ectoderm capping the top of the germ cells is described and figured by Goette in Hydractinia echinata[21]. The endodermal lamella has become much compressed and dense, but the nuclei can still be distinctly seen. In this as in the previously figured stage the outer ectoderm is greatly thickened at the top of the gonophore; this becomes less conspicuous in later stages and may entirely disappear at last. In fig. 18 is reproduced a male gonophore which is nearly ripe, and there is no difficulty in connecting it with the previously described stage; for the same parts are present in both, though much altered. The spadix has become greatly elongated and irregularly club-shaped, the tall endodermal cells presenting a typical epithelial arrangement, and enclosing a central cavity directly continuous with that of the blastostyle. The endodermal lamella is exceedingly thin, but can be clearly distinguished as a distinct layer separating the two supporting lamellæ enclosing it and directly continuous with the endoderm of the spadix at the base of the gonophore; the nuclei can be observed with extreme difficulty if they are present at all. The opening between the inner and the outer ectoderm was present in a

[21] Goette: '07, p. 73, pl. 6, fig. 132.

single section ($=7.5\,\mu$) in a nearly ripe gonophore examined for the purpose, the original communication being mostly cut off by the formation of a membranous septum of supporting lamella. It may also be remarked that the position of this opening may be apical or eccentric both in young and mature gonophores. The larger part of the contents of the gonophore at this stage consists of the germ cells which have become very small by repeated divisions. Numerous karyokinetic figures are however present, showing that the process of division is still actively going on. The figures probably belong to maturation stages. Careful observation shows the presence of the nuclei of the inner ectoderm cells here and there between the sperm cells, distinguishable by their smaller size, more or less elliptical shape and especially by their deeper and diffuse staining. The ripe male gonophores are, as already mentioned, slightly ellipsoidal in shape.

Relationships with other forms

In regard to the soft parts nothing particular need be said on the relationships of the present species, but the skeleton appears to lead us to a better understanding of some of the forms previously described, including certain fossil ones. Of the species having skeletons of the same general structure as H. sodalis, Stechow[22] mentions Hydractinia calcarea Carter,[23] Hydractinia angusta Hartlaub ('04), Hydractinia dendritica Hickson & Gravely,[24] Hydrodendrium gorgonoide Nutting[25] and Clathrozoön wilsoni Spencer.[26] Again Nutting[27] mentions the following families as being more or less closely related: Hydractinidæ, Ceratellidæ (Solanderidæ), Hydrodendridæ, Tubidendridæ (a new family to be described), Hydroceratinidæ and Milleporidæ. It seems to me that of the described species of Hydractinia, H. arborescens Carter is most nearly related to H. sodalis, if indeed it is not identical with the latter. Carter[28] had a single specimen of this species which "now

[22] *Loc. cit.*: '09, p. 22.
[23] Carter: '77, p. 50.
[24] Hickson & Gravely: '07, p. 9.
[25] Nutting: '06, p. 936.
[26] Spencer: '90, p. 123.
[27] *Loc. cit.*: '06, p. 938.

belongs to the British Museum, and was found, without any label or indication of its locality, among the late Dr. Bowerbank's collections." Carter ('78) however gives the locality as Polynesia with a query, and Steinmann[29] gives it as "wahrscheinlich die Philippinen." The figures both of Carter and Steinmann clearly show its close resemblance in the general form of the chitinous skeleton to Hydractinia sodalis, and it is not going too far to assume that the internal structure must also be closely similar, especially as Carter's description of the skeleton of Hydractinia echinata[30] shows essentially the same arrangement of parts, as in Hydractinia sodalis. Here it may be mentioned that Carter's description of '73 is much more accurate than that of '77, as may be seen by comparing the two descriptions with the results obtained by Colcutt ('98) through the use of modern methods. The later paper of Carter ('77) appears to me to have been influenced too much by a desire to bring out the supposed affinity with certain fossil forms (other than Hydractinia), which must in my opinion be said to be at most only remote. Renewed examination of the various fossil forms mentioned by Carter and Steinmann, especially if microscopical sections are prepared, will probably throw light on this question. In Carter's specimen of H. arborescens the hydroid skeleton did not entirely cover the shell which was that of Fusus sulcatus,[31] but this is clearly a point of secondary importance. Again in Hydractinia levispina[32] is clearly seen, as pointed out by Steinmann,[33] the tendency of the hydroid skeleton to grow beyond the mouth of the gastropod shell to form a "shell" of its own, and the presence of the same tendency in Hydractinia echinata can be inferred from Carter's description.[34] If now we compare the chitinous skeleton of Hydractinia with those of Solanderia, Clathrozoön and Hydrodendrium, they are all found to be on essentially the same plan derived from the well known fundamental structure of the hydroid colony. Are we to infer from this that they are all closely related phyletically? There can be no

[28] *Loc. cit.*: '78, p. 299. [29] Steinmann: '78, p. 109. [30] Carter: '73, p. 2.

[31] I.e., according to Steinmann. Carter gives it as Phos senticosusor Fusus sulcatus.

[32] Carter: '73, pl. 1, fig. 1. [33] *Loc. cit.*: '78, p. 109.

doubt that the corresponding parts are homologous in a general way, but it would be in my opinion a mistake to look upon these forms with complex skeleton as more nearly related to each other than to those without it. To clarify this point a much more detailed knowledge of the structure and development of these forms than we possess at present appears to me necessary. So far as I can see at present the development of a complex skeleton in these forms appears to have gone on independently in the different species; in other words, the resemblance is one of homoplasy. As to the relationships of the fossil forms mentioned by Carter[35] and Steinmann ('73), I have nothing to say, because I have not been able to study them. So far as I can see from the descriptions, however, their affinities to the living hydroids appear to me to be more remote than is supposed by Carter and Steinmann, with the exception of the species of Hydractinia.

2. HYDRACTINIA SPIRALIS, N. SP.

I can deal very briefly with this species, because the gonophores appear to be in all essential respects exactly like those of the preceding species. The form was first described by Inaba[36] as a species of Podocoryne as follows:

3. Podocoryne sp. (figs. 5, 6, 7,).

Trophosome.—Hydrorhiza consisting of numerous parallel small tubes, the perisarc covering them being fused together and forming a strong lamella. From this lamella spring small pointed chitinous spines. Hydranths also springing in large numbers from the lamella; they are of two forms, those without reproductive organs large and with 12-18 tentacles; those bearing reproductive organs small and with 4-8 tentacles.

Gonosome.—Medusoid, growing from the hypo-tentacular part of the hydranth; imperfectly developed and incapable of swimming, merely with four radial canals and a circular; manubrium, however, full of genital cells, enlarged and entirely filling the cavity of the umbrella.

Color.—Hydranth colorless; perisarc reddish brown.

[34] *Loc. cit.*: '73, p. 2. [35] *Loc. cit.*: '77, and '78. [36] Inaba: '09, p. 98.

Locality.—Between Misaki and Jogashima, 3 *hiro*[37] deep, covering worm-tubes resembling gastropod shells, inhabited by a hermit crab in place of the dead worm.

Date.—April, 1889. Collected by Mr. Shishido.

The hydrorhiza is very strongly built but very thin, hence it is easy to prepare sections of it. The original worm tube was probably very delicate and hardly leaves any of its traces; the whole lamella consisting of the creeping hydrorhiza of the Podocoryne. Perisarc not elevated in the form of a bowl at the base of the hydranths. The chitinous spines are hollow and filled with a coenosarc consisting of the two layers and ending blindly. Some of the spines have incomplete or exceedingly thin apices; these are probably growing ones.

The upper surface of the hydrorhizal lamella is covered by a naked coenosarc, which has been described as consisting only of the ectoderm, but which, according to my own observation, appears to contain also the endoderm; this point requires reëxamination.

The hydranths are very small, the larger ones being 1.5 mm. high and the smaller ones bearing medusoids not being over 0.5 mm.; the spines are 0.5–0.7 mm. high.

Of the medusoid gonophores there are generally two on a hydranth, the lower one being the larger; the full grown medusoid comparatively large, with a diameter of over 0.2 mm.

This is a very interesting species and probably new. The genus Podocoryne usually produces free medusae and Hydractinia gonophores which are never detached. The present species is intermediate on this point, the reproductive organs being medusoid and never detached. Hence it may be somewhat doubtful to which of these two genera to refer it, but the presence of the four radial canals in the reproductive organs (fig. 7), and of tentacles on the hydranths bearing them, or blastostyles, leaves no doubt that it belongs to the genus Podocoryne.

According to Allman, there is no doubt that the Hydra aculeata of Wagner is a Podocoryne. In this species the medusa does not complete its development, being never free, although there are four radial canals and four tentacles on the edge of the umbrella; hence it is evident that there are several stages in the development of the medusa within the genus Podocoryne. The description of P. aculeata agrees fairly well with my specimens; possibly they are the same species. R. Wagner is stated to have obtained it in 1833 on the coast of the Adriatic Sea, but it has not been obtained since.

[37] A "hiro" is an arm-span, equal to about 1.6 m.

I shall confine myself to the points on which my own observations differ from those of Inaba, but in criticizing his descriptions it must be borne in mind that his work was done under some peculiarly difficult conditions and with insufficient literature at his command.

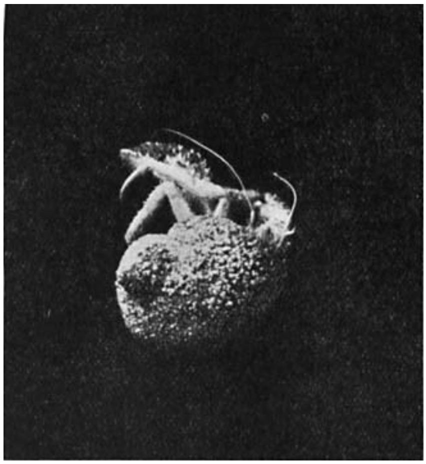
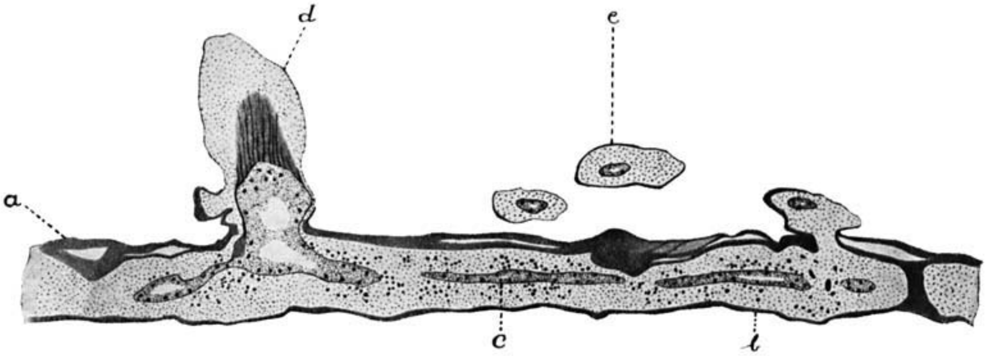


Fig. 19 A colony with polyps. Nat. size.

In the first place, what Inaba thought was a worm-tube is really the chitinous skeleton of the hydroid. It has the shape of a gastropod shell, is much more regular, judging from my specimens, than the corresponding structure in H. sodalis (fig. 19), and by far the larger part of it is soft and of a dirty greenish hue. The inner surface is perfectly smooth,and when examined with a hand lens shows exceedingly fine reticulations, due to the inner structure to be mentioned later. The thickness of the hydroid shell varies a good deal in different parts, being very thin near the mouth but becoming as thick as 2 mm. or more near the apex. On the outer surface are found much dirt, minute sand grains, diatoms, etc., and much of the thickness of the subapical part of the shell just mentioned appears to be due to the presence of these extraneous bodies. The chitin of the skeleton is flexible but very strong, so that it is relatively more difficult to obtain good serial sections of this species than in H. sodalis. These show that in the thinner part of the shell its hard parts consist of two parallel chitinous lamellæ about 7-22μ in thickness and 0.1 mm. apart, connected together at many points by strong chitinous trabeculæ of varying thickness (fig. 20). It was probably these trabeculæ that Inaba mistook for surface spines. The inner surface of the shell is bounded by the inner of the two lamellæ just mentioned; the outer surface is also largely bounded by the outer of the two lamellæ, but in many places chitinous tubes of the structure generally seen in monosiphonic hydroids take rise from the outer lamella and creep about on the outer surface of the shell in close apposition to the former. The interspaces between the two chitinous lamellæ are completely filled with ectoderm which contains numerous ramifying endodermal tubes forming a network, to which is due the appearance of the inner surface of the shell mentioned above. The superficial tubes above referred to are filled with the continuations of the endoderm and ectoderm filling the interlamellar cavities, exactly as in monosiphonic hydroids; but I have never seen them give rise to polyps, although my observations on this point are confessedly incomplete. As to the thicker part of the shell, I have not been able to obtain satisfactory serial sections owing to the presence of much dirt and sand grains. Where the chitin is of some thickness in any part of the shell it is seen to be composed of several superposed layers. According to my observations there is no coenosarc on the surface of the shell, and the relations of the soft part and the chitin are in this species nearer those found in the typical hydroids than in H. sodalis.

In this as in the preceding species there is always a small gastropod shell in the apex of the hydroid skeleton; in one case it was that of a species of Fusidæ only 6.5 mm. long, although the hydroid shell was 25 mm. in length. It is interesting to note that this species never grows so large as the preceding, although found in the same localities. The mother whorl of the hydroid shell is relatively very large and the turret very small.

So far as I have observed, the polyps are of two kinds, nutritive and reproductive. The former, or gasterozoöids, may be found in any part of the colony, but most frequently they are especially



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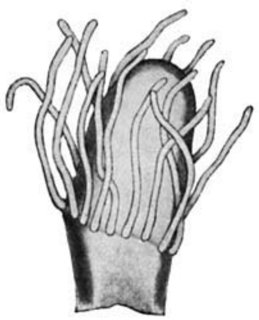

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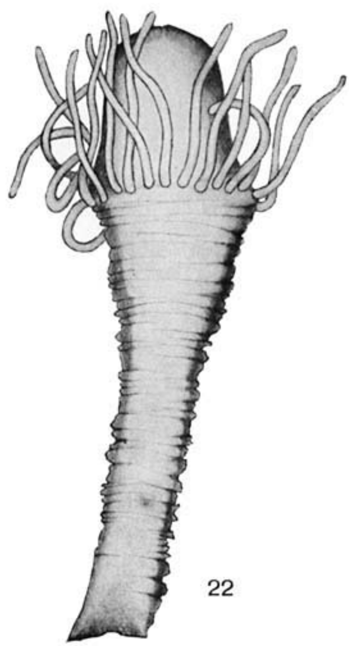

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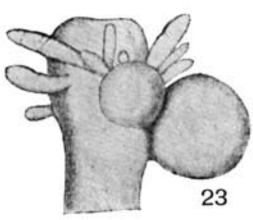

23

HYDRACTINIA SPIRALIS

Fig. 20 Transverse section of a colony at right angles to the mouth of the shell. The details of the cellular parts are not shown. *a* outer chitinous lamella, *b* inner chitinous lamella, *c* endodermal tube, *d* blastostyle, *e* superficial hydrorhiza. 90 diam.

Fig. 21 Nutritive polyp. 45 diam. Fig. 22 Nutritive polyp. 45 diam.

Fig. 23 Blastostyle. 45 diam.

numerous on the columnellar side of the last whorl, i. e., the side on which the hermit crab would slide along in locomotion. On the thinner part of the shell they are always very short and comparatively thick, with a single row of filiform tentacles 20-25 in number. The hypostome is very prominent and as long as the body when the mouth is closed, but flattened out when the latter is wide open (fig. 21). On the thicker part of the shell there are gasterozoöids of a quite different shape, with a slender funnel-shaped body, a prominent hypostome and a circle of about 30 tentacles (fig. 22). The relative numbers of these two forms of gasterozoöids appear to vary a great deal according to colonies, there being no essential difference between them.

The blastostyles are found where the gasterozoöids are few, so that we may broadly speak of blastostyle areas and gasterozoöid areas, although the two are not rigidly separate and pass into each other without any demarcation. The older blastostyles are difficult to recognize owing to the great development of the gonophores which they bear, and by which they are more or less pushed aside from their natural position. In young blastostyles bearing a few young gonophores their form stands out very clearly, and it is then seen that they are but little different from the slender gasterozoöids above mentioned, except that they are smaller all around and the tentacles are less numerous, there being only 6-12 on each (fig. 23). The hypostome is relatively very large, and the mouth is present in older ones. The gonophores are borne about midway between the base and the tentacles, and on an older blastostyle there may be as many as twelve or more of them. So far as I have observed the gonophores develop essentially in the same way as in H. sodalis. There are no canals, radial or circular, at any time and although in some gonophores the ectoderm is much thickened at the top and contains numerous nettle cells, there are no tentacles.

This species is common in different parts of the Bay of Tokyo and in the vicinity of Misaki, although it appears to be less so than H. sodalis.

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