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On *Stephanoscyphus* and *Nausithoë*

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With Plates XXI & XXII and 43 Text-figures

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Historical

Stephanoscyphus (= *Spongicola*).—The peculiar scyphozoon *Stephanoscyphus* ALLMAN (= *Spongicola* F. E. SCHULZE) was described first by EIMER (1872) from the neighborhood of Capri. He found there a polyp-like organism dwelling in a chitinous branching tube which was imbedded in stocks of various kinds of sponges. The

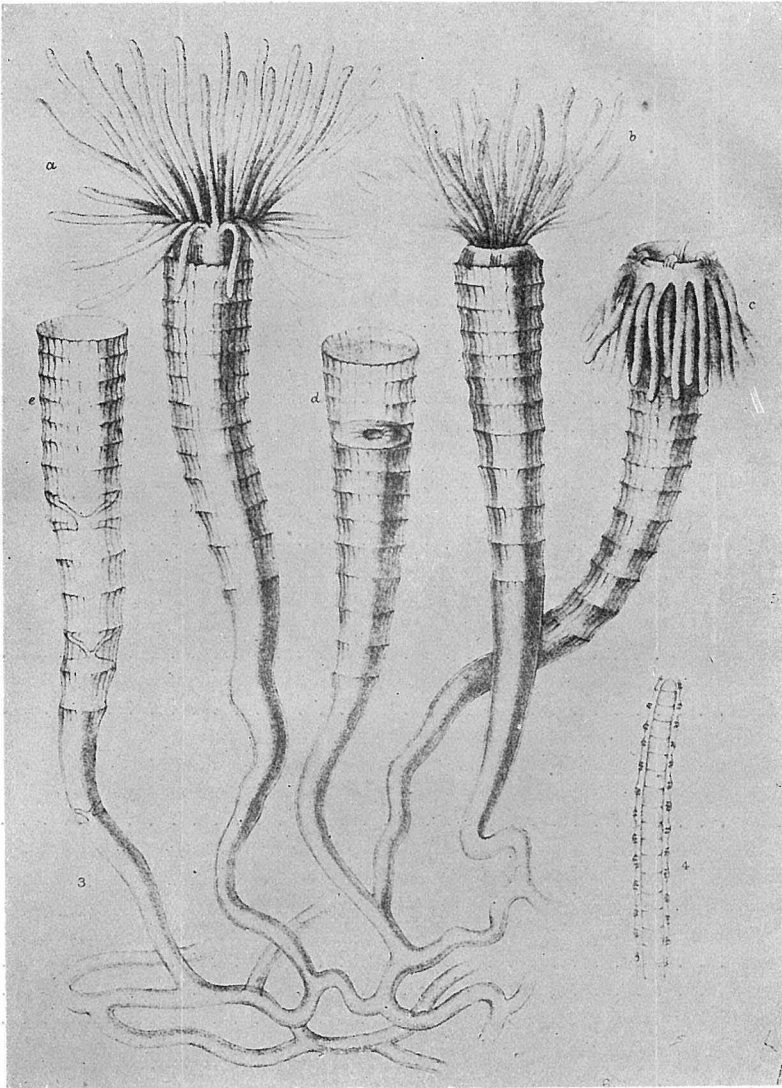


Figure 1. ALLMAN'S figure of *Stephanoscyphus mirabilis*; 1/2 the original.

organism was provided with tentacles, and some nematocysts. Because of these, he thought that it might be a hydroid parasitic on the sponges; but somehow the idea that it might be an essential component of the colony of the sponges prevailed on him. He therefore assumed that this polyp-like individual was a kind of trophic zoöid of the sponge. Further, he went on so far as to propound that the existence of such zoöids in the stock of the sponge, was an evidence of close affinity between the Porifera and the Cnidaria.

In the same year, CARTER (1872) observed some nematocysts in the specimens of *Reniera* which had been collected by W. THOMSON at Bon Bay on the north coast of Africa. However, he regarded the nematocysts as belonging to a polyp living as a parasite in the colony of the sponge.

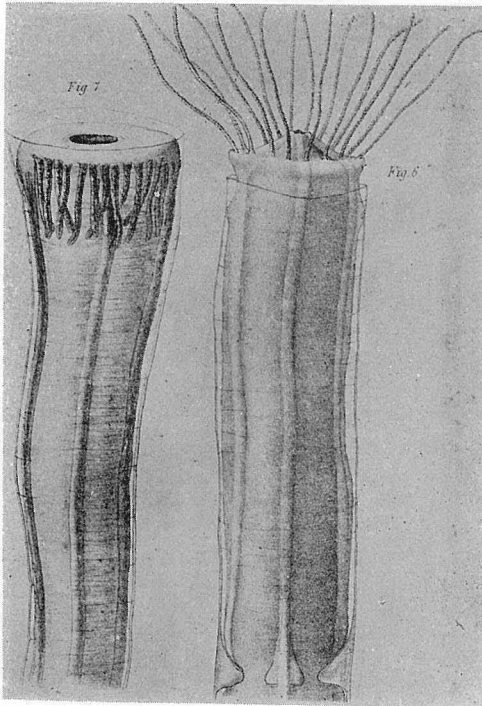


Figure 2. SCHULZE's figure of *Spongicola fistularis*; 1/2 the original.

Two years later, ALLMAN (1874) found in Antibes on the south coast of France, a hydroid-like coelenterate inhabiting the oscula of some demosponges (Fig. 1). At the first glance, the coelenterate appeared like a hydranth of *Campanularia*. But closer examination revealed that it was more like a medusa than a hydranth. It was provided with a circular canal and four symmetrically disposed longitudinal canals, though it lacked gonad, velum and ocelli. The name of *Stephanoscyphus mirabilis* was given by him to this curious coelenterate. As to the systematic position of the same, this author has stated:

“. . . . It is obvious that *Stephanoscyphus* must form the type of a distinct order of Hydrozoa. With the order Hydroida it possesses very decided affinities, but it is nevertheless removed from the Hydroida by a distance at least as great as that which separates

these from the Siphonophora. For the new order I propose the name of Thecomedusæ" (1874, B, p. 65).

Next in 1877, F. E. SCHULZE described '*Spongicola fistularis*' that he had found in the colony of the sponges, *Reniera*, *Suberites*, etc. collected from the Adriatic (Figs. 2, 3). This he took for a hydrozoon. He had known of ALLMAN'S *Stephanoscyphus*; but he found some points of discrepancy between his observation and ALLMAN'S statements, and he referred his material to the distinct genus mentioned above. He records at some length his findings on this new coelenterate. However, he does not seem

to have sectioned his material. So it is but natural, that his descriptions contain several misleading statements. He failed to observe any of the circular or longitudinal canals which ALLMAN had been able to recognize. Nevertheless, SCHULZE realized that the coelenterate possesses some characteristics of the scyphistoma of an acraspedote medusa. He consequently expressed his conviction that, in order to decide the systematic affinity of that coelenterate, it was necessary to have its entire cycle of reproduction worked out.

Some four years previous to the publication of SCHULZE'S paper, KOWALEVSKY seems to have observed strobilation of a kind of parasitic scyphistoma which was found in a colony of sponge. Evidently, this is the first record of the developmental cycle of *Stephanoscyphus*. But the original account remains still unknown to the wider zoological circle, except through an incidental remark of METSCHNIKOFF (1886).

METSCHNIKOFF studied the early developmental stages of *Nausithoë marginata* in Messina. When the planula of this medusa is fixed on the substratum, the basal part stretches on it and secretes a thin sheet of periderm. From the center of this sheet a funnel-like elevation develops around the polyp which has in the meantime acquired four tentacles (Fig. 4). METSCHNIKOFF'S attention was

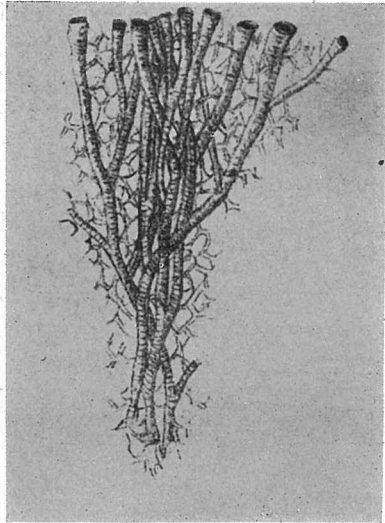


Figure 3. The same; the periderm of a part of colony; $\times 1.7$ the original.

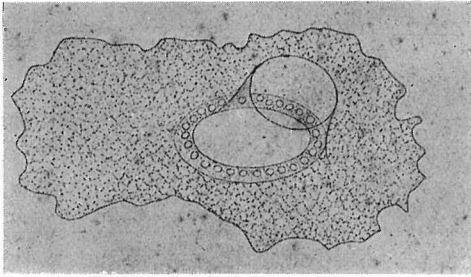


Figure 4. METSCHNIKOFF'S figure of the fixed stage in the development of *Nausithoë marginata*; $\times 1$ the original.

directed to the similarity of this stage to *Spongicola*. This observation, coupled with KOWALEVSKY'S account mentioned above, led him to the conclusion that *Spongicola* probably represents a developmental stage of *Nausithoë*.

Next in June 1890, LO BIANCO and P. MAYER observed in Naples a number of ephyrae swimming in a jar which contained a stock of sponge harboring colonies of *Spongicola*. They identified these ephyrae with those of *Nausithoë* figured in CLAUS' paper (1883). They thus confirmed KOWALEVSKY and METSCHNIKOFF'S view on the relationship of *Spongicola* and *Nausithoë*.

The above is a comprehensive review of the previous investigations on this remarkable scyphozoon *Stephanoscyphus*. Our knowledge however, is quite deficient regarding the details of its structure and development.

Nausithoë.—Since the first report on it by KÖLLIKER in 1853, *Nausithoë* has been observed by various investigators such as CLAUS (1883), HAMANN (1883), METSCHNIKOFF (1886), VANHÖFFEN (1892, 1902, 1906, 1908), A. MAYER (1900, 1902, 1910), H. B. BIGELOW (1904, 1909) and KRAMP (1924). CLAUS worked on the structure of this medusa and also described the ephyra, while METSCHNIKOFF, as mentioned above, recorded the early stages of its development. The habit and distribution have been dealt with mainly by VANHÖFFEN, KRAMP and KRUMBACH (1925).

Many text- and handbooks mention the names of *Stephanoscyphus* and *Nausithoë*, because the scyphozoon bearing these names is remarkable on account of the formation of an unusually extensive colony by *Stephanoscyphus* and the very primitive organization of *Nausithoë*.

Stephanoscyphus

External Appearance

Specimens found at Seto.—In my first summer at the Seto Marine Biological Laboratory in 1922, I was informed by men living in a neighboring village of a 'stinging alga.' This 'alga,' they said, which occurs in abundance in the littoral of the neighborhood, gives much annoyance to fishermen and especially to divers, by causing severe pain and itch to anyone who happens to touch it with the more sensitive parts of his skin. Moreover, inflammation often develops on those parts. Those who are sensitive to the poison frequently suffer from high fever for some days or weeks. The effect may come upon men who only swim in the water where the 'alga' grows in abundance.

At my request the 'alga' was brought me for examination. But I was unable to identify it with anything I had seen before, except that I found it to be a sort of colony-forming coelenterate. It took me some labor to identify it as *Stephanoscyphus*. Ever since that time, I have been working on this material intermittently. Although there still remains a good deal to be elucidated, it may be well to report now what I have been able to find so far. In pursuing this study, I have been favored with the generous help given by the resident members of the Seto Marine Biological Laboratory, Messrs. S. SHINO, H. SUGINO and Y. SAIKA. To all these gentlemen my hearty thanks are due.

Colony.—The colony of *Stephanoscyphus* is found in abundance in the littoral of Seto. It grows on submerged cliffs and in crevices of rocks at the depth of a few fathoms. The colony is imbedded usually in stocks of various sorts of sponges belonging to the group Demospongiae, e. g. *Reniera*, *Chalina*, *Euspongia*, *Suberites*, as mentioned by previous authors. The polyps, however, are not harbored in the oscula, but they are simply imbedded in the bulk of the sponge (Plate XXI, fig. 1). They are not parasitic on the sponge, nor do they necessarily occur with the latter. Colonies of *Stephanoscyphus* without any sponge associated with them are found sometimes, though not very often. Beside the sponges, the colony may be accompanied by various encrusting organisms, such as bryozoa, hydroids, ascidians and algae. Also many kinds of small marine animals like *Alphæus*, *Galathea*, *Tanais*, *Caprella*, small polychætes and ophiurians find shelter in the colony of the coelenterate. I have

also seen specimens of a kind of spider-crab, *Chlorinodes* carrying a small colony of this coelenterate imbedded in a piece of sponge on its back.

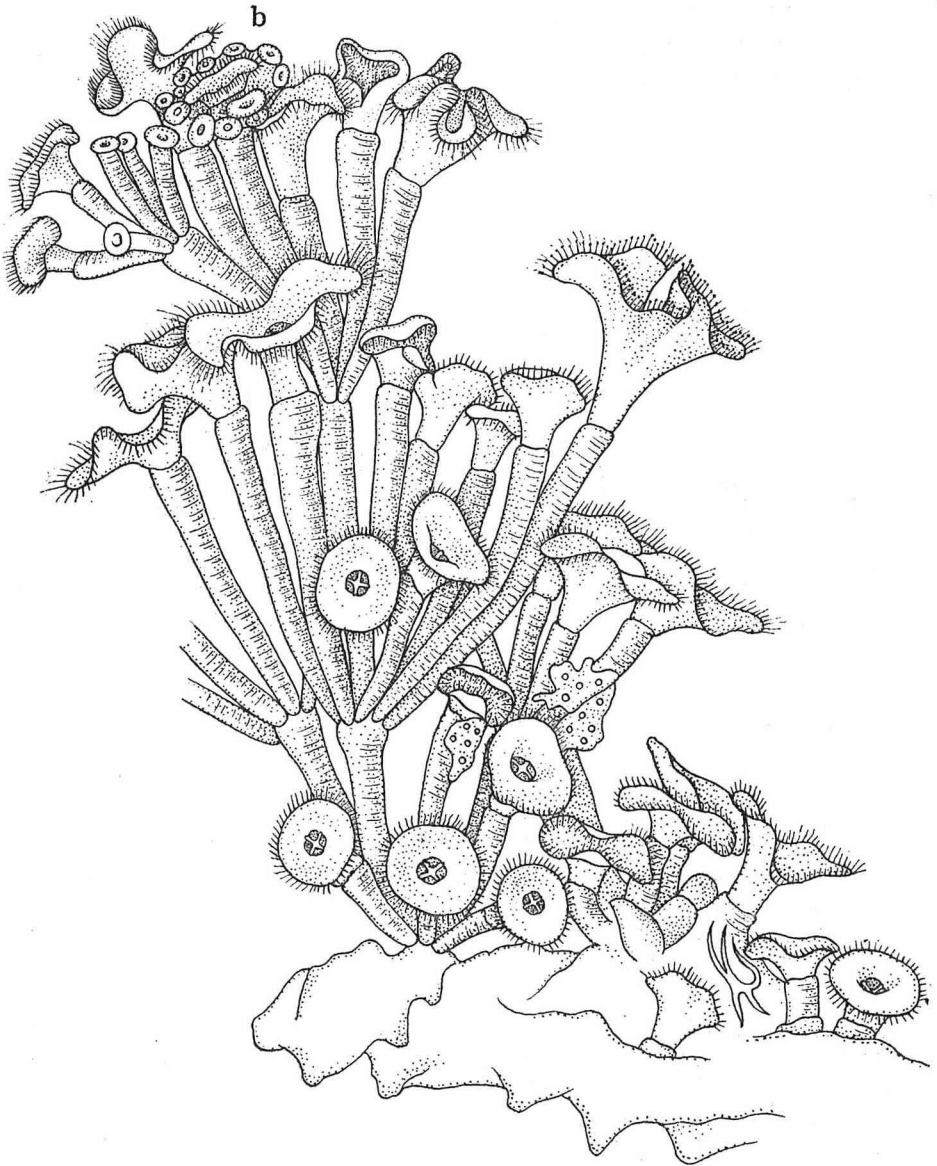


Figure 5. A sketch of a colony of *Stephanoscyphus* after the removal of the large part of the encrusting sponge; $\times 3$.

When a colony is put into a jar and left a while, the polyps extend. Such a colony appears something like a flowering herb, say, of the *Dianthus*-family (Fig. 5, Pl. XXI, fig. 1). The head of the polyp is funnel-shaped, brownish in color, and with the margin fringed with a number of delicate tentacles. The polyps shrink on slight disturbance, the margin of the head curling inside, exposing the whitish underside.

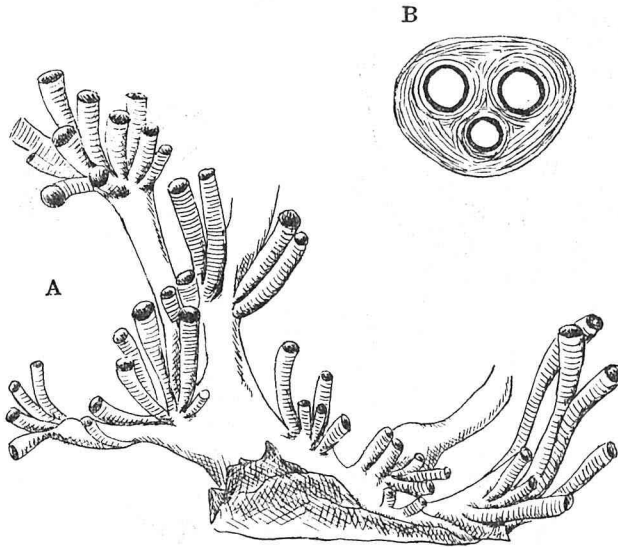


Figure 6. A. A part of the periderm of a colony, $\times 2$.
B. Cross-section of the periderm from the basal part of the colony; $\times 3$.

Periderm.—*Stephanoscyphus* possesses a well-developed chitinous periderm (Figs. 5, 6). Each polyp dwells in a thin tubular theca. From ten to twenty such thecae are borne on a common stalk. Several such stalks again are borne on a common stalk of a higher order. Thus a large colony comprises four or five storeys of racemose branchings of the tubular periderm, and the entire periderm system resembles the inflorescence of the Umbelliferae. The new branching is initiated by a peculiar group of polyps consisting of a central polyp and several smaller polyps encircling it (Fig. 5, b). The central polyp is apparently different from ordinary polyps from its origin, and it alone possesses the capacity of developing polyp buds around it.

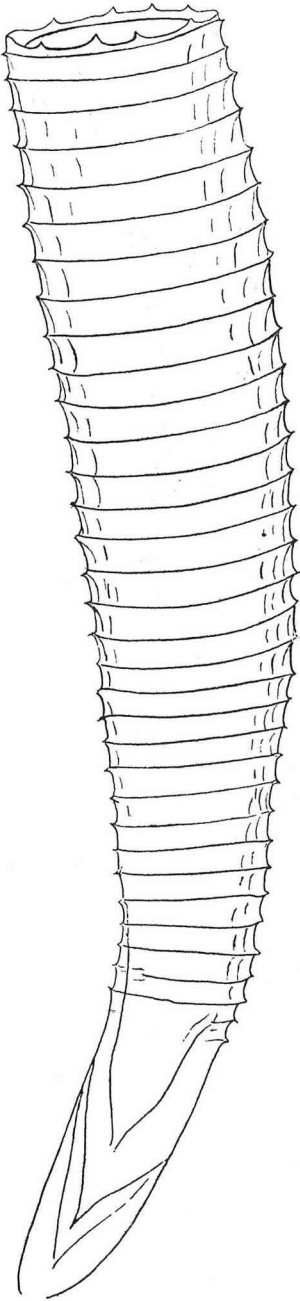


Figure 7. A theca of the polyp; $\times 20$.

The theca enclosing each polyp consists of numerous lamellar rings superposed one upon another (Fig. 7). Each theca is usually ca. 10 mm. in length, though it may be as long as 20 mm., and has a diameter about 2 mm. at the distal end and 1 mm. at the base. The stalk usually has a thicker wall and retains an axial lumen which communicates with the gastric cavity of the polyp. Thicker stalks near the base of the colony are penetrated by two or three separate axial lumina, showing that they are double or triple structures (Fig. 6, B). How such duplicity or triplicity of the stalks has been brought about remains to be investigated.

The above description of the mode of branching of the periderm differs somewhat from either ALLMAN's or SCHULZE's observation. ALLMAN illustrates the thecae as arising directly from what appears to be a network of stolon (Fig. 1), while SCHULZE's figure shows the branching of the periderm to be very irregular (Fig. 3). Thus nothing suggesting the characteristic racemose branching is to be found in either author's work. This I take to be due to the deficiency of the material at their disposal rather than to a specific distinction between the Mediterranean and Japanese specimens.

Polyp.—The polyp is trumpet-shaped and consists of the terminal funnel or head and a tubular stalk (Figs. 5, 8, 9). Larger polyps may measure 7 mm.,

but smaller ones are only 2 mm. across the head. The margin of the head is fringed with 100–200 delicate tentacles; the number does not vary much with the size of the polyp. The longest tentacles measure about 2 mm. when fully stretched.

At the center of the terminal funnel is found the mouth opening (o). When fully open it is rounded, about 0.7 mm. in diameter, and shows inside four small prominences symmetrically disposed. These mark the termini of mesenteries. The mouth is closed in quick response to slight stimulus. Then it becomes cruciform, and a depression is formed at each interradius between the arms of the cross.

The color of the inside of the funnel is brownish, ranging from light-brown to sepia, and often tinged with emerald green. Sometimes it is almost milky white. The parts around the mouth are deeper in color. The external side of the funnel is whitish. The tube is light brown and is translucent. The brownish color is due to zooxanthellae inhabiting the entoderm, the variable tone of the inside of the funnel depending upon the amount of this com-

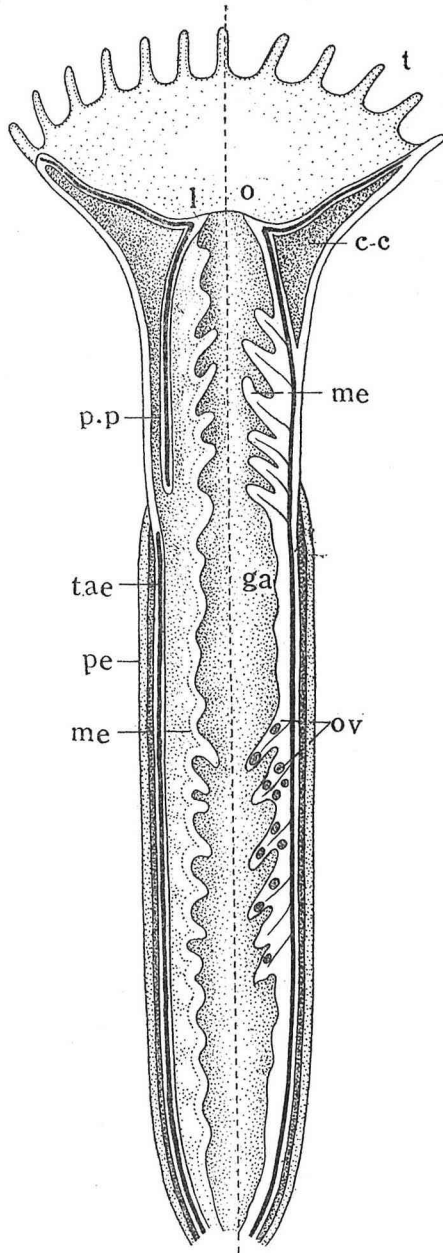


Figure 8. Semidiagrammatic figure of the organization of the polyp; longitudinal section through the perradial plane is in the left half, longitudinal section through the interradiial plane is in the right half.

menal alga. The greenish tint is given by a kind of zoochlorellae also found in the entoderm but in much smaller quantity. The whitish color of the outer side of the funnel is largely due to nematocysts which occur in great numbers in this part. The nematocysts are much fewer in the tubular part of the polyp, so that this part is translucent and shows through it zooxanthellae occurring in the entoderm.

The colony may be kept alive in the aquarium for a week or more especially in milder seasons.

Structure

General Scheme (Figs. 8-10)

The theca including the polyp was cut with the scissors at the base and fixed in BOUIN's fluid. The theca was removed before imbedding in paraffin. FLEMMING's material showed no advantage over BOUIN's material; consequently, even the histology was worked on BOUIN's material.

Fixed material is so contracted that the interpretation of the structure of the polyp appears somewhat difficult at the first glance at the sections. By a little practice, however, the difficulty may be overcome.

The head of the polyp contains a spacious internal cavity which may be termed the coronal cavity (c. c), ('Kranzdarm' or 'ring sinus' of certain previous authors). Proximally this cavity extends as four perradial entodermal pockets each of which communicates with the general gastric cavity by a small hole (p. p). Evidently, the coronal cavity and the perradial pockets correspond with the 'circular canal' and the 'longitudinal canals' respectively mentioned in ALLMAN's paper. The central gastric cavity (ga) extends from the mouth all through the polyp and communicates at the basal end with the cavity of the stalk.

On the wall of the central gastric cavity in each interradi- al plane is found a prominent longitudinal ridge—the mesenteries (me). In length the mesentery exceeds the polyp to a considerable degree, consequently the former is folded so much that in the tangential longitudinal section of the polyp the mesentery exhibits a very undulating course (Fig. 9 A, left half), while in the interradi- al longitudinal section it appears as a series of villiform processes superposed one upon another (Fig. 9 A, right half).

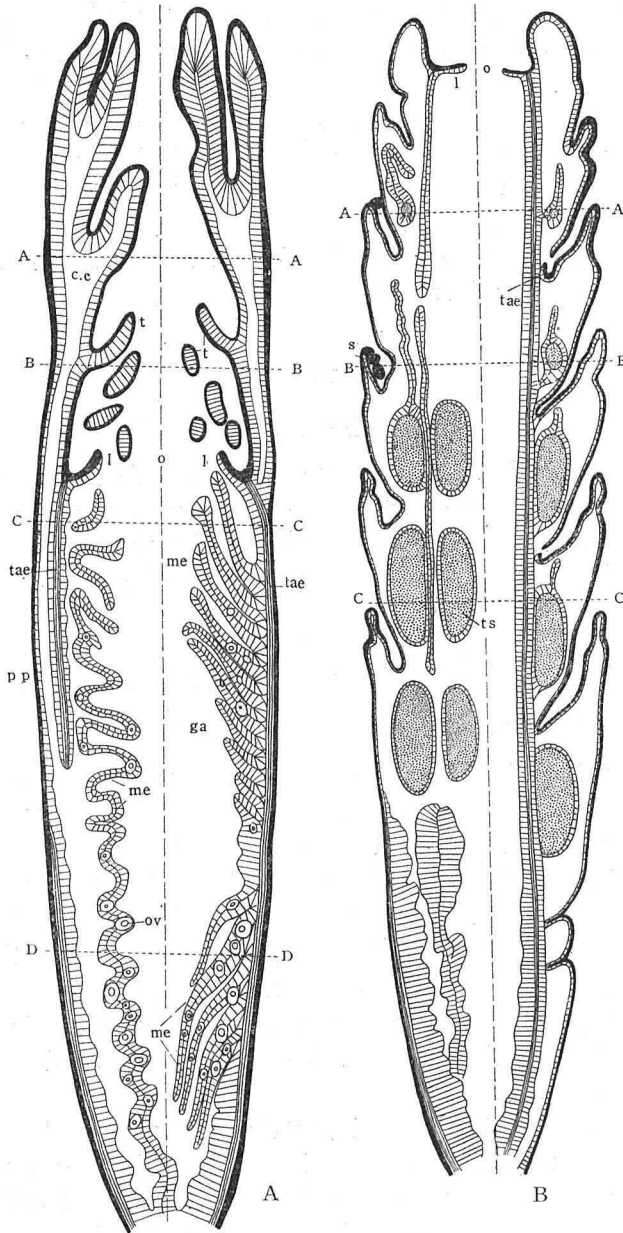


Figure 9. Semidiagrammatic figures of the longitudinal sections of the polyp. A. Of ordinary state. B. During strobilation. In both A and B, the section through the perradial plane is in the left half and the section through the interradianal plane is in the right. a-a, b-b, c-c, d-d (in A) indicating the levels of cross-sections shown in Fig. 10, A-D respectively; a-a, b-b, c-c (in B) indicating the levels of cross-sections shown in Fig. 28, A-C respectively.

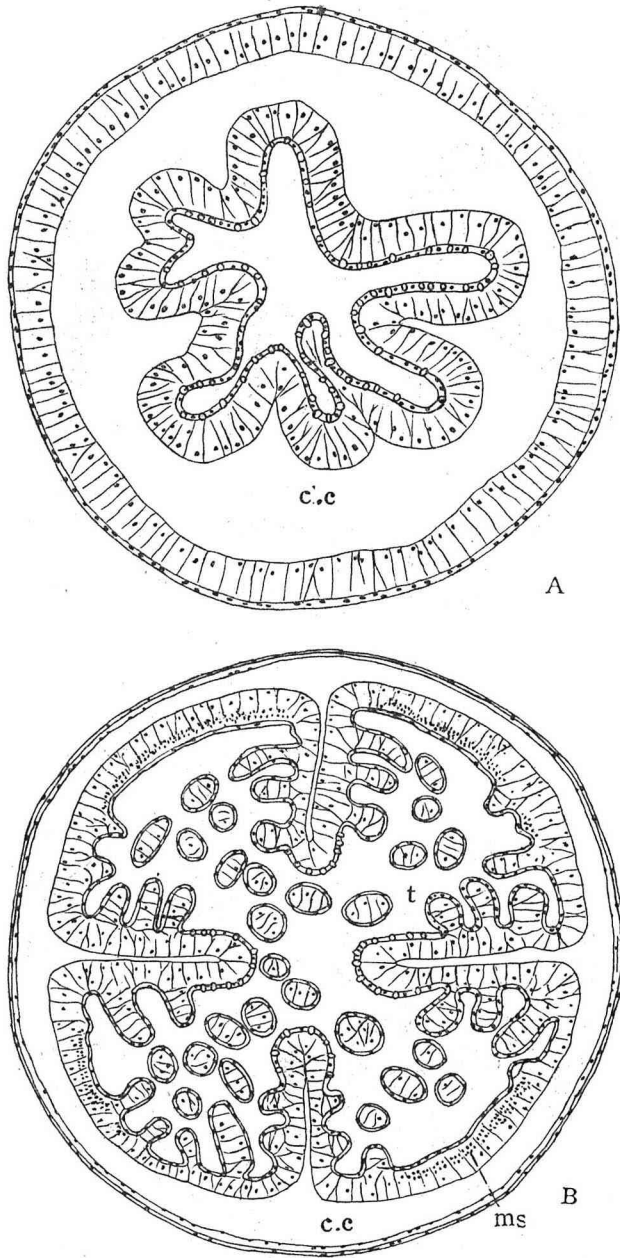


Figure 10. A, B. Semidiagrammatic figures of cross-sections of the polyp in the ordinary state on the levels a-a, b-b, respectively in Fig. 9, A.

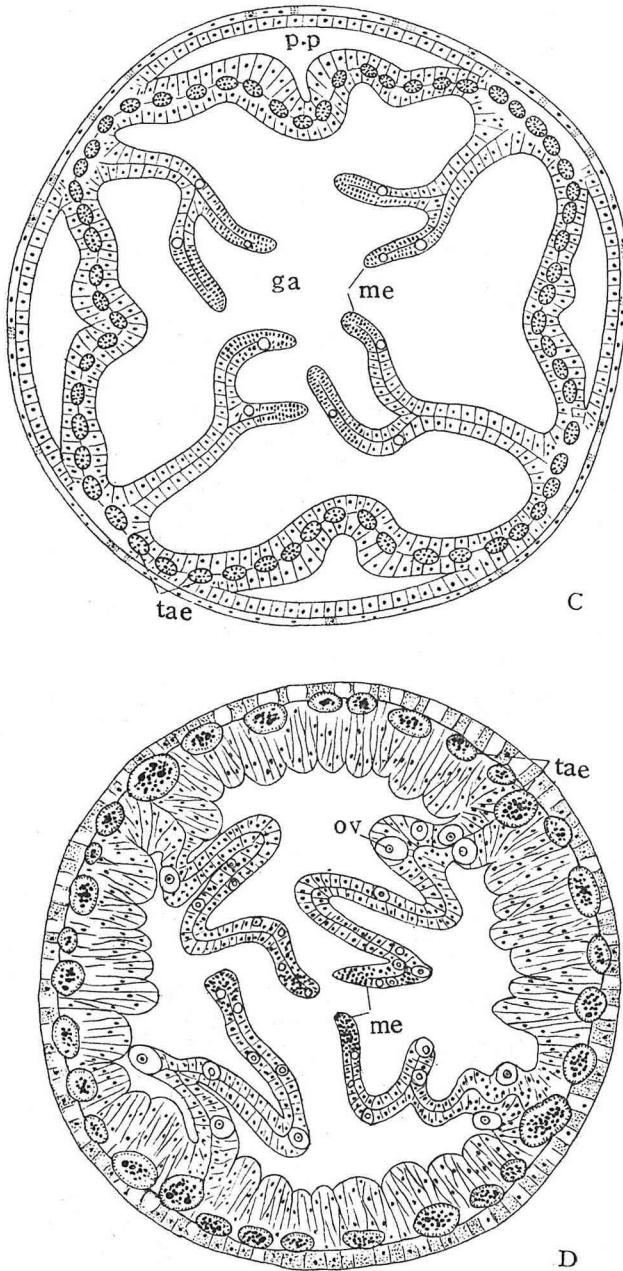


Figure 10. C, D. Semidiagrammatic figures of cross-sections of the polyp in the ordinary state on the levels c-c, d-d, respectively in Fig. 9, A.

The whole external surface of the polyp, the head as well as the tube, is covered by the ectoderm, while the gastric wall and the wall of the coronal cavity and perradial pockets are lined with the entoderm. No stomodæum is found.

Between the ectoderm and the entoderm of the tubular portion of the polyp are inserted a number of longitudinal strands in a

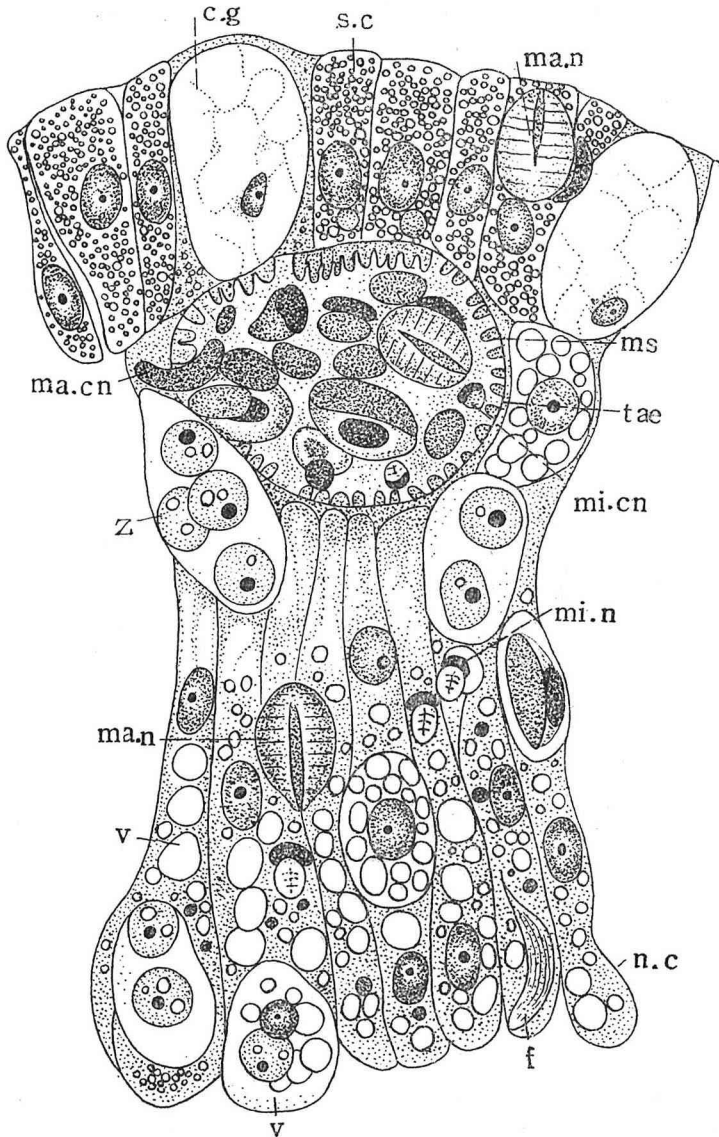


Figure 11. A part of the wall of the tubular portion of the polyp; $\times 1000$.

nearly complete circle. These strands are so-called tænioles (tae). In the scyphistoma of other medusae there occur only four such tænioles, one at each interradius at the base of the mesentery. *Stephanoscyphus* is distinguished from those scyphistomas in that there are a number of tænioles instead of only four. The tæniole is stuffed with nematocysts in various stages of development, and is circumscribed by a layer of longitudinal muscle-fibers.

Histology

Ectoderm (Figs. 11, 12, 14).—As in other cœlenterates, the ectoderm consists of the supporting cells (s. c), two kinds of gland

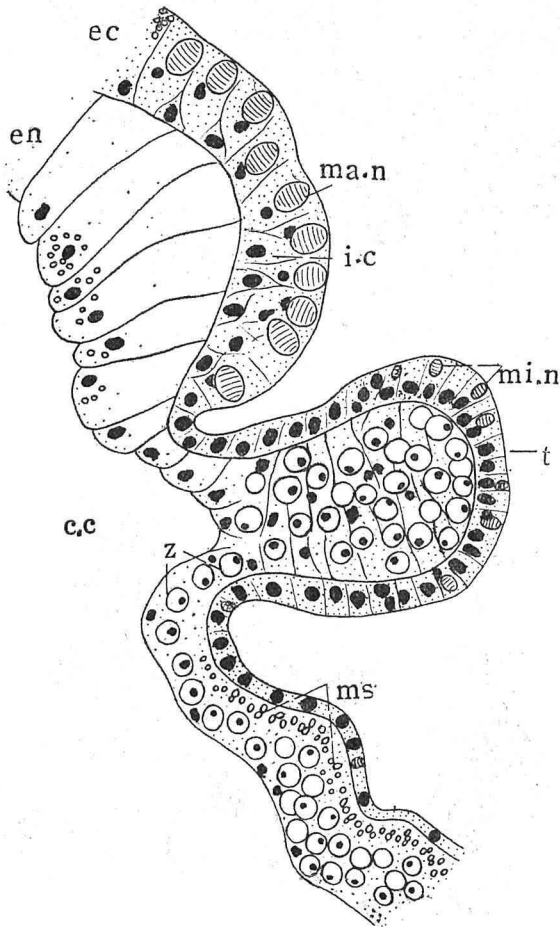


Figure 12. Longitudinal section of the part adjoining the margin of the head funnel of the polyp; $\times 230$.

cells, the granular (g. g) and the clear gland cells (c. g), interstitial cells (i. c) and nematocysts. Besides, there seem to be flagellated cells and sensory cells as will be pointed out later. The supporting cells sometimes have granular inclusions, so that the gradation from the supporting cell to the granular gland cell is insensible. The granular gland cells contain a quantity of secretory granules which stain rather strongly in acid dyes. In shape the granular cells differ little from the supporting cells, except that they may be somewhat flask-shaped. The clear gland cells are sharply distinguished from the other kinds of cells in that they contain apparently mucous substance that stains more or less in basic dyes, and also in that they show always a much inflated appearance, the nucleus being small and shrunken. The interstitial cells occur scattered among the other kinds of cells in the basal layer of the ectoderm.

Entoderm (Figs. 11-13, 15).—The entoderm is made up of the nutritive cells (n. c), flagellated cells (fl. c), granular gland-cells (g. g) as well as nematocysts. The nutritive cells vary greatly in shape and size; but usually they are taller and larger than the ectodermal cells of the corresponding part. They contain a large quantity of inclusions, and often have amoeboid appearance at the free extremities. The inclusions are mostly food-particles and vacuoles which represent various stages of digestion and assimilation, and probably of excretion as well. Another important cell-inclusion is zooxanthellae (z). These occur mostly in the basal parts of the nutritive cell; but cells stuffed with the algae, leaving scarcely any space for cytoplasm, are by no means uncommon.

The flagellated cells (fl. c) are thin and columnar, and occur mostly at the free end of the mesenteries, and in the lip surrounding the mouth. Probably they are found in other parts also, but they are far less conspicuous, if they occur at all. The gland cell is of only one kind, the granular gland cell (g. g) which contains highly eosinophilous granules. The granular cells are developed particularly well in the mesenteries (Fig. 15).

Nematocysts (Fig. 16).—The nematocysts are clearly of two kinds which may be termed macronematocysts (ma. n) and micronematocysts (mi. n). The macronematocyst is ca. 0.17 mm. in length and 0.13 mm. in breadth; the coil of the stinging filament makes about 20 turns. In the discharged macronematocyst one notices the existence of a lid of the capsule, a neck-like swelling of the filament, and a spiral tract passing all along the neck and filament (Fig. 16,

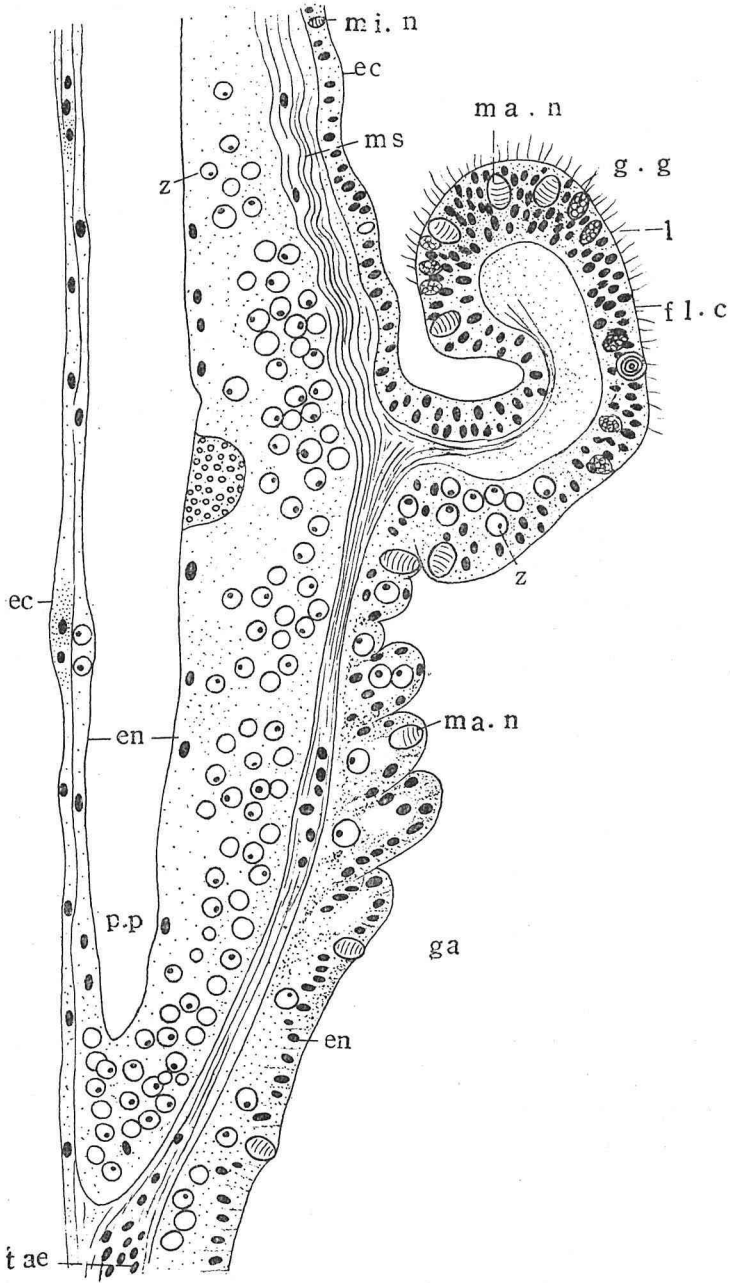


Figure 13. Longitudinal section through the part surrounding the mouth; $\times 230$.

C). The micronematocyst is only one-third the macronematocyst either in length or in breadth; the coil of the filament makes about 10 turns; they are only with difficulty induced to discharge.

Head (Figs. 10, 12, 13).—In the head of the polyp the ectoderm on the concave side is thin, being only $5\ \mu$ in thickness and contains a few micronematocysts. Slight ciliation seems to exist here, as small particles are often observed to be moving on it toward the mouth. Comparatively conspicuous muscle fibers (ms) run radially under the ectoderm, from the point of insertion of the tænioles to be described later, into the base of tentacles. These without doubt serve for the contraction of the head. The entoderm of this part is ca. $40\ \mu$ in thickness and filled with zooxanthellae.

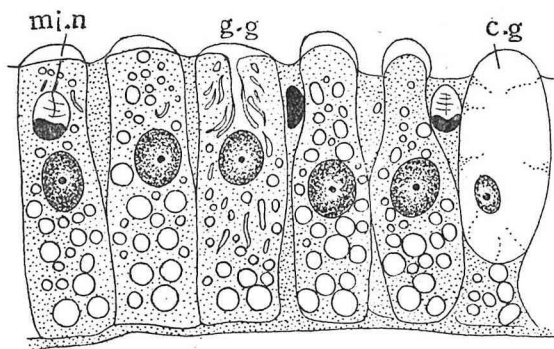


Figure 14. A portion of the epidermis of the neck, composed of gland cells; $\times 1000$.

The margin of the mouth, the lip (l), is composed of columnar flagellated cells (fl. c) sprinkled with granular gland cells (g. g). The region inside the mouth is provided with some macronematocysts (ma. n). This indicates that this region is entodermal, because macronematocysts are missing in the adjacent ectoderm, but found in the entoderm. Thus *Stephanoscyphus*, like ordinary scyphistomas, possesses no stomodæum.

The convex side of the head, the region between the margin of the funnel and the tubular portion of the polyp, is lined with an ectoderm of ca. $30\ \mu$ in thickness. This region is thickly beset with macronematocysts intermixed with a smaller number of interstitial and granular cells. It is exposed and covers up all the rest of the polyp, when the latter is contracted, and the battery of nematocysts gives a severe sting to any enemy that comes to attack the polyp. The entoderm underlying the ectoderm is as high as

100 μ , and contains a few eosinophilous granules near the free extremity; otherwise it looks uniformly clear.

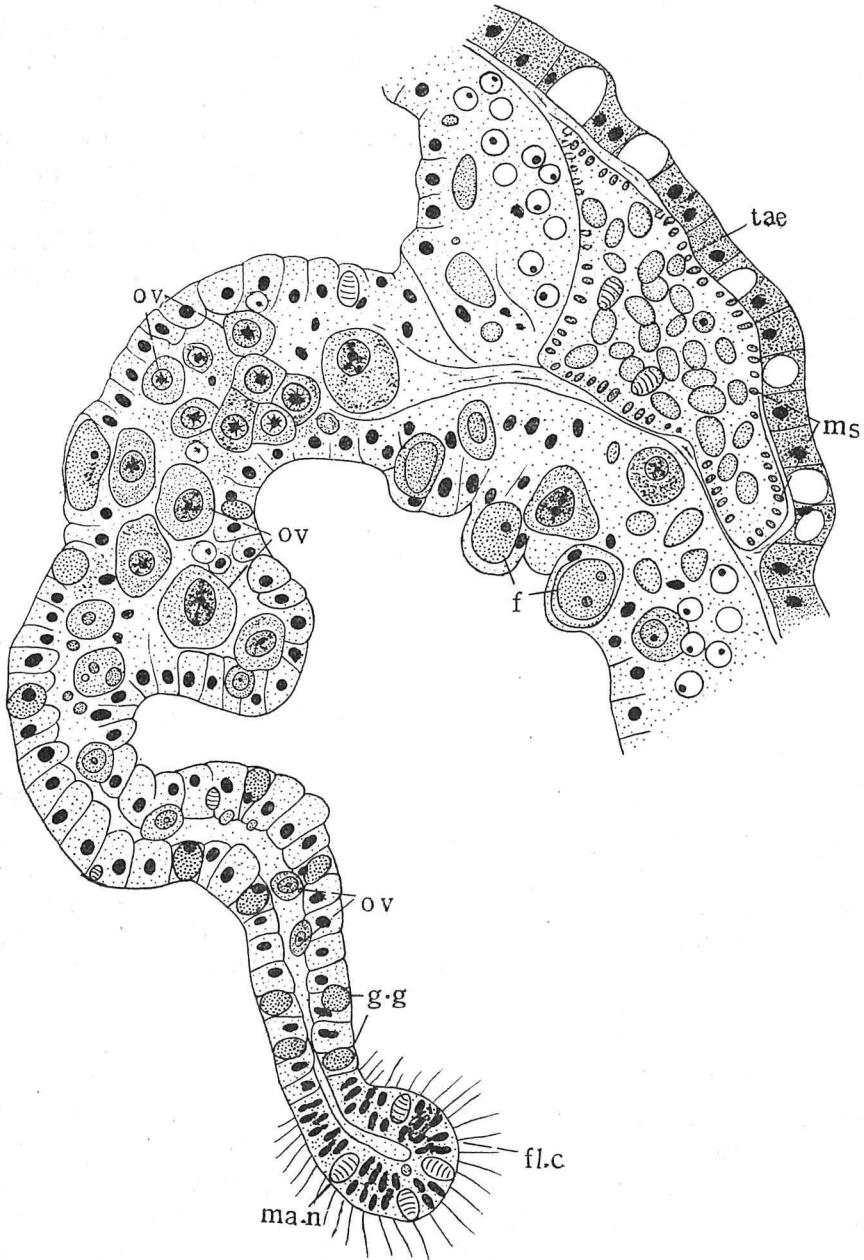


Figure 15. Cross-section of a mesentery; $\times 230$.

Tentacles (Figs. 12, 17).—The tentacles (t) consists of a thin coat of ectoderm and a core of entoderm. The former is formed by small rectangular cells among which are dispersed a few micro-nematocysts. The core is made up of a row of large cells stuffed with zooxanthellae. When the tip of a living tentacle is examined under a high power, a number of long stiff bristles are visible (s. h). SCHULZE regards them as cnidocils. This does not seem to be the case; more probably, they are sensory hairs. Flagella (fl) also occur, though very sparsely.

Neck (Fig. 14).—The part between the head and the tube which may be termed neck, has a thick epidermis (35–50 μ), which contains numerous granular and clear gland cells. There are also a few nematocysts of both types. It is evident that the epidermis of this

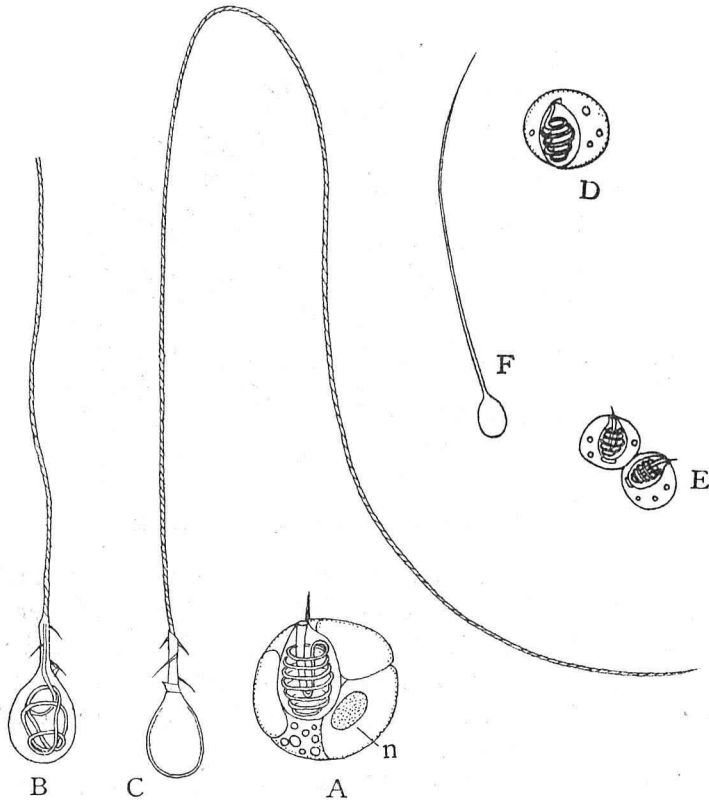


Figure 16. Nematocysts from a living specimen. A-C. Macronematocyst. A. quiescent, B. half-discharged, C. wholly discharged. D-F. micronematocysts. D. E. quiescent, F. discharged; $\times 750$.

region plays an important part in the secretion of the periderm. The growth in length of the theca is apparently due to the secretion of new rings from this part, while the growth in thickness is brought about by the addition of new substance to the periderm by the more proximal part of the epidermis of the tube.

Tubular portion.—The tubular portion of the polyp has an epidermis composed of cells mostly glandular. There are both granular and clear gland cells besides nematocysts of both types. Some of the secretory granules appear somewhat linear in shape.

The entodermal cells lining the gastric wall (Figs. 11, 15) are large and contain a quantity of food-particles (f) and waste products. Of the food particles, pieces of bodies of small crustaceans are very common, showing that such constitute the main food material of the polyps. The more basal portion of the cells enclose zooxanthellae.

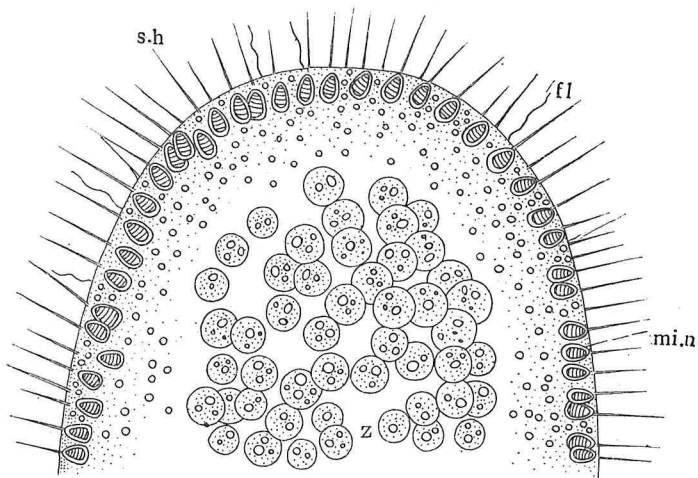


Figure 17. Tip of tentacle of a living specimen; \times ca. 500.

Mesentery (Fig. 15).—The mesentery shows a differentiation similar to that found in Anthozoa, but decidedly of a lower grade. The free extremity is made up of flagellated cells (fl. c) and macronematocysts (ma. n), the part next to it contains a fairly large number of granular gland cells (g. g), while the more basal part may harbor germ-cells (ov).

Tænioles (Figs. 10, 11, 13, 15, 18).—As pointed out above, *Stephanoscyphus* shows the important difference from the ordinary scyphistoma that tænioles occur in large numbers instead of being only four. They lie between the epidermis and the gastric entoderm,

forming a nearly complete circle around the gastric wall. In cross-sections they are rounded, oval or triangular. They have their origin in the head of the polyp at the base of the lip (Fig. 13), and pass all through the length of the polyp to its basal end. Several of them converge into one, and some disappear, as they approach the base, so that there are fewer and fewer tænioles toward the basal end, and none is left at the very base of the polyp. The four

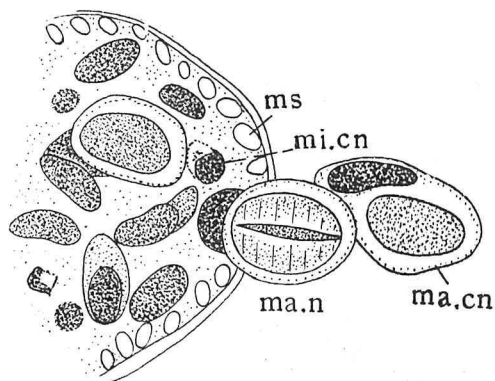


Figure 18. Migration of nematocysts from a tæniole; $\times 1000$.

tænioles situated at the bases of the mesenteries may be distinguished from all others by their greater thickness (Fig. 15). It may be unnecessary to add that these represent the tænioles occurring in the ordinary scyphistoma.

Each tæniole is encircled by a thin mesogloea. Directly within it occurs a layer of longitudinal muscle-fibers (ms). The internal

space is filled with formative cells of nematocysts.

At the distal end of the tænioles, some of the muscle-fibers are directly continuous with the fibers of the radial muscles of the head (Fig. 13). But there is scarcely any fiber going into the lip.

Development of nematocysts (Fig. 19).—It is easy to trace the process of development of the nematocyst. The initial stage is represented by the cell with clear plasm and a large vesicular nucleus. Next comes the stage in which the plasm shows a cloudy area stained more deeply than the rest (A,B). This area is gradually con-

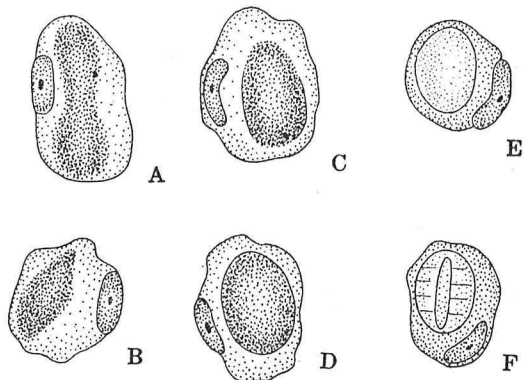


Figure 19. Developmental stages of macro-nematocyst; $\times 700$.

densed and becomes an oval opaque mass which has neutral staining reaction (C, D). The reaction changes gradually into strong acidophily, and the outline of the mass becomes more definite (E). Then a coiled filament is formed in the mass (F), and the formation of the nematocyst is completed. In the meantime the nucleus has been transformed into the crescent body which is characteristic of the nucleus of the cnidoblast.

Thus the tæniole is the matrix of nematocysts. Apparently most, if not all, nematocysts found in tissues of the polyp

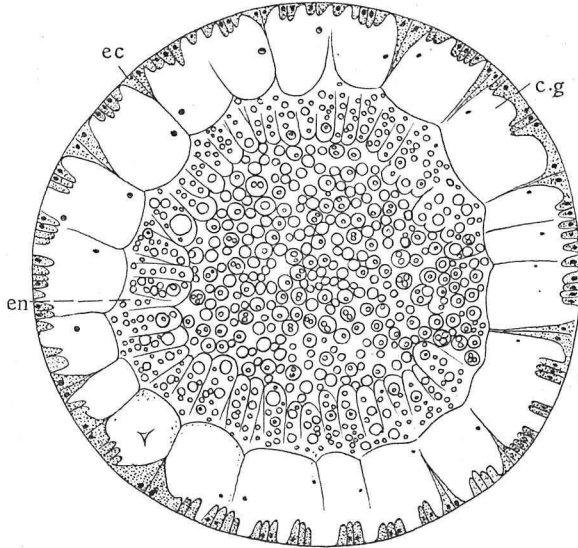


Figure 20. Cross-section of a part of stalk; $\times 100$.

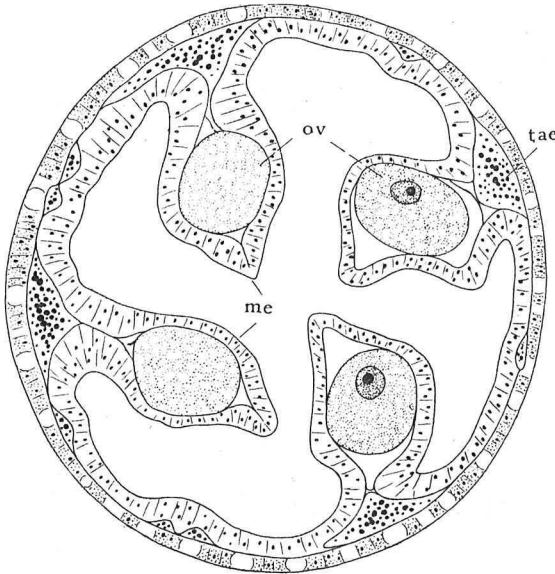


Figure 21. Cross-section of a polyp containing very large eggs; $\times 80$.

originate in the tænioles and migrate to their definitive sites. The migration may occur in the mature stage, or during the developmental change. One often perceives nematocysts or their developmental stages on the way through the mesogloea surrounding the tæniole toward the epidermis, or into the gastric entoderm (Figs. 11, 18). It is also common to find nematocysts or their younger stages imbedded among cells of these tissues.

Stalk (Fig. 20).—Near the base of the polyp, mesenteries become obscure, tænioles disappear, and entodermal cells are full of inclusion. In the stalk the epidermis is high and comprises a large number of clear gland cells, and the entoderm is stuffed with inclusion. The gastric cavity also contains a great quantity of free plasmic spherules which carry much inclusion. These are no doubt pieces of cells which previously formed the entodermal wall.



Figure 22. Longitudinal section of a polyp containing a number of full-sized eggs; $\times 80$.

Germ cells.—In the specimens collected in August and November 1930, and also in July and August 1934, germ cells were found. In no specimen collected on other occasions have I seen the germ cells. The young germ cells (Fig. 15, Pl. XXII, fig. 2) occur in mesenteries of the region near the bottom of the polyp. They are imbedded mostly in the mesogloea in the basal part of the mesentery, but may be scattered among entodermal cells. Primordial egg cells are amœboid in appearance and have without

doubt the power of locomotion (ov). Several specimens collected in August 1930 and in July and August 1934 contain many eggs as large as the largest eggs found in *Nausithoë* (diameter about 0.2 mm.) (Figs. 21, 22, Pl. XXII, fig. 3). In some of these specimens, such large eggs are arranged in almost continuous series (Fig. 22). Other specimens contain a great quantity of male germ cells. These also occur in almost continuous series (Figs. 23, 27, A). The



Figure 23. Longitudinal section of a polyp containing spermatogonial cells; $\times 80$.

component cells are in various stages of differentiation, apparently from spermatogonium to spermatid. In the cases where such large eggs or great quantity of testicular cells are found, the mesenteries bulge out conspicuously on both sides, and the covering entoderm is reduced to a very thin membrane. But I have never come across any mature spermatozoa or eggs in *Stephanoscyphus*. It remains to be demonstrated whether such eggs or sperm cells do take part in fertilization or not. In any case, the occurrence of germ cells es-

pecially of such advanced stages in a scyphopolyp, is a fact worthy of special attention.

Strobilation

Strobilation has been observed. But its occurrence is comparatively rare, apparently because propagation by budding is predominant. Among the materials obtained in the later part of August 1930 were some specimens which were undergoing strobilation.

My observation on these materials agrees in the main with the accounts given by previous authors, such as CLAUS (1892), HEIN (1900), FRIEDMANN (1902), HERIC (1909), HADZI (1909), HARGITT (1910), PERCEVAL (1923), TCHFOU (1930) on various discomedusae. So I shall describe the phenomenon only briefly.

Preparatory changes.—Strobilation is accompanied by changes

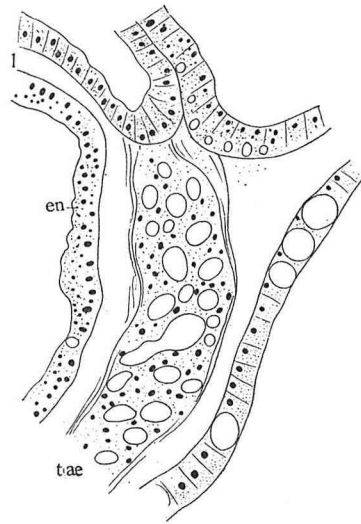


Figure 24. Degenerative change of tæniole before strobilation. A longitudinal section through the region adjacent to the oral end of the tæniole; $\times 150$.

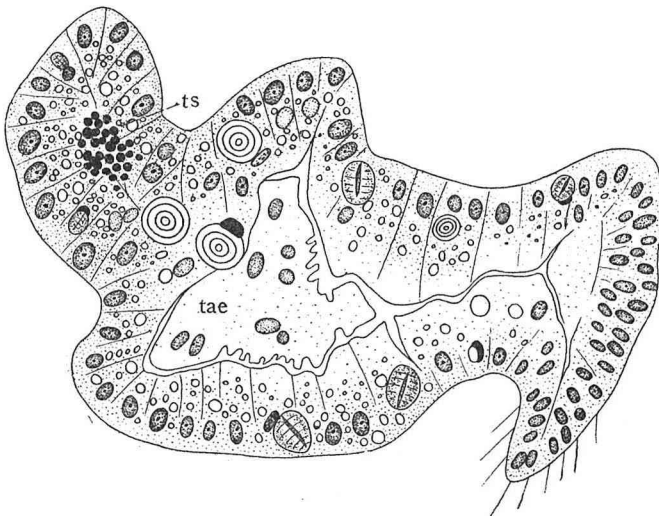


Figure 25. Degenerative change of tæniole and gonad during strobilation. A transverse section across a mesentery; $\times 500$.

of a very profound nature resembling those occurring in the cases of metamorphosis of various animals. First the gastric entoderm diminishes uniformly in thickness. This seems to result from the fact that the terminal portions of the component cells are constricted off. These liberated pieces of cells become corpuscles circulating in the gastric canal. In the meantime, *tænioles* disintegrate (Figs. 24, 25); the muscle-fibers which they contain become attenuated and broken into pieces, and the nematocysts and their younger stages are liberated in the gastric cavity. Eventually the *tænioles* disappear completely, except only the four which are at the bases of the mesenteries, and even these have undergone a good deal of degeneration. As a consequence, the gastric cavity enlarges greatly, and its peripheral part almost encircles the *tænioles* at the bases of the mesenteries.

Hand in hand with these disintegrating changes in the tubular portion of the polyp, the tentacles disappear (Fig. 26). This seems to be brought about in the manner that HARGITT (1910) and TCHÉOU (1930) have described in the case of disco-medusae: the tissues composing the tentacle disintegrate and are absorbed by the neighboring tissues; the ectoderm is absorbed by the entodermal cells forming the core, and these latter in turn become free one after another from the base of each tentacle and are devoured by the adjacent entodermal cells. In consequence, no tentacle is left when the strobilation begins.

Thus, as has been described above, when the polyp enters the stage of strobilation, there occurs the disintegration of tissues on a large scale. Most of the disintegrating tissues are absorbed by the entodermal cells, especially in the basal region of the polyp. These cells accordingly become stuffed with inclusions. The majority of

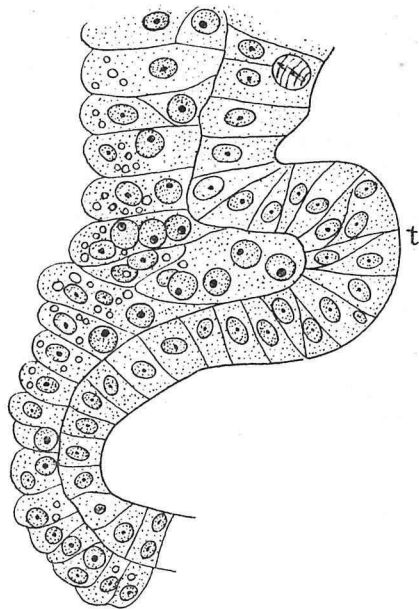


Figure 26. Degenerative change of tentacle before strobilation; $\times 500$.

these inclusions are the substance which was previously the components of the more distal portion of the polyp. These are probably utilized as material for the development of ephyrae as well as for the regeneration after strobilation.

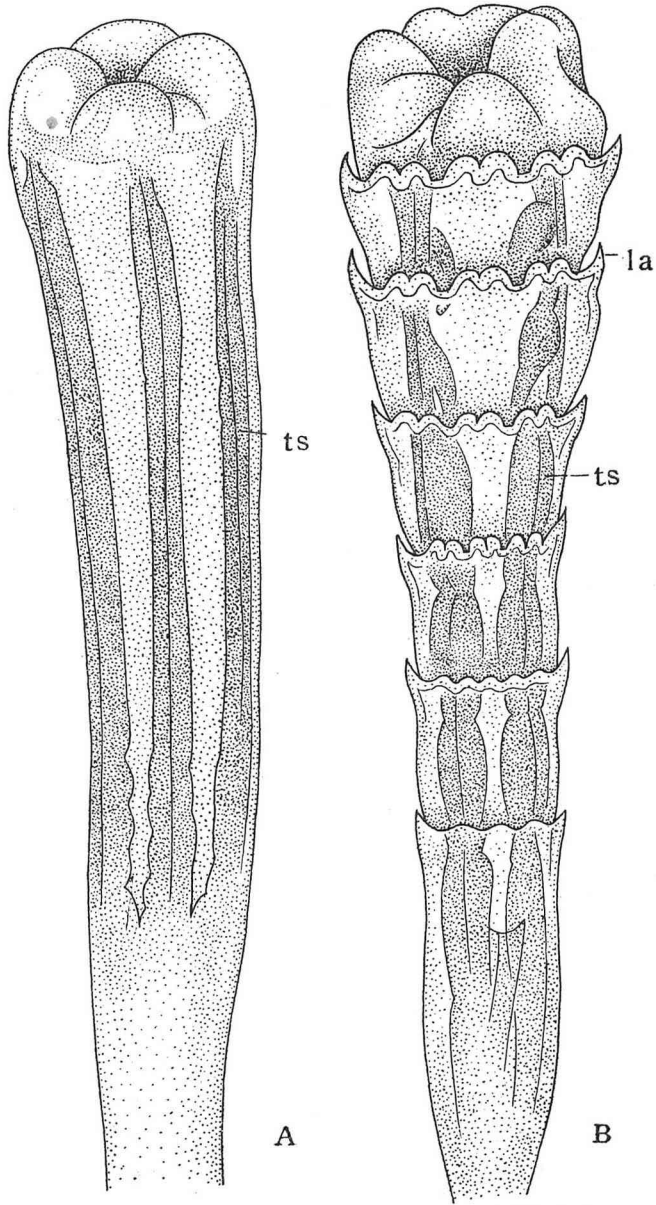


Figure 27. Total views of male polyps (A) before and (B) during strobilation. Fixed and clarified materials; $\times 20$.

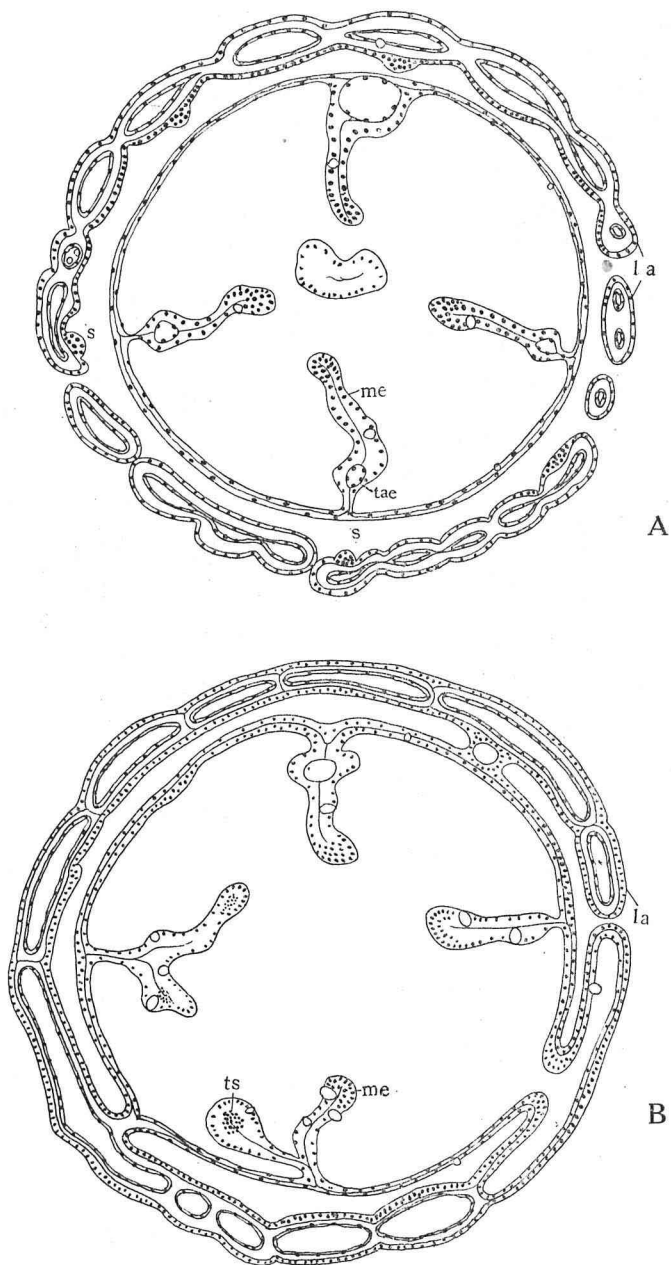


Figure 28. A, B. Semidiagrammatic figures of transverse sections through the male polyp during strobilation. Levels of sections are shown in a-a, b-b, respectively in Fig. 9. B.

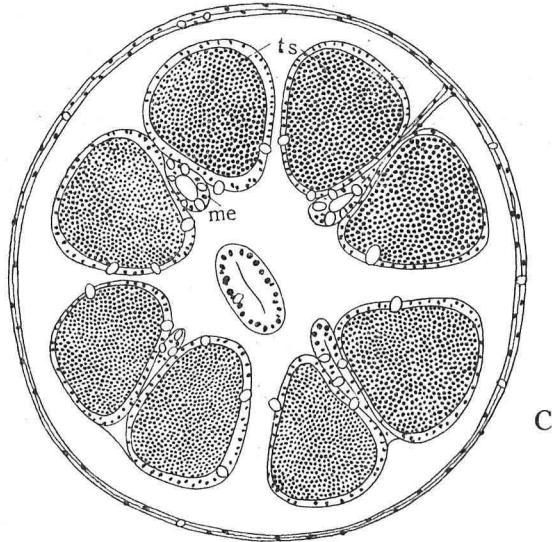


Figure 28. C. Semidiagrammatic figure of transverse sections through the male polyp during strobilation. Level of section shown in c-c in Fig. 9. B.

Development of transverse constrictions.—The transverse constrictions of the strobila arise and advance nearly in the same manner as described by HERIC (1909), PERCIVAL (1923) and TCHÉOU (1930) in various discomedusae. The strobilation belongs to the polydisc type, several constrictions being formed at the same time (Figs. 9B, 27, 28; Pl. XXII, figs. 4-6).

The constriction is initiated by the thickening of both the epidermis and gastral entoderm of the polyp. This is brought about by the component cells becoming taller and also multiplying by division. As a consequence, a fold develops in the same region (Fig. 29, A). In a longitudinal section, this region shows a sigmoid outline, there being an invagination above and an evagination below. The folding increases and both the invagination and the evagination become deeper (Fig. 29, B, C, Fig. 30). The invagination does not seem to proceed equally around the circumference of the polyp. It proceeds fastest at the interradii, so that a pocket is formed for a time at each interradius.

The evagination has on its external side an ectoderm which is made up of tall cells containing fine eosinophilous granules sprinkled with macronematocysts (Fig. 29, C). On the internal side, the entoderm is thinner and has in its basal layer muscle-fibers which

are the primordia of circular muscles of the medusa (ms). Near the distal end of this side, is found the primordium of the sense-organ (s). As is known in other cases, the organ develops by the collaboration of the ectoderm and entoderm, the former forming the covering and the latter the core. Here the ectodermal cells become particularly tall and slender, comprising nuclei in two or three

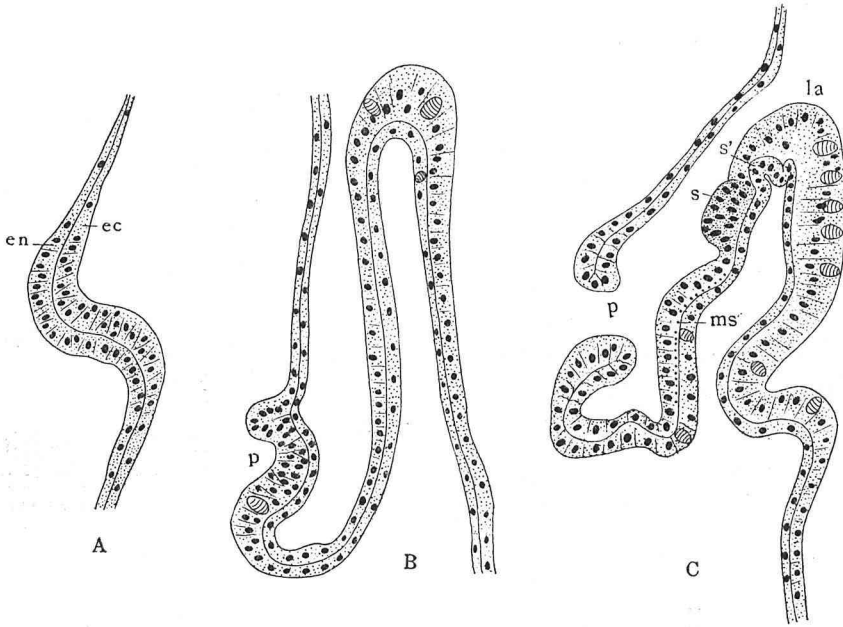


Figure 29. Longitudinal sections of a part of the wall of the polyp during strobilation, showing the progress of constriction and perforation; $\times 150$. s—ectodermal component of the primordium of sense-organ. s'—entodermal component of the same.

layers, and are marked off from the surrounding parts as a knob-like mass. The entoderm develops a small swelling directly above this knob (s'). The two structures become united subsequently to form a sense-organ.

The process of cutting off the ephyrae is initiated by perforations of the wall of the strobila in the region slightly above the bottom of the invagination (Figs. 29, 31, 32, p). The perforation seems to appear first at the perradii. Here the entoderm thickens and forms a spherical swelling, which grows rapidly and finally forms a round hole. Similar perforations appear at interradii and adradia also (Fig. 32). Although the subsequent stages are not

found in my material, there is no doubt that these perforations are united transversely, so as to become a continuous rift all around the circumference.

The mesenteries and gonads are cut by these constrictions into as many sections as there are primordia of ephyrae in the same polyp (Figs. 9 B, 27, Pl. XXII, fig. 6). The distal primordia contain fewer germ-cells than the proximal ones. This appears singular at first sight. But as will be stated below, this is probably due to degeneration of germ cells.

I have never seen the actual process of the liberation of ephyrae, nor have I ascertained that the ephyrae of *Nausithoë* originate from strobilation of *Stephanoscyphus*. Still there seems to be no room for doubting that this is the fact, since

1. LO BIANCO and P. MAYER observed in Naples a number of ephyrae apparently of *Nausithoë* swimming in a jar containing a colony of *Stephanoscyphus*. 2. The season of appearance of ephyrae and young stages of *Nausithoë* in the waters of Seto coincides with, or comes shortly after, the season of strobilation of *Stephanoscyphus*. 3. No other ephyra or young medusa occurs in the vicinity of Seto in these seasons.

Nausithoë

Material examined.—This peculiar scyphomedusa is not uncommon in the neighborhood of Seto, though it is much rarer than *Aurelia*, *Dactylometra* or *Mastigias*. It appears in the late fall and in winter. One is fortunate if after searching a whole day he can secure as many as ten specimens. The *Nausithoë* found round Seto is decidedly smaller than the same species occurring in the tropics, reaching a maximum of 8 mm. in diameter as contrasted

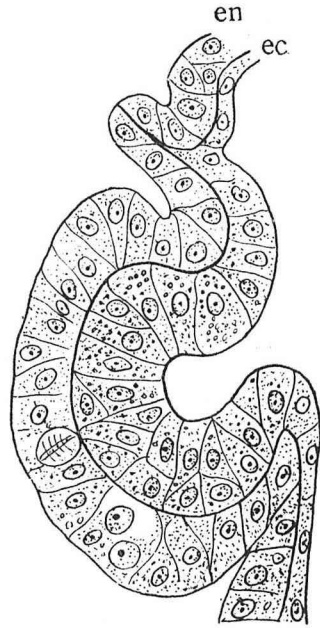


Figure 30. Longitudinal section of a part of the wall of the polyp during strobilation. A stage between A and B in Fig. 29, more highly magnified; $\times 500$.

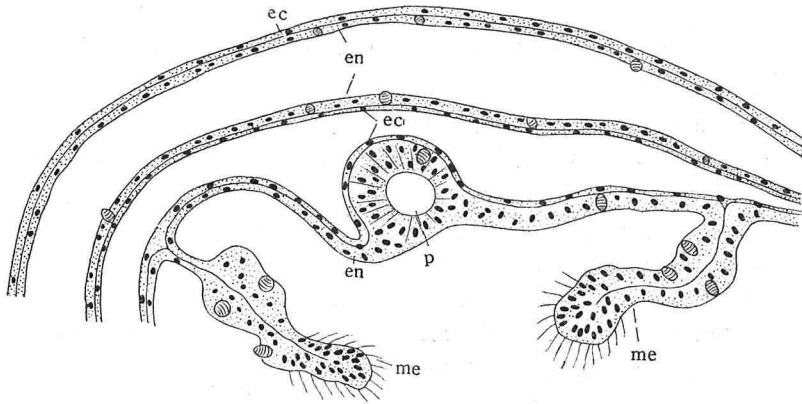


Figure 31. Transverse section of a part of the wall of the polyp during strobilation; $\times 150$.

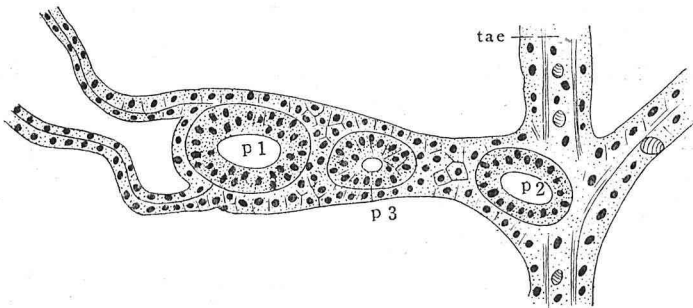


Figure 32. Tangential section of a part of the wall of the polyp during strobilation, showing especially the perforations; $\times 150$. $p_1 \dots p_3$ — showing perforation in the perradial, interradial and adradinal plane respectively.

with 15 mm. recorded in the tropical specimens (KRAMP, 1924, KRUMBACH, 1925). I have obtained at Seto more than a hundred examples of various stages of this medusa, ranging from ephyra to the stage ca. 8 mm. in diameter. Moreover, by the kindness of Prof. T. UCHIDA and Prof. A. POLOMBI, I was able to secure three specimens from Misaki, eight from Kagoshima Bay and about ten from Naples for comparison, besides the eight examples from Naples in custody of the Zoological Institution of our university. My findings on these materials have largely confirmed the accounts given by previous authors, so there is hardly need of detailed statements.

Ephyra and young medusa.—The ephyra of this medusa has a characteristic appearance (Fig. 34, Pl. XXI, fig. 2). It measures 1.5–2 mm. in diameter, and has its margin divided equally into 16

lappets. It has no tentacle, but is provided with a sense-organ in each adradius and also a gastral filament in each interradius. The filament is still fastened to the subumbrellar entoderm at both ends (Fig. 35). The whole body of ephyra is colorless and highly transparent, except a number of granules which are nothing but nematocysts scattered over the whole body. There occur also some yellowish refringent crystals in the margin of the lappets. These

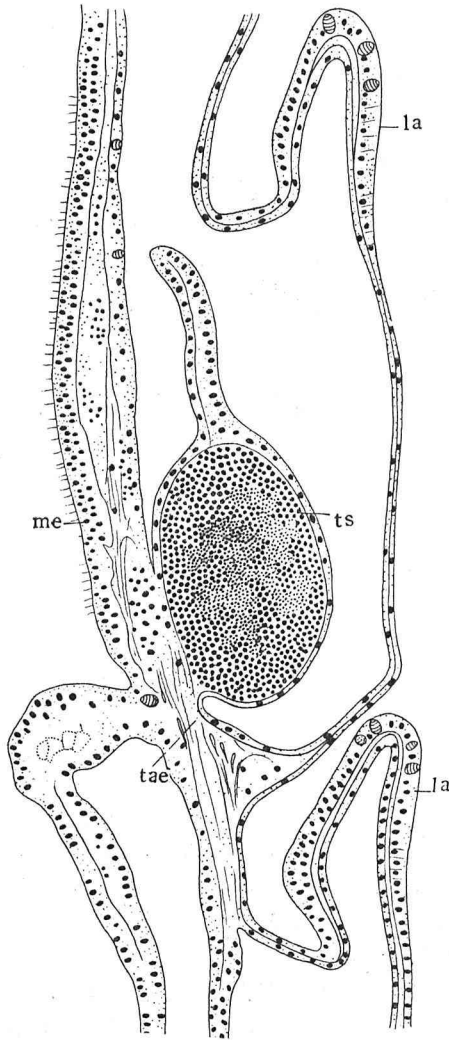


Figure 33. Longitudinal section through a part of the polyp during strobilation; $\times 110$.

crystals are depicted faithfully in CLAUS' figure. They are hexagonal pillars of various lengths. The origin of these crystals is not clear, but they seem to have some relation to zooxanthellae in origin. In young *Nausithoë*, one often sees some dirty-yellow spherules resembling in appearance zooxanthellae, imbedded in the endodermal cells in the region of the circular muscle, and in these spherules are enclosed the crystals (Fig. 36 B).

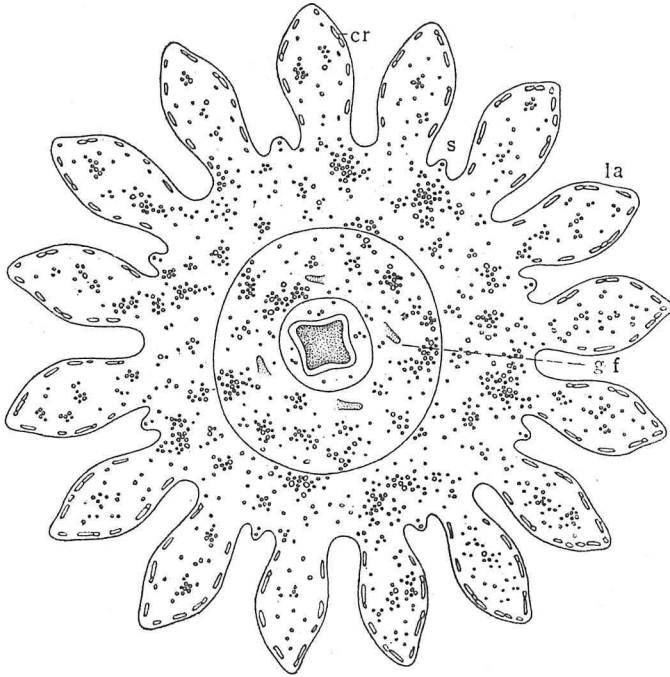


Figure 34. Ephyra of *Nausithoë*. Sketch of a living specimen; $\times 50$.

The stage slightly more advanced (Fig. 37), is distinguished from ephyra, by the formation of short tentacles, the elongation of gastral filaments, and also by the appearance of the crescent-shaped primordia of gonad in each adradius on the level midway between the ring-furrow and the base of the tentacle. In specimens about 3 mm. in diameter the tentacles are nearly half as long as the lappet, and there are two gastric filaments in each radius and the primordia of gonad are more conspicuous than in the younger stage.

Development of gonad.—The first primordia of gonad occur in ephyra (Fig. 35). Although they are hardly recognizable in living specimens, they may be found in sections. The sections of the

adradial region show on the level between the margin of the umbrella and the margin of the mouth, the existence of a few free cells with particularly large nuclei in the subumbrellar entoderm. These are primordial germ-cells. In a slightly later stage when the gonadal primordia may be recognized easily from outside, the cells form a marked aggregate at the corresponding spot. Still the sex cannot be told (Fig. 38). In a stage slightly more advanced, the sex is differentiated, and a genital sinus is formed among the germ-

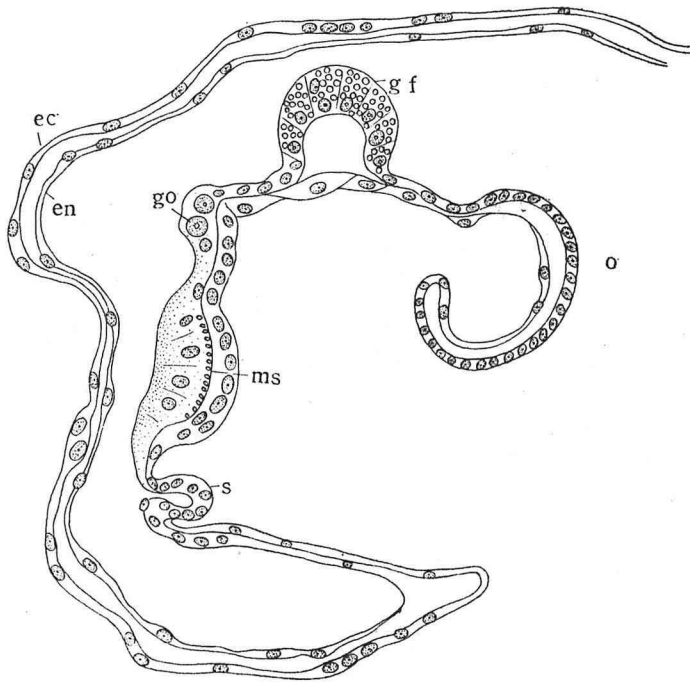


Figure 35. Longitudinal section of ephyra. The material is shrunken and shows, gastral filament (g. f) gonad (go) and sense-organ (s) in the same section; $\times 400$.

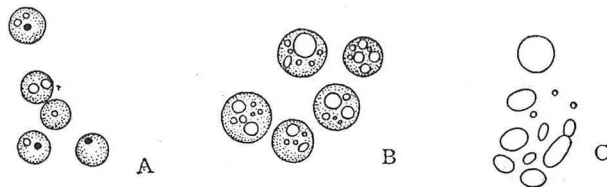


Figure 36. A. Zooxanthellae found in *Stephanoscyphus*, B. Yellowish spherules found in some young specimens of *Nausithoë* and containing crystals. C. Crystals found in young specimens of *Nausithoë*; $\times 400$.

cells in either sex (Figs. 39, 40). Further development is due to the rapid multiplication of the germ-cells and the growth of each cell. The medusa which has attained 5 mm., contains mature sperms and ova (Fig. 41, Pl. XXI, 3). HAMANN (1883) maintains that in ephyra of *Nausithoë* the primordium of gonad appears at each interradius at the base of each gastral filament, and these primordia gradually migrate to the adradial. However, this is not the case; the primordia are formed at the adradial spots from the start.

The structure of gonad in full development has been described by previous authors notably by CLAUS (1883) and VANHÖFFEN (1892).

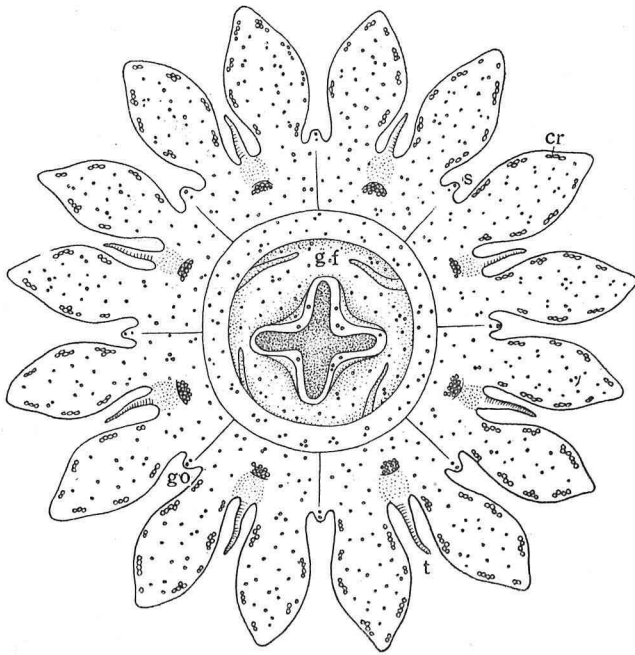


Figure 37. Young specimen of *Nausithoë* with diameter 3 mm.

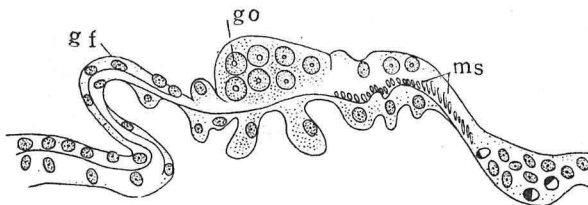


Figure 38. Gonad in *Nausithoë* of a slightly more advanced stage than ephyra; $\times 400$.

The sexes can be distinguished from the external appearance of the gonad (Fig. 41). The testis is sausage-shaped (B), and opaque yellow in color, with a longitudinal shaded area occupied by ripe sperms. The ovary on the other hand (A), is oval or even sub-spherical, wine-yellow, and nearly transparent, and has no shaded area.

Fate of germ cells of Stephanoscyphus.—As stated above, I have met with several cases of strobilating polyps or of polyps in

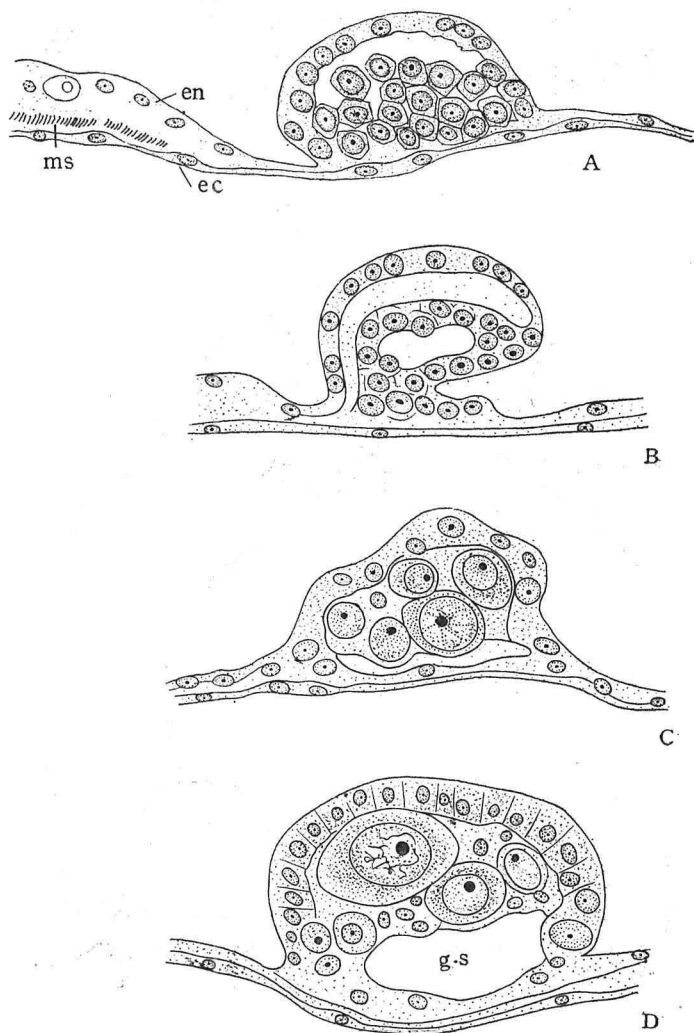


Figure 39. Successive stages of the development of ovary of *Nausithoë*; $\times 400$.

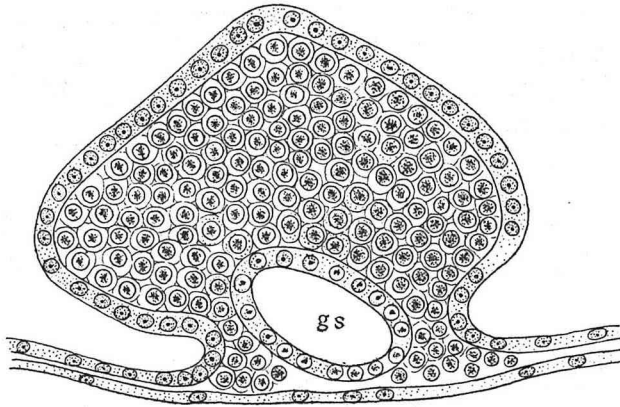


Figure 40. Section of a young testis of *Nausithoë*; $\times 400$.

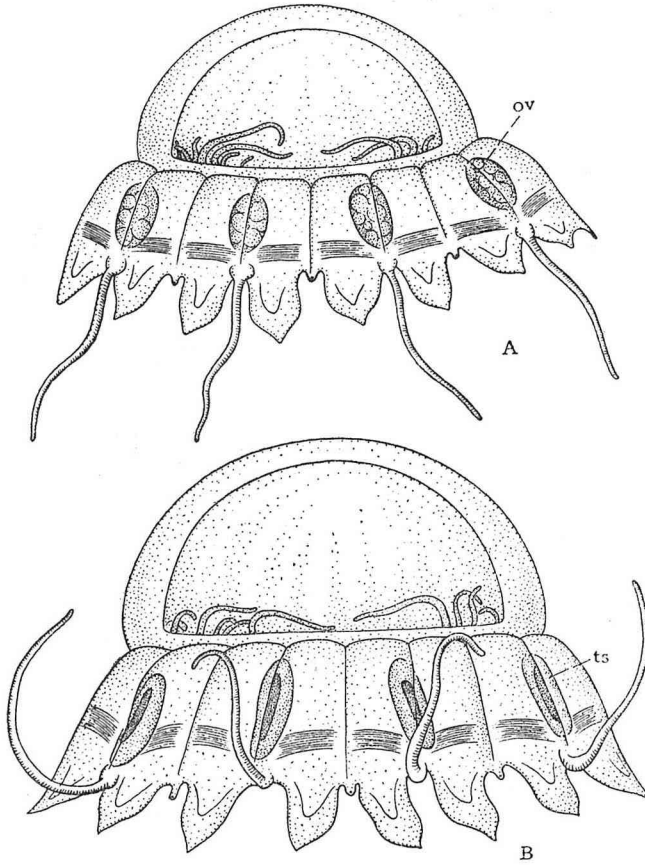


Figure 41. Side views of mature specimens of *Nausithoë*; \times ca. 20.
A. Female. B. Male.

the stage before strobilation. These contain a great quantity of sperm-cells apparently of the spermatid-stage, or ova as large as the mature ova occurring in *Nausithoë*. But very singularly, in no individual of ephyra or young *Nausithoë* have I found germ-cells in such advanced stages. To reconcile the above apparent inconsistency in my own observations, it seems necessary to assume one of the following alternatives: the gonad found in *Stephanoscyphus* undergoes complete degeneration before the liberation of ephyrae, after once attaining the stages mentioned; or it develops fully-formed sperms or ova which are all liberated in water. As a matter of fact I have found in the strobilating specimens that the more distal ephyra rudiments generally contain a smaller quantity of sperm-cells, than the more proximal ones. Moreover, in those more distal ephyra rudiments there can be seen unmistakable signs that the once highly developed testes have undergone quick degeneration, and the membrane that had once covered the testes remains as mere strands on either side of the mesentery. It also seems

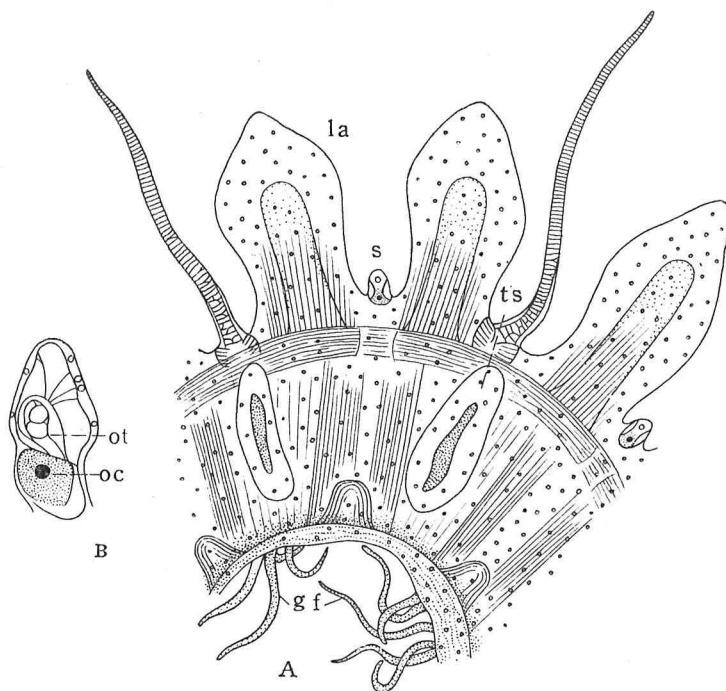


Figure 42. Subumbrellar view of a part of a mature male specimen of *Nausithoë*, showing some details of structure; $\times 25$. B. Sense-organ more highly magnified.

significant that I have never met with any mature spermatozoa in the strobila. These observations no doubt favor the first alternative rather than the second.

In female polyps, however, I have never seen any sign of degeneration of eggs. On the contrary, I have come across several cases of fully developed eggs surrounded by a very thin coat of entoderm. In such cases it appears more probable that these eggs are shed and fertilized in water than that they degenerate *in situ*. But I have no decisive evidence for either possibility.

Irregular specimens.—As a general rule, the tentacles, gastral filaments and gonads of *Nausithoë* develop nearly at the same rate.

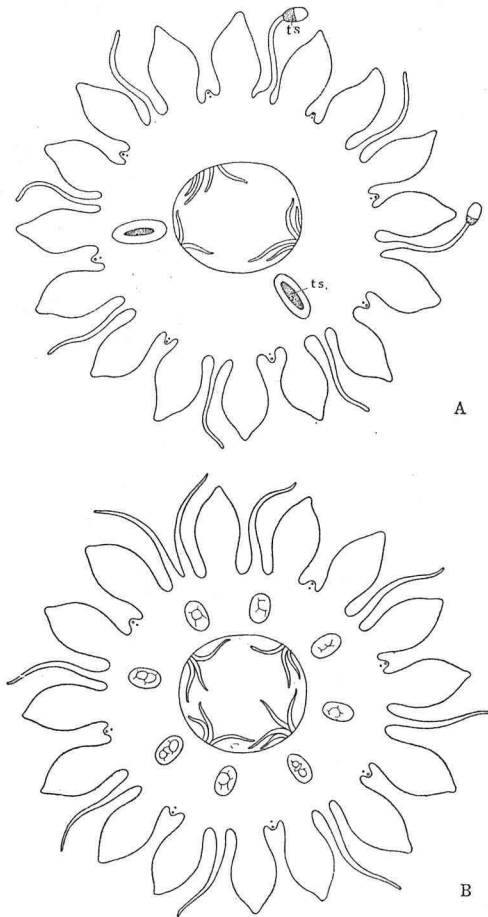


Figure 43. A, B. Irregular specimens of *Nausithoë*.
A. Male. B. Female.

But exceptions are quite common. The individuals of the medusa occurring at Seto quite frequently show irregularities of various sorts. Both the number and the position of umbrella lappets, tentacles, gastral filaments or gonads vary greatly (Fig. 43, A-H). Especially the gonads show a high degree of irregularity. I have seen cases where a fairly large specimen is without any rudiment of gonad or has it in a single octant (E), or where a gonad occurs at the center of a lappet (F), or even in the distal end of the tentacle (A).

Specimens of Seto as compared with those from other localities.—As compared with the specimens found at Seto, those from Naples are apparently larger and with more spherical gonads, and with less irregularity in structure. But a few individuals from Seto have gonads of exactly the same shape as the latter specimens.

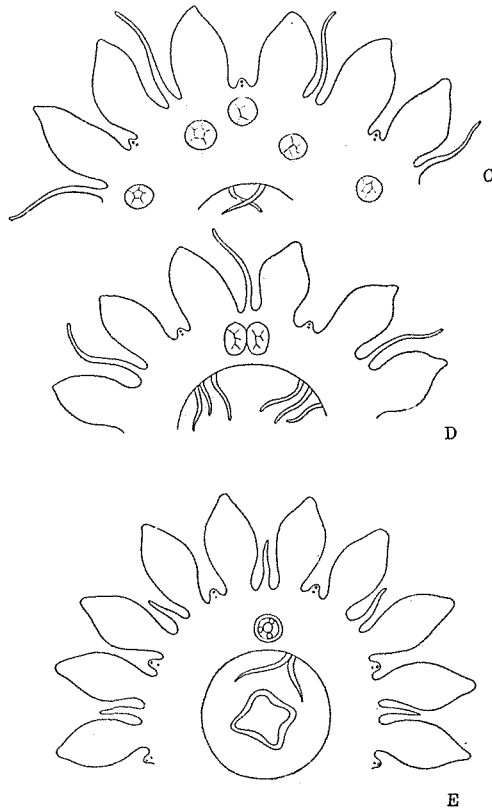


Figure 43. C, D, E. Irregular specimens of *Nausithoë*.
Females.

Moreover, the examples from Kagoshima show little difference from the Neapolitan specimens either in size or in the shape of gonads. Thus we seem warranted in identifying the Japanese form of this medusa with *N. punctata*.

According to the detailed statements by VANHÖFFEN (1909), KRAMP (1923) and KRUMBACH (1925), the distribution of *Nausithoë* is restricted to the tropical seas of the world. Although it occurs in the Mediterranean as well, the examples are undersized. The individuals found in Seto are even smaller than the Mediterranean specimens. This is due without doubt to the unfavorable environmental conditions around Seto. Especially, the too low water temperature seems to be responsible for the greater part of this arrest of development. According to KRUMBACH, the habitat of



Figure 43. F, G, H. Irregular specimens of *Nausithoë*. F, G. Females. H. Male.

Nausithoë usually retains an average water temperature in winter no lower than 22°. C, whereas the corresponding temperature at Seto is only ca. 12°. C.

At any rate, it appears to me very strange that in spite of the very wide distribution of *Nausithoë* throughout the eastern and western hemispheres, *Stephanoscyphus* has been known only from a part of the Mediterranean. Whether it is rare or has been overlooked, remains to be investigated.

Remarks

Stephanoscyphus as a scyphopolyp.—*Stephanoscyphus* possesses all the characteristics essential for a scyphopolyp. In addition it has several features which are not found in other scyphopolyps. First the tænioles occur in large numbers and around the whole circumference of the polyp, instead of only four, one at the base of each mesentery. Second, the polyp has such strong power of budding as to produce an extensive colony. In scyphistomas of certain discomedusae also, lateral budding is known. But this occurs to a limited degree, and never results in the formation of a stock which deserves the name of colony. In *Stephanoscyphus*, further, the periderm is much more developed than in ordinary scyphistomas. The high development of germ cells is also a very striking phenomenon which is shared by no other scyphopolyp. In fact *Stephanoscyphus* might well be called an adult scyphopolyp, if only those germ cells were discharged and fertilized. At any rate *Stephanoscyphus* represents the zenith of development of the scyphopolyp, and serves as a good sample of the scyphopolyp in general.

Stephanoscyphus probably an ancestral type of scyphopolyp.—As to the question whether *Stephanoscyphus* is an ancestral or a differentiated scyphopolyp, it seems to me that it represents an ancestral type. First the tænioles which occur in great numbers, and all around the periphery of the polyp, apparently represent a primitive feature. Such tænioles seem to have been derived from the longitudinal muscle-fibers which originally formed a continuous layer around the gastral cavity. The development of germ cells in the mesenteries also seems to favor the above assumption. The branching periderm is apparently more ancestral than the rudimentary pedal disc of the scyphistoma of Discomedusae. Moreover, it is universally recognized that *Nausithoë* is a scyphomedusa in the most

primitive type of organization. These facts seem to stand for the assumption that *Stephanoscyphus* represents the ancestral type of scyphopolyp, whereas the scyphistomas found in Discomedusae show a degenerated state.

Configuration of gastric cavity in different orders of Scyphomedusae.—Stauromedusae are known to develop without strobilation. The same is probably true of Cubomedusae, although this has not been demonstrated as yet. Of the Stauromedusae, Cleistocarpidae seem to show the more primitive feature in that gonad develops in the central gastric cavity. In Eleutherocarpidae, on the other hand, gonad develops in the perradial pockets. The same is true for Cubomedusae also. In Eleutherocarpidae and Cubomedusae the perradial pockets retain the original state found in the scyphopolyp: they are long and spacious cavities and the partitions (septa) between them are complete. The coronal cavity, on the contrary, are very inconspicuous, represented merely by the circular canal. Among Coronatae such deep-sea forms which seem to develop without strobilation, *Periphylla*, *Pericolpa*, etc., have fairly long perradial pockets separated by incomplete septa. In *Nausithoë* where strobilation is initiated, the perradial pockets are diminished, and the coronal cavity has been extended. Semostomae and Rhizostomae are probably groups which have undergone farther evolution from the state represented by *Nausithoë*. The septa are gone and the coronal cavity is very spacious, although this varies in configuration in different groups. Thus, as a general tendency we can recognize that with the differentiation of the medusa-like form, the perradial pockets are shortened and the coronal cavity is extended.

Scyphopolyp as contrasted with hydropolyp and anthopolyp.—As to the phylogenetic relationship of the scyphopolyp with the other two kinds of polyps, there has been much discussion by previous authors. Some of them, e. g. GOETTE (1887) HYDE (1894) DELAGE et HÉROUARD (1901), HÉROUARD (1909), MAAS (1912) support the view of the closer affinity between the scyphopolyp and the anthopolyp than between the former and the hydropolyp. They have proposed to unite the two groups of coelenterates that possess those two kinds of polyps into a common class Scyphozoa. The other authors including CLAUS (1892), CHUN (1891) and most recent investigators, consider the Scyphozoa as an independent class standing between Hydrozoa and Anthozoa. In their opinion the scyphopolyp represents a distinct type of polyp differing both from the

hydropolyp and from the anthopolyp. This difference of opinion on the systematic position of Scyphozoa is due in the main to the difference in their observations on the germinal layer which lines the part inside the lip. Whereas GOETTE and HYDE, etc. strongly maintain the presence of the stomodæum in that part, the other investigators deny it. At present this question seems to have been largely settled in favor of the latter group of investigators. The observation on the histology of that region in *Stephanoscyphus* also, as mentioned above, shows fairly clearly that it is entodermal, in spite of HÉROUARD's contrary histological finding (1909). Next, the tæniole is a structure which has no equivalent either in the hydropolyp or in the anthopolyp. The coronal cavity also seems to be of a different nature from the cavity around the gullet of Anthozoa: while this forms a continuous ring cavity in the former, it is interrupted by mesenterial partitions in the latter. Both the tentacle and the periderm are similar to the corresponding structures occurring in Hydrozoa. The presence of mesenteries, on the contrary, shows the undeniable affinity between Scyphozoa and Anthozoa. In short, the scyphopolyp is to be regarded as a special type of polyp differing from both the hydropolyp and the anthopolyp. Consequently Hydrozoa, Scyphozoa and Anthozoa should be ranked as independent classes.

Summary

(1) The chitinous periderm shows triple or quadruple racemose branchings and resembles the inflorescence of the Umbelliferae.

(2) The polyp has a structure essentially of the scyphistoma; but it shows a higher order of differentiation. It is trumpet-shaped, and consists of the head-funnel and the tube. The former is fringed with 100–200 tentacles on the margin, and has a mouth-opening at the center of the concave side; the convex side is thickly beset with large nematocysts.

(3) The head contains a spacious cavity which continues proximally into four perradial pockets which communicate with the gastric cavity.

(4) The stomodæum is not found; the ectoderm goes over into the entoderm at the margin of the mouth.

(5) The tubular portion of the polyp contains a gastric cavity in which project four mesenteries situated in the interradial planes.

(6) Between the epidermis and the gastric wall are a number of tænioles arranged in a nearly complete circle, in contrast to the ordinary scyphistoma which has only four tænioles at the bases of mesenteries.

(7) Each tæniole is encircled by a layer of longitudinal muscle-fibers and is filled with nematocysts which are in various developmental stages.

(8) The development of nematocysts is briefly described. The nematocysts in various stages wander out from the tæniole to their definitive sites.

(9) The mesenteries become obliterated near the base of the polyp and they disappear entirely in the stalk.

(10) In many specimens collected in August and November 1930, and in July and August 1934, germ cells of both sexes are found. These are imbedded mostly in the basal parts of the mesenteries. The eggs may be as large as the mature eggs found in *Nausithoë*, while the sperms are apparently in the spermatid or spermatocyte stage.

(11) Some specimens collected in the same season show strobilation of the polydisc type.

(12) Previous to the strobilation the polyp undergoes profound changes, such as the thinning out of the entoderm, the absorption of tentacles and the distintegration of tænioles.

(13) Then series of constrictions is formed around the polyp. With the advancement of this process, indentations appear in the margin of each section, and carve it into lappets. The primordia of sense-organs also make their appearance.

(14) The cutting off of the ephyra-rudiments is accomplished by the transverse union of the perforations which appear near the bottom of constrictions in various radial planes.

(15) No liberation of ephyrae was actually observed; but for various reasons there is no doubt that *Nausithoë* develops from these ephyrae.

(16) In the ephyra the primordia of gonads are found as aggregates of primordial germ cells in each adradius.

(17) The fate of the germinal elements in *Stephanoscyphus* is unknown; but probably they (at least male cells) degenerate entirely before liberation of ephyrae.

(18) There is a considerable degree of irregularity in the number and arrangement of various organs of *Nausithoë*.

(19) The *Nausithoë* found at Seto are evidently undersized specimens which have developed under unfavorable conditions as compared with the specimens occurring in the tropics and even with those found in the Mediterranean.

(20) In various features *Stephanoscyphus* attains a higher grade of development than ordinary scyphistomas. It probably represents an ancestral type of scyphopolyp.

(21) Different orders of Scyphomedusae are compared as to the configuration of gastric cavity.

(22) The scyphopolyp represents a distinct type of polyp differing from either the hydropolyp or the anthopolyp.

Literature

- AGASSIZ, A. and MAYER, A. G., (1902). Reports . . . expedition to the tropical Pacific, 'Albatross,' Aug. 1899-March, 1900. III. Medusae. Mem. Museum Comp. Zool. Harvard Coll., 39, 263, pl. 6, fig. 21.
- ALLMAN, G. J., (1874). A new order of Hydrozoa. Ann. Mag. Nat. Hist. Ser. 4, 14, 237-238.
- (1874). On the structure and systematic position of *Stephanoscyphus mirabilis*, the type of a new order of Hydrozoa. Trans. Linn. Soc., Ser. 2, Zool. 1, 61-66, pl. 14.
- BIGELOW, H. B., (1904). Medusae from the Maldive Islands. Bull. Mus. Comp. Zool. Harvard Coll., 39, 263, pl. 6, fig. 21.
- CARTER, H. J. (1872). Proposed name for the sponge-animal, viz "Spongozoon"; also on the origin of thread-cells in the Spongiadae. Parasitic polypes and thread-cells in the parenchyme of a sponge. Ann. Mag. Nat. Hist. Ser. 4, 10, 50.
- CLAUS, C. (1883). Untersuchungen über die Organization u. Entwicklung der Medusen. Prag. u. Leipzig.
- (1892). Ueber die Entwicklung des Scyphostoma von *Cotylorhiza*, *Aurelia* u. *Chrysaora* sowie über die systematische Stellung der Scyphomedusen. Arb. Zool. Inst. Wien, 9, 85-128, Taf. 1-3.
- CHUN, K. (1891). Coelenterata in Bronns Klassen u. Ordnungen.
- DELAGE et HÉROUARD. (1901). Traité de Zoologie Concrète, Coeléntérés.
- EIMER, Th. (1872). Nesselzellen u. Samen bei Seeschwämmen. Arch. mikr. Anat. 8, 281-294, pl. 2.
- FEWKES, J. W. (1888). Report on the medusae . . . Lady Franklin Bay Expedition, 40, pl. 1, figs. 1, 2.
- FRIEDMANN, O. (1902). Untersuchungen über die postembryonale Entwicklung von *Aurelia aurita*. Z. w. Z. 71, 227-267, Taf. 12, 13.
- HADZI, J. (1909). Einige Kapitel aus der Entwicklungsgeschichte von *Chrysaora*. Arb. Zool. Inst. Wien. 17, 17-44, Taf. 1, 2.
- HAMANN, O. (1883). Beiträge zur Kenntnis d. Medusen. Z. w. Z. 38, 419-429, Taf. 23.
- HARGITT, CH. W. & G. T. (1910). Studies in the development of scyphomedusae. Jour. Morph. 21, 217-262.

- HEIN, W. (1900). Untersuchungen über die Entwicklung v. *Aurelia aurita* Z. w. Z. 67, 401-438, Taf. 24, 25.
- (1902). Untersuchungen über die Entwicklung v. *Cotylorhiza tuberculata*. Ibid. 71, 302-320. Taf. 20, 21.
- HERIC, M. (1909). Zur Kenntnis der polydisken Strobilation von *Chrysaora*. Arb. Zool. Inst. Wien. 95-107, Taf. 9.
- HEROUARD, E. (1909). Sur les entéroïdes des acraspèdes. C. R. A. S. Paris, 148, 1225-1227.
- HYDE, I. (1894). Entwicklungsgeschichte einiger Scyphomedusen. Z. w. Z. 58, 531-565. Taf. 32-37.
- KOWALEVSKY, A. (1873). Observations on the development of coelenterates (Russ.) Mem. Imp. Soc. Lovers of Natural History, Moscow, 10. 7. (Cited in METSCHNIKOFF, 1886).
- KRAMP, P. (1924). Report on the Danish Oceanographical Expedition 1908-1910. 2 (Biology), H. 1. Medusae.
- KRUMBACH, Th. (1925). 'Scyphozoa' in Kükenthal and Krumbach's Handbuch d. Zoologie.
- LO BIANCO, S. u. MAYER, P. (1890). *Spongicola* und *Nausithoë*. Zool. Anz. 687.
- LO BIANCO, S. (1899). Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del Golfo di Napoli. Mitt. Zool. Stat. Neapel. 13, 463.
- MAAS, O. (1904). Méduses provenant des campagnes des Yachts Hironnelle et Princesse-Alice (1886-1903), 54.
- (1909). Die Scyphomedusen. Ergebn. u. Fortschr. Zoologie. 1, 189-238.
- MAYER, A. G. (1900). Some medusae from the Tortugas, Florida. Bull. Mus. Comp. Zool. Harvard Coll., 37, 67, pl. 23, figs. 67, 68, pl. 26, figs. 87, 88.
- (1910). Medusae of the World. III. The Scyphomedusae, 554.
- METSCHNIKOFF, E. (1886). Embryologische Studien an Medusen. Wien.
- PERCIVAL, E. (1923). On the strobilation of *Aurelia*. Q. J. M. S. 67, 85-100, pl. 6.
- SCHULZE, F. E. (1877). *Spongicola fistularis*, ein in Spongien wohnendes Hydrozoön. Arch. mikr. Anat. 13, 795-817, Taf. 45-47.
- TCHÉOU-TAI-CHUIN. (1930). Le cycle évolutif du scyphistome de *Chrysaora*, étude histophysiological. Trav. Stat. Biol. d. Roscoff, Fasc. 8.
- VANHÖFFEN, E. (1892). Die Akalephen d. Plankton-Expedition. 13, Taf. 3, fign. 8, 9.
- (1902). Die acraspedoten Medusen d. deutsch. Tiefsee-Exped., 29.
- (1906). Nordisches Plankton, Nr. 11, 43, fign. 2, 3.
- (1908). Die Lucernariden u. Skyphomedusen d. deutsch. Südpolar Expedition, 10, Zool. 2, 37.

Abbreviations used in plates and text-figures

b bud initiating new branches	ga gastric cavity
c. g clear gland cell	g. f gastric filament
c. o circum-oral cavity	g. g granular gland cell
cr crystals	go gonad before sexual differentiation
ec ectoderm	g. s sinus in gonad
en entoderm	i. c interstitial cell
f food-particle	l lip
fl flagella	la lappet of ephyra
fl. c flagellated cell	ma. cn. developmental stage of macronematocyst

ma. n . . . macronematocyst	pe periderm
me mesentery	p. p perradial pocket
mi. cn . . . developmental stage of micro-nematocyst	s sense-organ
mi. n . . . micronematocyst	s. c supporting cell
ms muscle-fibers	s. h sensory hair
n nucleus	t tentacles
n. c nutritive cell	tae tænirole
o mouth-opening	ts testis
ov ova	v vacuoles in entodermal cell
p perforations initiating the liberation of ephyra-primordia	z zooxanthellae

Explanation of Plates

Plate XXI. Fig. 1. Sketch of a colony of *Stephanoscyphus* imbedded in a stock of sponge. Green spheres are *Valonia*, a green alga. $\times 25$.

Plate XXI. Fig. 2. Ephyra of *Nausithöë*. $\times 30$.

Plate XXI. Fig. 3. Mature specimens of *Nausithöë*. $\times 7$. Upper half - female; Lower half - male.

Plate XXII. Microphotos of sections of *Stephanoscyphus*. $\times 80$ Fig. 1. Cross-section of a polyp on the level where the mesenteries are highly developed; corresponds roughly with Fig. 10, D.

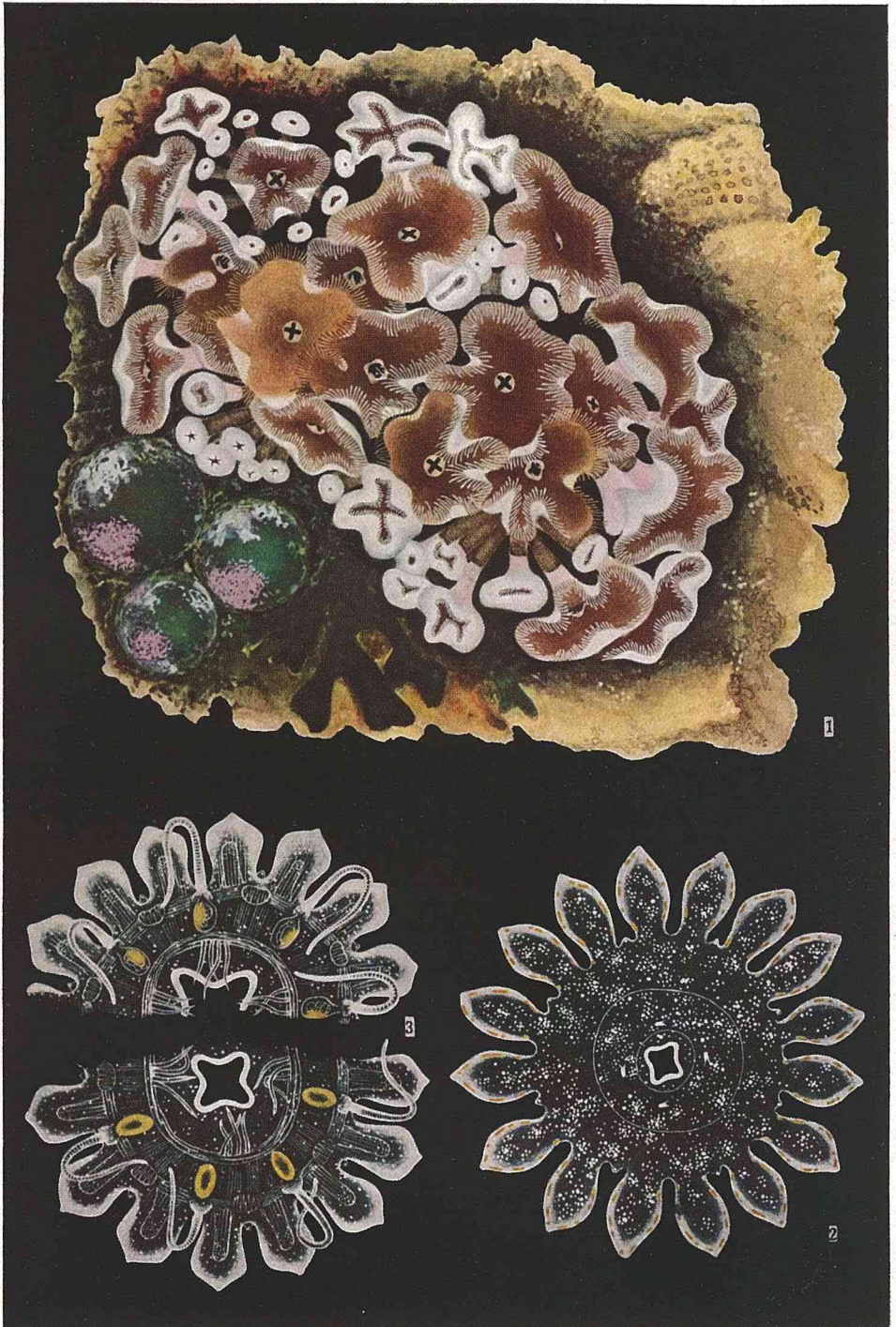
Plate XXII. Fig. 2. Longitudinal section of the basal portion of a polyp in the interradian plane; corresponds with the right half of Fig. 9 A.

Plate XXII. Fig. 3. Cross-section of a polyp containing large eggs in all mesenteries; corresponds with Fig. 21.

Plate XXII. Fig. 4. Cross-section of a polyp undergoing strobilation on the level near the distal end; corresponds with Fig. 28, B.

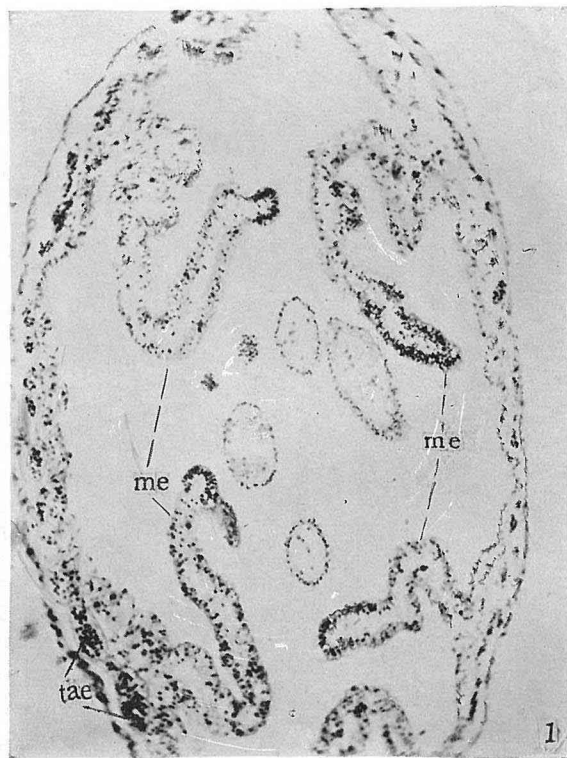
Plate XXII. Fig. 5. Cross-section of a polyp undergoing strobilation on the level where testes are highly developed; corresponds with Fig. 28, C.

Plate XXII. Fig. 6. Longitudinal section of a polyp undergoing strobilation; corresponds with Fig. 9, B.

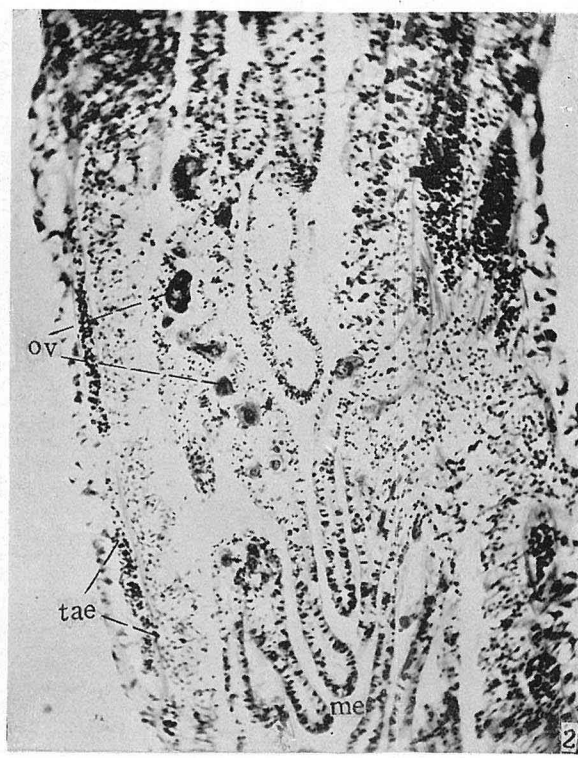


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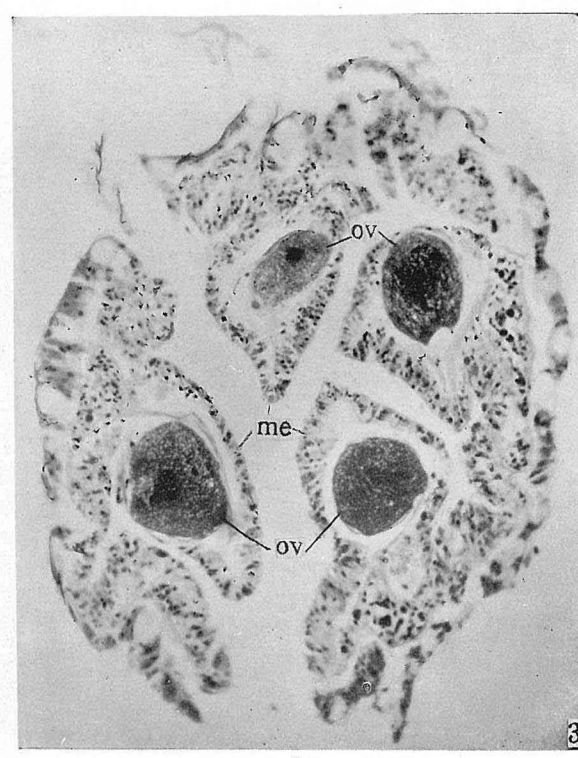
K. SHIMADA, del.



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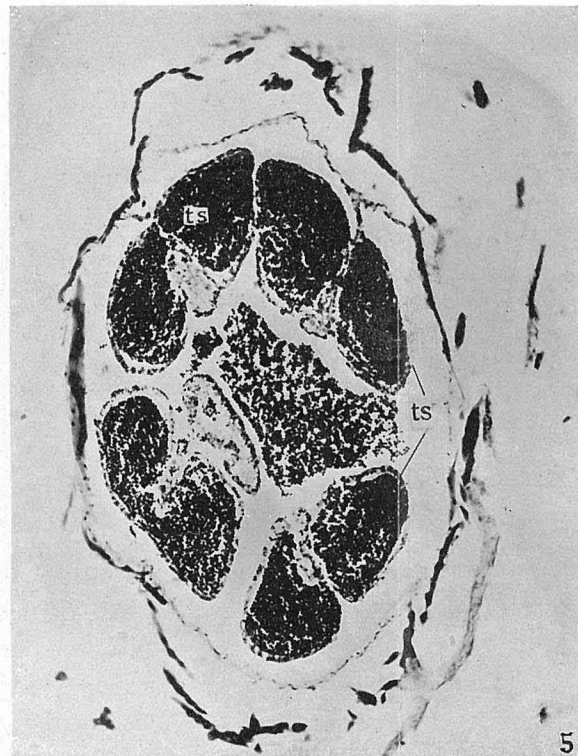
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