

## ALTERNATE PHASES IN FOLLICULINA.

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As long ago as 1858 it was independently affirmed by Wright (7) and by Claparede and Lachmann (6) that the sedentary marine infusorian once known as *Freia*, but called now by the more prosaic term, the bottle animalcule, *Folliculina*, could reduce itself to a more simple larva-like form and then swim free, subsequently to make for itself a new dwelling in which to differentiate again into the perfect form.

So great was the difference in structure that the free swimming form was regarded by Daday (3) as a new genus to be placed in a family quite different from the family of Stentors in which the adult sedentary *Folliculina* belongs.

Even as late as 1916 Sahrlage (4) after much study of *Folliculina* denies the reality of any process of alternation of differentiated and dedifferentiated phases in *Folliculina*. He also denies the credibility of the evidence that *Folliculina* is found in fresh waters as well as in the sea.

In both these negations he is shown to be wrong by Penard (5) who studied fresh water *Folliculinas* and describes the transformations from one phase to the other back and forth.

However, both these authors, overlooked the fact that in 1914 (1, 2) the same alternation of sedentary and free swimming phases early claimed for *Folliculina* in Europe had been found in American waters.

The present paper will serve to reaffirm the reality of this alternation in *Folliculina* and to emphasize its fundamental nature.

*Folliculina* being the most specialized of the highly complex Stentors presents in its anatomy an unusually high grade of complexity, while its ability to fabricate a complex dwelling by secretion is the acme of accomplishment among the ciliated protozoa.

Under the conditions elsewhere described (1, 2) *Folliculina*



passes readily back and forth from more complex sedentary to more simplified free-swimming phases of form and activity.

In the sedentary phase the animal occupies a house or case from which it may protrude two very long ligulate lobes that make its feeding apparatus so effective. In this phase the animal presents the maximum differentiation and is capable of division, as described in part by Mobius (9) and more in detail by Sahrlage (4). This is the adult or perfect phase. In the free-swimming phase the animal lacks the feeding lobes, the mouth and the special organ for attachment and it is in fact a simplified, retrograded or dedifferentiated form which some have called a larval form. It is, however, the free-swimming form that fabricates the house which it will occupy when it has differentiated into the perfect form, from which state it may again retrograde back into the simplified free-swimming stage and again leave its house.

Briefly, the general structure of these two forms is as follows: The free-swimmer is cylindrical, capable of great extension and contraction with spiral and lateral bendings. It moves by means of about 100 lengthwise lines of cilia. At the posterior end the cilia are absent over an area within which is a complex, problematical organ into which the myonemes converge. At the anterior end there is a very small, nearly circular spiral of membranells which though active seem to have no special use. Where the infundibulum and mouth might be expected there is a small microscopic vestige of no conceivable use. The animal captures no food. The food that may be inside of it was obtained in the previous phase when the feeding lobes and mouth were present. Essentially this free-swimmer is the adult broken loose from its former attachment to the bottom of its house or case and dedifferentiated to the extent of entire resolution of its lobes, pharynx, and hypostome. The only vestige of all its former feeding apparatus being the above-mentioned minute ectosarcular cup and the single limb of a spiral hypostome.

On the other hand the anatomy of the adult sedentary form is more complicated. In addition to the long lines of cilia and pigment underlaid by very highly specialized myonemes, there is at the posterior or foot end a special organ of fixation to the



bottom of the house and at the oral or anterior end the remarkable lobes, arms, or flat ribbon-like extensions of the body which have been likened to the ears of a rabbit. These like the rest of the body are exceedingly pliant and almost always in active movement. Where the two arms or lobes arise from the main mass of the body a funnel leads into the interior and ends in a mouth with complex activities. In addition to the longitudinal lines of cilia which run on both the outer and inner faces of each lobe there is a very highly organized band of membranells. This starts near the edge of the funnel ventrally on the right side, runs out along the entire inner face of the right lobe almost to its tip, then returns parallel to itself along the dorsal part of that same lobe to the main body, makes a dorsal course around the funnel to the left side and out along the dorsal edge of the left lobe almost to its tip, then back parallel to itself near the ventral edge of the left lobe to the edge of the funnel down which it goes in a spiral of about 2 turns, ending very near the cytostome. On the left ventral face of the exterior of the body there is a definite region which opens and closes as the functional anus.

While the two phases thus differ remarkably in the high specialization of the adult feeding apparatus as compared with its nearly obliterated condition in the free-swimmer, both phases have essentially the same character of nucleus, namely one long many-lobed moniliform macro-nucleus accompanied by very many minute micro-nuclei. The function of the free-swimmer is not only to transport the animal from one place to another, often for considerable distances, but also to build up the house in which it will live after it has become differentiated into the adult form.

The method of making the house will be described elsewhere but it consists of a series of activities; first, the selection of the site; second, the making of the sac or bottom; third, the making of the spiral tube; and finally, the finishing of a lip around the orifice on top of the tube. After all this is accomplished, the free-swimmer inside the case that it has built, rapidly differentiates into the adult form, capable of stretching out of the case and getting its food. It is this adult form which may later dedifferentiate or retrograde into a free-swimmer and break loose and escape from the house and later construct a new house somewhere else.



The times consumed in the various elements of this alternation of phases vary very greatly, being hastened by high temperatures in general. Often the animals that have been feeding adults during the night pass into the swimming form in the morning, settle down toward the middle of the day and transform into adults again before night so that an entire wave of rise to the adult and recession to the swimming form and rising again to the adult may be about 24 hours. However, in some cases an entire alternation was accomplished in perhaps as little as 6 hours.

The following anecdote relating to a single individual *folliculina* acting under unusual conditions may serve to illustrate the pertinacity with which these alternating phases are adhered to and to raise a number of questions which it would require experimentation to solve.

August 28, 1914 which was very near the end of the season for the occurrence of *Folliculina* in the Severn River, a number of perfect animals in their houses were placed in a hanging drop over water in a hollow slide for the purpose of seeing how they retrograde into the free-swimming form. One group had 17 or 18 perfect cases, another had 5.

By some accident one of these cases had the tube jammed at the tip so that it was closed off. August 29 at 7:50 A.M., temperature 75° F., the *folliculina* in this tube which from its color was evidently an old one, not recently formed, was found to be in a late stage of reduction of the arms in the process of becoming a free-swimmer (Fig. 1). It revolved on its foot as normal, with reversals of direction and the arms had been, as it were, melted down to a castellated ridge or membrane while the long complex adoral zone was now but a semicircular band running along the edge of the very obliquely truncated end of the body, opposite to the above elevated ridge. At 9:50 the arms were reduced to nothing and the *folliculina* was ready to break loose as a free-swimmer with normal spiral adoral band (Fig. 2). This larval stage then broke free from its foot and proceeded to go out of the tube as is normal, but was prevented from emerging by the closure of the tube near its tip. Then began a long series of advances and retreats in which the free-



swimmer vainly tried to force itself out of the tube end, but did not succeed in boring its way out with the narrower tip of the body and all possible efforts (Fig. 3). After two hours and a half of this free-swimming life inside of the case, the free-swimmer settled down to the bottom of the case and became attached there by its foot end again, thus settling down as it naturally would have done after the same interval of time had it, as normal,

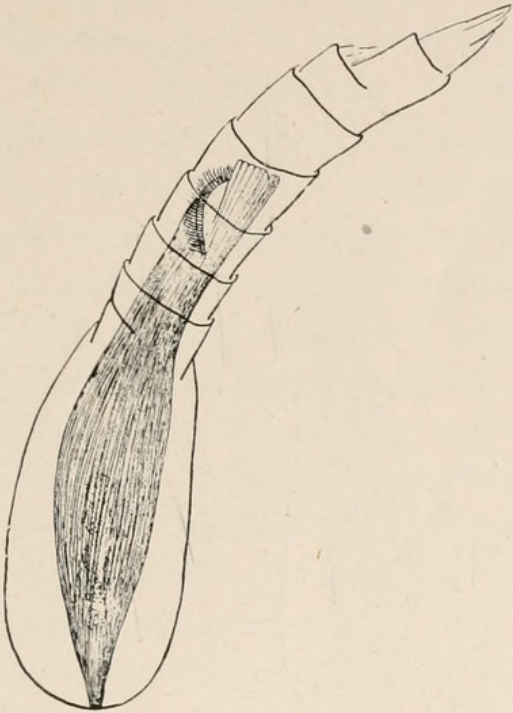


FIG. 1.

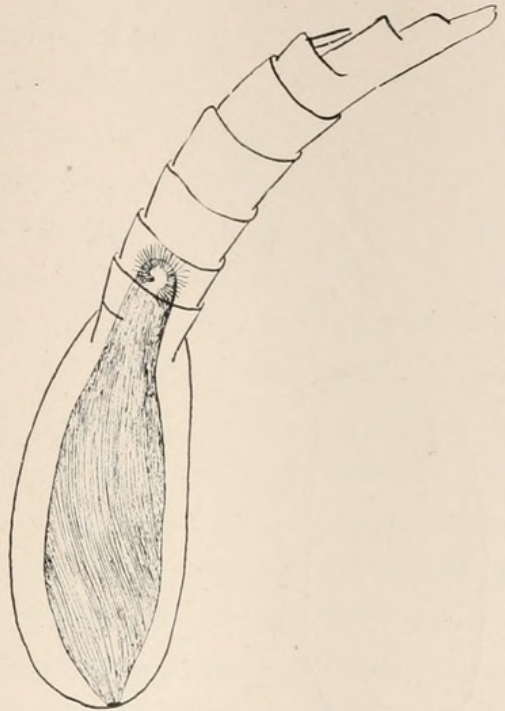


FIG. 2.

FIG. 1. *Folliculina* trapped inside closed case, dedifferentiating its lobes at 7.50 A.M., August 29, 1914.<sup>1</sup>

FIG. 2. Same at 9.50 with lobes gone and free-swimming form completed.

swum free through the water to some distant point of contact and selected a new solid surface to become attached to, far from its old dwelling.

From 12:50 onwards the newly attached larva at the bottom of the case was seen to be reconstructing its lobes (Fig. 4) and this process was completed at 10 P.M. In this process of making lobes (Fig. 4) the usual series of phenomena took place just as is the rule after a free life and formation of a new tube; but here the old tube was used to dwell in and no new tube was formed.

<sup>1</sup> *Explanation of Illustrations.* All sketches outlined with camera lucida, Zeiss, 4, D, that is enlarged about 700 diameters and then reduced to one third in diameter.

All sketches are successive views of one individual *Folliculina*.



In making lobes the old adoral band of membranells sank down into the interior and was apparently entirely melted away during a remarkable loss of organization of all the terminal region of the body accompanied by especial internal circulation of the now very fluid endoplasm, rapid currents passing dorsally from the foot end up to the peristomal end, across that end and down again to the foot ventrally to complete a circuit. The appearances sug-

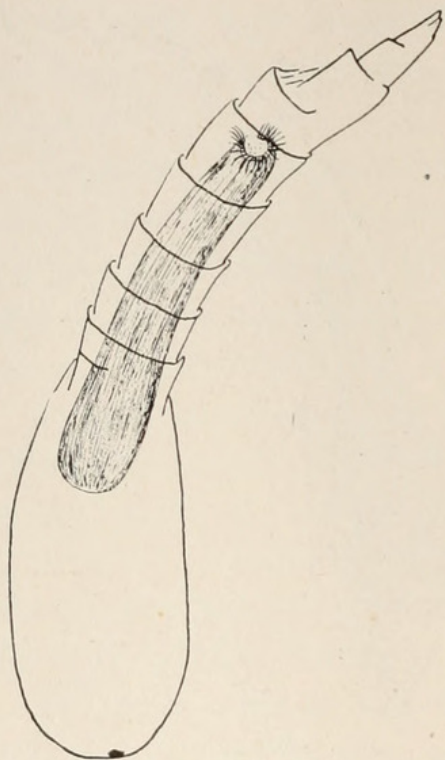


FIG. 3.

FIG. 3. Same at 12.30 swimming in vain attempts to get out.

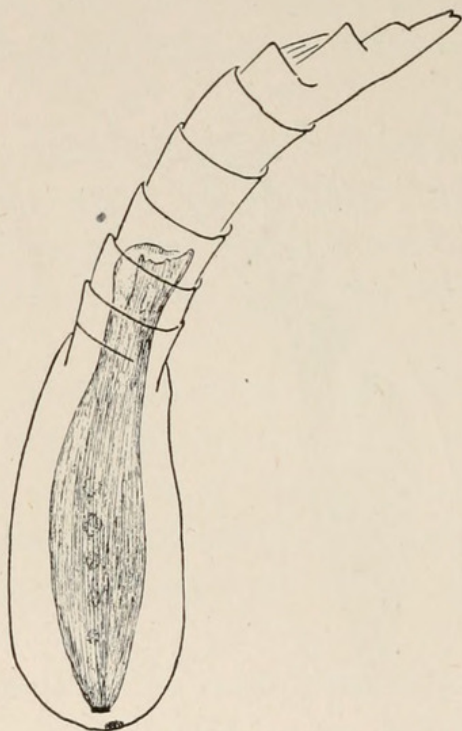


FIG. 4.

FIG. 4. Same at 4 P.M. again attached by new base inside case and with new lobes differentiating. A stage like that in Fig. 1 but going toward differentiation and not the reverse.

gest that the usually well organized and rather rigid anterior end of the animal as well as much of the interior rather suddenly breaks down into a fluid state as if a solid were melted, or a gell changed to sol, and then this begins to rotate violently from unknown causes. The animal now is a cone of stiffer ectosarc with ciliated lengthwise bands and subjacent myonemes attached at end, which is tip of cone, while the base of cone is oblique and liquid out to a mere superficial pellicle, apparently (Fig. 4). This oblique soft face has lost all myonemes and cilia as well as the former rigid adoral band of membranells and the pigment patch.



This oblique cone-base then elongated down one side of the cone like a candle that is gutted down one side, but meanwhile the edges of the soft base rose up more and more as walls like the edges of end of a burning candle. The elevated walls were irregular and fantastic at times, with castellated edges. One side was greater than the other and for long one of the lobes which is the left, was greater than the other. But it is not the elongation of the edges of the cone base that makes the lobes, so much, but the actual splitting down of the base internally into right and left halves. That is, the soft end divides more and more to form a deep groove between the tips of the lobes and so the bases of the lobes are produced more and more down into the interior till finally the two lobes are nothing more or less than the right and left halves of the basal third, or more, of the original cone separated from one another by a deep median space. The new adoral zone that is to follow the edges of the arms arises at an early stage and seems to have no connection with any previous formation but to be differentiated *de novo* from the softened and disorganized terminal and lateral areas. The adoral band starting at one end from within the minor or right arm rudiment, or papilla that is to be its tip, sweeps in a circular arc dorsally and then along the left side central to the rudimental tip of the larger left arm to then pass down the ventral face of the animal where it extends very far toward the apex of the cone. As the animal becomes twisted spirally and has the habit of rotating and of changing the direction of rotation from time to time, it becomes difficult to ascertain how the band is completed, but it is evident that the tip of the band nearest the foot burrows inward into the protoplasm as the future spiral within the peristomal funnel and ultimately acquires a mouth or cytostome at its innermost termination; but in proportion as the two lobes are separated from one another as halves of the animal's body, the two lateral sides of the hypostome curve (Fig. 5) are pulled out as lateral loops that run up and down each arm till the ultimate course of the membranell band is that of two long inverted Us or tuning fork curves connected dorsally by a short dorsal part of the curve, beginning abruptly on the inner face of the base of the right lobe and ending at the opposite



base of the left lobe as that inner spiral that runs within the animals peristomal funnel to terminate at the cytostome.

All the complex organizations having been accomplished in usual order, there resulted at 10 P.M., Aug. 29 (Fig. 5) a creature with great powers of extension and with the anterior third of the body split into two very mobile and responsive arms bearing the collecting membranells destined to produce in the water outside the case such powerful currents as rotifers, bryozoa and the close relatives of *Folliculina*, Stentors, make to bring food particles within control of the selective mechanisms near the mouth. As this individual with its newly formed feeding and

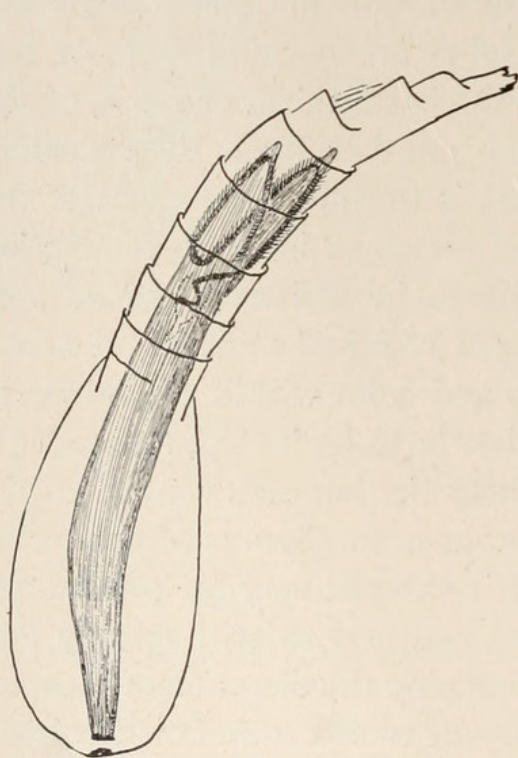


FIG. 5.

FIG. 5. Same at 10 P.M. with fully differentiated lobes, mouth, and feeding apparatus, but with lobes not fully expanded inside closed tube.

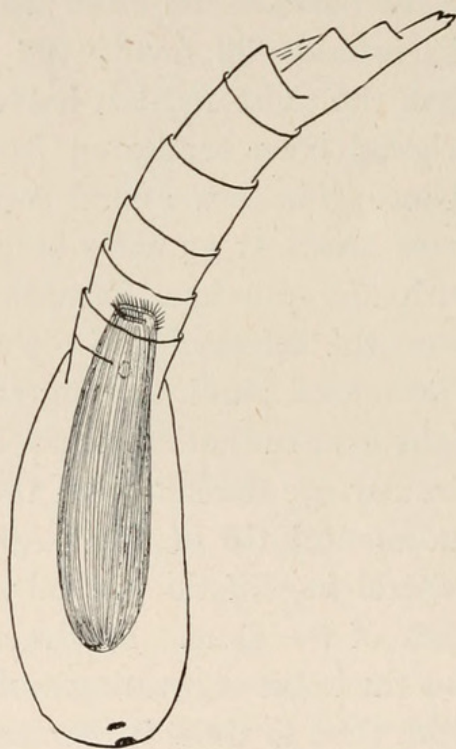


FIG. 6.

FIG. 6. Same August 30, 6.45 A.M., now dedifferentiated into swimming stage again, with two scars of former attachments to base of sac.

responsive organs elongated for the first time, as is normal when first reaching out of the tube it had made before possessing such organs, it, in this case of closed up tube, came to a physical resistance that it could not overcome. Very many trials were made in attempts to complete the normal expansion from mouth of tube; sometimes one lobe alone was thrust up into the closed



tube, the other being bent back alongside of the body like the ear of a lop-eared rabbit; sometimes both lobes were thrust forward. With repeated contractions toward base of tube and repeated expansions and stretchings out, much time was spent in the vain endeavor to complete the expansion which alone would lead to function of the feeding apparatus.

Sometime in the night of August 29 this series of trials must have come to an end, for at 6:45 A.M., August 30, it was found

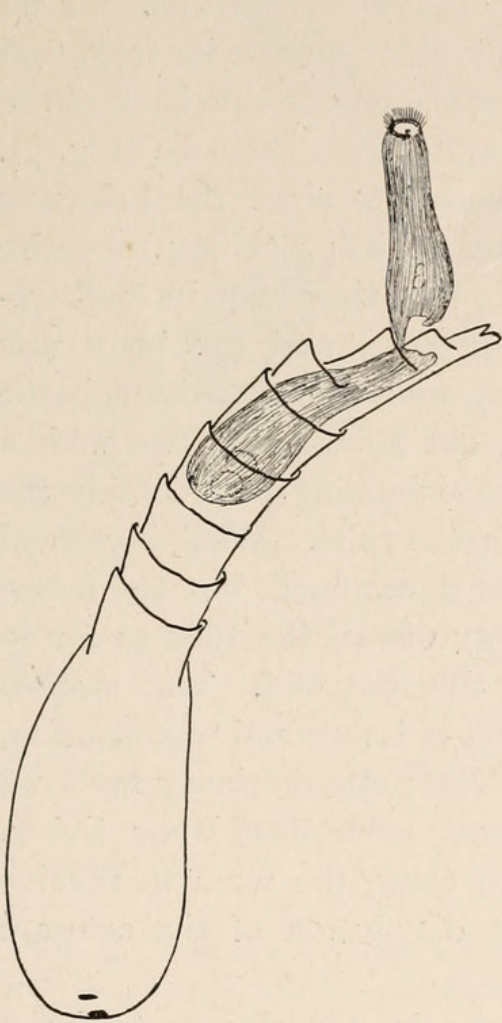


FIG. 7.

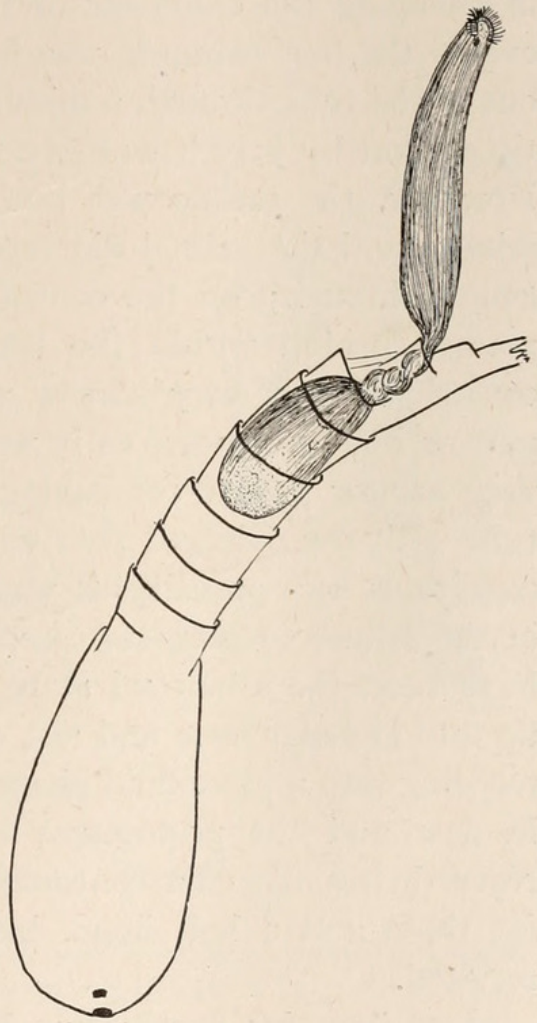


FIG. 8.

FIG. 7. Same at 8.57 when the anterior part had succeeded in forcing its way out of tube, but major part remained inside nearly severed from anterior moiety.

FIG. 8. Same at 9.09 showing revolution of anterior part, twisting connection with posterior part inside tube, and healing over of torn base of anterior part.

that these useless lobes had been resorbed or dedifferentiated and again the animal was in the form proper to a free-swimming phase (Fig. 6).

When this new free-swimming phase broke loose from its foot



attachment there were two scars left on base of tube sac, one for each of the two secessive periods of attachment of the animal to the base of the same dwelling.

Upon swimming up to the top of the tube to escape, as is normal, the free swimmer now met with resistance as before but for some reason the tube was not entirely closed as it seems to have been the day before, possibly the force exerted by the pushing of the lobes of the animal the day before had some effect in changing the character of the closure of the tube. At all events the free swimmer was finally able to force its front end out of the tube through a minute orifice on one side back of the tip so that by 8:45 it was seen escaping from the tube (Fig. 7). However, the escape was but incomplete since the hole was minute and the animal did not succeed in propelling its entire length through; on the contrary, more than half its bulk remained behind within the tube (Fig. 7) and the body was constricted to a very narrow waist when passing through the narrow hole, and was, as it were, cut almost into two with a very narrow pedicle connecting the swimming part outside the tube with the enlarged part within the tube. What abnormal conditions here prevailed it was not determined, but one factor in the failure to progress completely out of the tube seems to have been the abnormal state of the foot end. This swelled up into globular form and lost much of its normal organization, receding into a more fluid phase. The contents slowly revolved in flow and the protoplasm seemed more dead than living. Nevertheless the cilia continued to cause the mass to revolve for three and a half hours before dissolution of the ectosarc resulted.

Meantime, for nearly two hours, the anterior part of the animal now outside the tube continued to swim with its numerous rows of cilia and exerted strain upon the part within the tube; this gradually led to the pulling out of a lengthening isthmus or cylindrical waist between the active outside and the passive inside swollen part. The base of the outside part became pinched off nearly to complete severance from the rest. It formed an oblique base of ragged form sending out pseudopodial processes but ever at one corner, continuous with the hind part



of the animal by a very slender strand that reached through the hole in the tube to the rest of the animal still imprisoned. Within the tube this slender strand became twisted as the outside part swam in its usual spiral revolving way (Fig. 8). Gradually, this dark green strand was at first twisted, drawn out longer, made

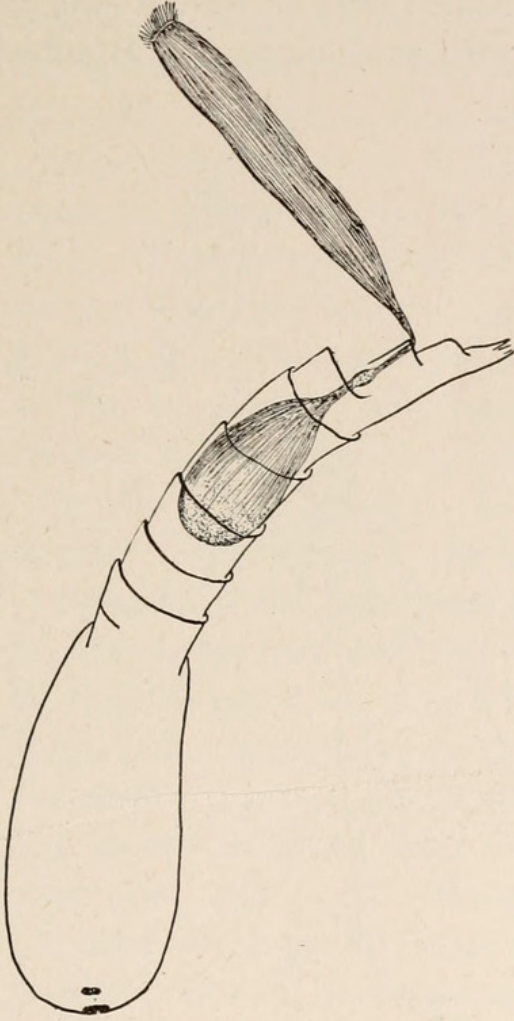


FIG. 9.

FIG. 9. Same at 10.05 when the anterior part swimming powerfully stretches out both its own body and the connecting strand that binds it to posterior region within tube.

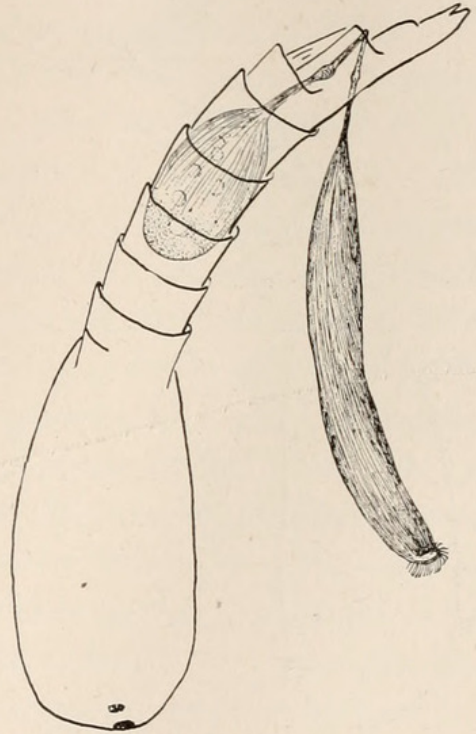


FIG. 10.

FIG. 10. Same at 10.10, showing change of direction of swimming that tends to wind the connecting strand about the tube.

an ever lengthening and very slender string connecting the active outside animal with its dying foot (Figs. 8, 9, 10, 11). The animal revolving swung its head end in wide circles while the slender string held its other end firm to the hole in the tube. Moreover, the direction of pull exerted by the combined stroke of the many cilia was changed so that the strain now pulled



the string out at right angles to the tube (Fig. 9), now parallel to the tube length. Within the tube the string was also pulled out long (Fig. 9) but did not break loose either from the dead swollen foot mass nor from the swimming part. It is to be remarked that the ragged base of the free animal had by 10 A.M., that is, in about an hour's time healed over so that it was no longer ragged, oblique, provided with projections and attached

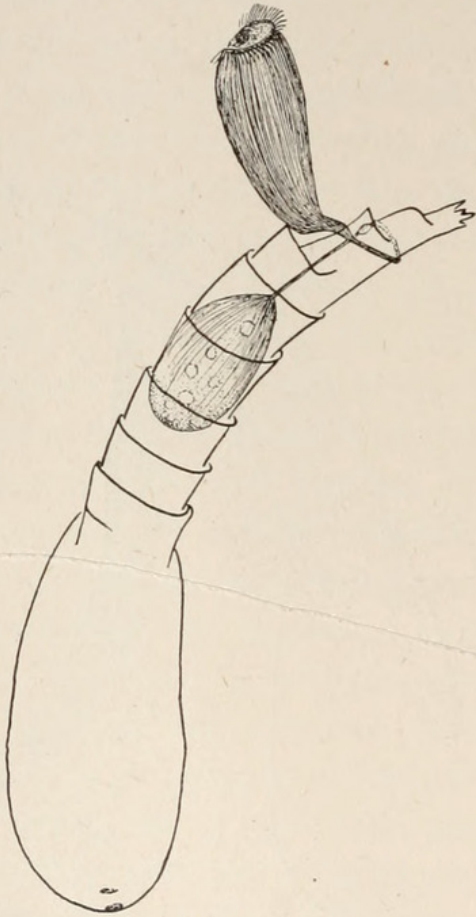


FIG. 11.

FIG. 11. Same at 10.40. The strand wound about the tube brings base of swimming part against tube and the swimming form contracts to take on the sedentary phase.

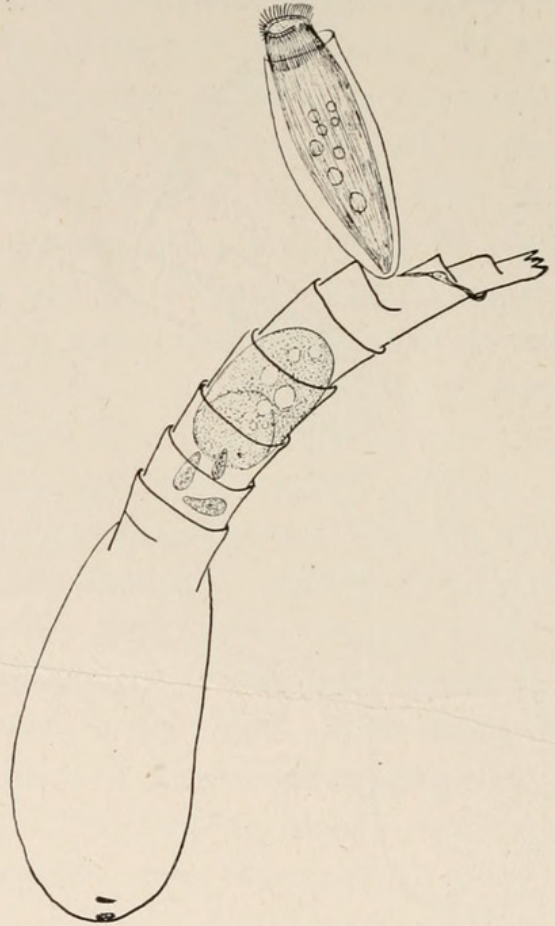


FIG. 12.

FIG. 12. Same at 11.40. The free-swimming stage having terminated, the anterior part has secreted a sac attached to old tube; while the posterior part is disintegrated and being eaten by scavengers within the tube.

by one corner only to the string, but was smoothly finished as a cone with its central part passing smoothly forth (Fig. 9) as the cylindrical slender string of protoplasm which would not break. With the elongation of this strong filament of firm protoplasm, the free animal had more and more wide excursions bound by this



tether, and came to swim entirely around the end of the tube, pulling its cord with it till it became wound up like any larger animal so tied (Figs. 10 and 11). Fig. 10 shows the result of an excursion about the end of the tube in which the string was drawn out very fine and long, but later the animal relaxed and ceased to swim vigorously so that the string shortened and thickened somewhat. Its elasticity pulled the body back toward the tube. The effete mass within the tube still seemed alive on the surface at 9:25 as it had myoneme bands, and cilia that caused it to revolve, but by 10:32 it had come to rest. At 10:40 (Fig. 11) the animal ceased to struggle and now having spent the normal time of a free-swimmer in the swimming activities thus carried on by the anterior part with the limitations of tethering to the imprisoned posterior part, the internal conditions of fixation and tube building had become ripe for expression. The base of the external moiety flattened out on the tube surface and acquired attachment to the tube after the manner of a nascent foot, while at the same time breaking off the long-lasting tether or strand that had held it to the posterior moiety within the tube. Of the old animal was now left the anterior part which proceeded to make a new dwelling on the outside of the old tube (Fig. 12), the swollen posterior part within the old tube which became more and more a rounded dead mass to be destroyed by protozoan scavengers and the slender connection string or middle of the old body which partly inside and part outside the tube soon was lost to view, as if disintegrated or eaten by scavengers.

The fate of the dead posterior was as follows: A rounded mass (Fig. 12) containing portions of the original macro-nucleus was attacked by protozoa which forced themselves against it and indented it as if it were jelly-like with more firm exterior though the original myonemes and colored bands had disappeared. At 11.53 the scavengers entered into the original foot end of the mass which now had become liquified or disintegrated where attacked. At 1 o'clock the mass was broken up into fine granular matter (Fig. 13) scattered about by the movements of thirteen scavengers and into certain refractive shells, apparently representing lumps of the macro-nucleus of greater firmness eaten out on one side by the scavengers which



pushed them about as they ate into them. By 8 o'clock the next morning (Fig. 14), August 31, nothing visible was left to represent the old dead posterior end except a few of the scavengers, six in place of thirteen, and these moved sluggishly, and the following day only dead remnants were left, imprisoned in the

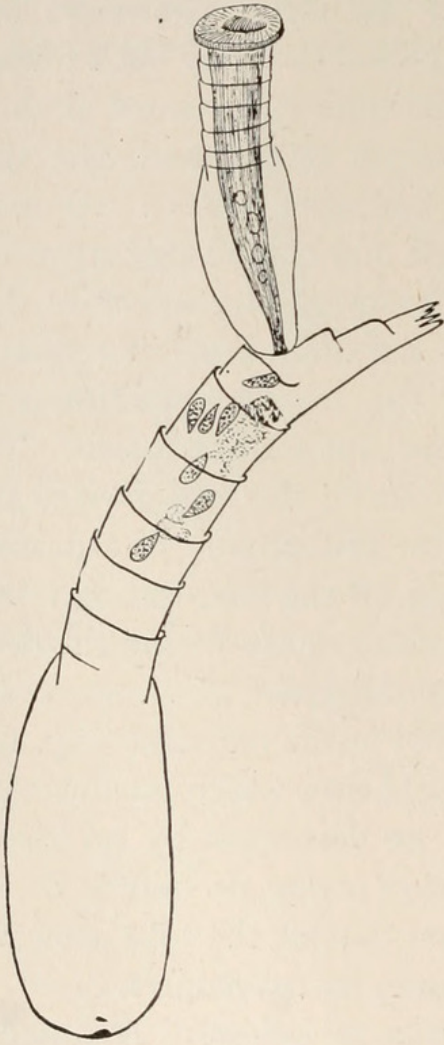


FIG. 13.

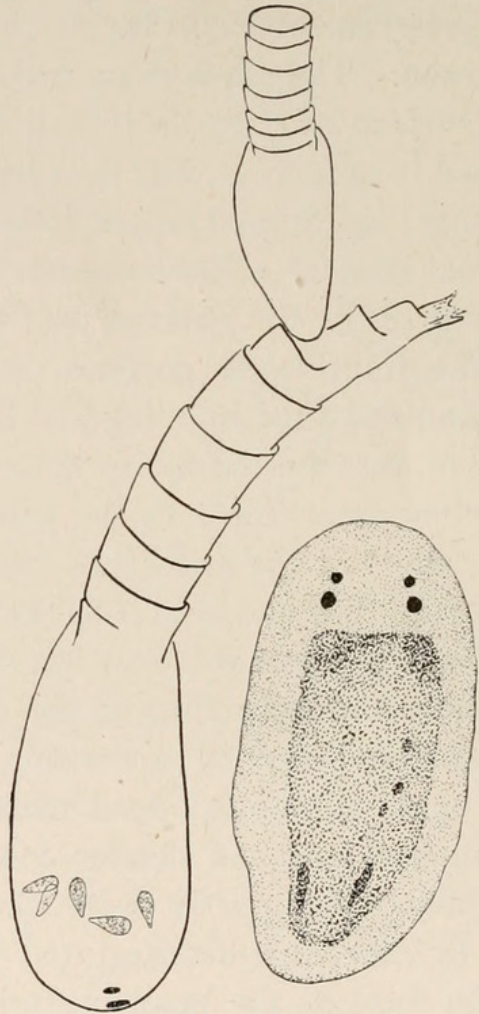


FIG. 14.

FIG. 13. Same at 12.59 after the sedentary form has completed a spiral tube and has assumed the mushroom form preparatory to finishing the secretion with a terminal lip. The old posterior part within tube nearly all eaten up by scavenger protozoans.

FIG. 14. Same August 31, 8 A.M. after a planarian (which is indicated below on right), had sucked out the sedentary folliculina when about to differentiate into the perfect form.

old tube base, as greenish detritus. The scavengers seemed to be the ciliated protozoon, *Urotricha*.

The anterior living part of the animal, however, outside the tube while attached to the tube continued to advance in the



normal cycle of rhythmic activities characteristic of an entire animal; that is, it proceeded to make for itself a new dwelling with all the developments of form that underlies that architectural result. To be sure this new dwelling was small as was the bulk of the anterior half animal that made it and it was not as perfect as normal tubes in the open, but yet it was merely lacking in finish and some perfections of proportion and in no wise deficient in fundamental traits nor more unfinished than many dwellings of whole animals when made in conditions of poor food, etc., incident to long stay in a hanging drop.

The process of making the tube was continuously observed for nearly one hour during which time a dozen camera lucida sketches of successive phases were made. In making the dwelling the new animal which had regenerated from the anterior part of old one followed the traditional sequences as below described.

The dwelling or case of *Folliculina* comprises a sac or attached swollen part and a long tubular continuation which is ornamented by a spiral ridge (Fig. 1). The orifice at the end of the tube is completed normally by a very pretty everted lip, made after the spiral part is finished. In this case of dwelling making, the anterior part animal having become attached, proceeded as if entire, assuming for its attached and adjacent areas the same functions as were normally carried on by the old foot which had degenerated within the tube it was imprisoned in. The first action after becoming fastened by the foot consists in contraction into a form which will be that of the future sac end of the dwelling (Fig. 11) and then in this shortened and swollen form the animal secretes from all its general surface, excepting the anterior face that bears the adoral zone, a material which hardens in the water and forms a complete envelope about the animal partaking of its form and thus molding a sac with end open where the anterior face of the animal projects and does not secrete. This secreted sac lies all in one plane and generally has marked bilateral symmetry, since it is attached along one face which is flattened, but in such examples as the present where standing out rather free into the water the sac (Fig. 12) is not so markedly bilateral.

After the sac is completed it is continued as the tube, but this



always forms an angle with the axis of the sac (Figs. 1-14). To produce this abrupt change of angle and to form the spiral tube the animal has the habit of modifying the anterior region to make a sort of temporary head or cylindrical plug which projects out of the sac and acts differently from the region of the animal that remains within the sac. This plug-like head sticking out of the sac like a cork in a bottle turns upward at a large angle to the main axis of the sac, and thus generally at a large angle with the surface of attachment, be it vertically above or below. This angle in the main axis of the animal is maintained during the making of the tube and the tube is made round about the head region, little by little as the head region is extended farther and farther away from the foot by the gradual elongation of the whole animal. The length of the head or secreting region is such as to produce one of the component rings of the tube and it makes first the bottom one, then the next. However, these are not commonly made as mere rings but as parts of a continuous spiral, since, in proportion as the head slowly advances the head revolves and bends laterally, or nutates, secreting successively left, ventral, right, dorsal and so on. There are then three co-ordinated actions in this making of a spiral tube: first, the slow elongation of the animal, second the contractions of its anterior end to make a mold or form about which secretion is deposited, third the revolution of the head and also what might at first be called a fourth, the localization of secretion so that it is not uniform all round about at any one moment. This latter factor is the least readily made out and involves the appreciation of the fact that the spiral is really bounded by a hollow ridge due to a duplication of the tube wall and this duplication arises from the form and revolution. That is, as one side of the head is more flat it makes the straight walls of tube but as opposite side is bulged out it makes convex ridge and as revolution brings these sides into play successively the bulged out secretion is lined inside by the flat wall. The tube is smooth within but presents a spiral hollow ridge on the outside only.

The animal here considered proceeded normally with this spiral activity till five or six rounds had been finished (Fig. 13) and then made ready to complete the dwelling by the addition



of the everted lip. The making of the lip is one of the most specialized associations of form and secretion in the whole gamut of changes that the animal can run through. As indicated in Figs. 12-13 the head that has been held for more than an hour during the secretion of the spiral tube like a short plug or cork in form and position now suddenly changes into a flat terminal disk which projects outward all round about the mouth of the tube like a mushroom cap from the body of the animal as a stalk. In this mushroom, or disk-phase, of the head the adoral zone becomes excentric on the terminal face of the disk and soon disorganizing changes of the central parts initiate the future completion of dedifferentiations that are to be followed by the differentiation of new arms or feeding organs. But first the overhanging rim of the mushroom normally secretes from its lower surface an annular continuation of the tube which lacks any spiral element and terminates the tube as a horizontal shelf, convex on top; that is, an everted rounded collar comparable to the everted lip of many a potter's jar. However, in this particular instance the collar was never completed, since at 1 o'clock, August 30, a small planarian imprisoned in the hanging drop came over the incomplete dwelling of the *Folliculina* and in one minute, thrusting its proboscis into the tube as the *Folliculina* withdrew, with a few gulps, sucked the entire *Folliculina* up into its digestive cavity.

But for this unexpected event the *Folliculina* would probably have soon completed the lip of its dwelling tube and then have differentiated the usual feeding apparatus, with the aid of which it might have accumulated energy and eventually have returned to normal size after successive alternations of form and of activity.

Comparing the alternations of phases of the normal with those in this individual hampered by restrictions, we observe that the normal was nearly attained, except in the function of secreting a house; and in periods of time closely alike in the two cases.

There is here remarkable adherence to the normal rhythm despite changed external conditions. When the feeding form could not expand and feed as normal it retrograded into the swimming mouthless phase and this after the usual time of



swimming activity though not exposed to outside environment but still within the same house in which the feeding phase had lived, settled down and differentiated the feeding apparatus again, though it skipped the usual making of a house. This feeding stage not functioning as such again reverted to the swimming phase which partly escaped from confinement but was held tethered for such a long time that the next phase, the settling and house building phase came into expression, with the result that the anterior part of the animal made such a house as is normally made by the entire animal while the posterior part of the animal underwent cytolysis.

This comparison may be put in tabular form:

| The Average Folliculina.        |   | The Imprisoned Folliculina.                |                |
|---------------------------------|---|--|----------------|
| To use and resolve arms.....    | Many hours  | About twelve hours                         |                |
| Only to resolve arms.....       | Several hours                                     | Two hours and more                         |                |
| Free-swimming phase.....        | Two hours and more                                | Two hours and more                         | (inside house) |
| To make sac.....                | One half hour                                     |  |                |
| To make tube.....               | Few hours   |  |                |
| To make lip.....                | Quarter to half hour                              | All omitted                                |                |
| To make whole house.....        | Four to eight hours                               |  |                |
| To differentiate arms, etc..... | One and three quarter to<br>four and a half hours | Six hours                                  |                |
| Again to use and resolve arms.. | Many hours  | Nine hours or less                         |                |
| Free-swimming phase.....        | Two hours and more                                | Four hours (partly out<br>of house)        |                |
| To make sac.....                | One half hour                                     | One hour                                   |                |
| To make tube.....               | Few hours   | Two hours                                  |                |
| To make lip.....                | Quarter to half hour                              | Seventeen minutes<br>(when stopped undone) |                |

It is then evident that long journeys through the water are not necessary preliminaries to the settling down of the swimmer to secrete and to differentiate. That the use of the feeding apparatus is not necessary preliminary to the dedifferentiation of the complex form into the simple; and that the anterior part of the animal can act like a whole animal. In brief the external conditions are not, for a time at all events, the necessary determining factors in the transformations back and forth from sedentary complex to migratory simple forms, or phases. Some internal factors must be decisive in the alternation of forms.

That time is spent in one phase and again in the next phase



suggests a series of internal events that must be accomplished before each phase must give place to the next.

As is often the case in normal specimens the free swimming phases in this imprisoned animal were in the daytime and the sedentary phases in the night-time so that one might suppose the phases to be dependent upon some concomitant of day and night alternations, especially as the animal is deeply pigmented both in its granules and also throughout its plasma, so that it should be affected by light and heat; however, there were many instances where the transitions from phase to phase seemed to be quite independent of alternations of light and darkness. The free swimming forms are very responsive to light and generally positive and this favors their swarming out in the daytime. However the dedifferentiation that precedes swarming may be associated with metabolic changes that have but remote connection with diurnal changes. How far these internal factors may be thought of along the lines suggested by E. J. Lund (8) remains for future experimentation to discover.

As in *bursaria* so in *folliculina* the nuclei remain apparently unchanged during the transformations from phase to phase and the transformations are those of the organs of external relation, feeding, muscular and ciliary movements and responsiveness.

Regarding the closure of the tube as presenting problems to be solved by the *folliculina*, it is difficult to see how an intelligent animal could have solved them more satisfactorily with the implements at hand: and were there a complex nerve system present we might assume activities within it like those of a higher animal, such as would lead to omission of the secretion of a useless dwelling after some tactual appreciation of the existence of one formerly secreted.

Granting some internal sequences that lead to alternate forms despite usual or unusual external conditions the most difficult question is why the secretion of a dwelling was omitted when the animal was held confined within the old dwelling. The omission of this series of activities that normally takes place like a chain of reflexes, leads to the appearance of a remarkable parsimony, as if the presence of the old dwelling was a signal for the neglect to construct a new one.



In this connection it should be pointed out that in several instances it was observed that free-swimmers intruded into dwellings already occupied and nevertheless when the time for transformation arrived, these intruders, one in each tube, secreted a new house within the host's house; thus showing that the presence of a surrounding house need not necessarily inhibit the making of a house within a house. In such instances also there was no intelligent result, since the new house blocked the passage and neither host nor guest was ever able to feed nor to escape from the predicament (except in one instance when a tear in the side of the old tube enabled both animals to protrude their feeding arms).

#### SUMMARY.

In the protozoan *Folliculina* an individual imprisoned continued to pass from differentiated to dedifferentiated phases, though both were exposed to the same restricted conditions.

Imprisoned in the night of August 28 the feeding adult dedifferentiated into a swimming form which was active within the prison all the forenoon of August 29.

It then passed into the sedentary phase and omitting to construct the usual dwelling, being inside the old one, differentiated again into the perfect form by ten o'clock.

During that night it again dedifferentiated into the swimming form, still within the old dwelling to the bottom of which it had twice fastened itself.

At 8:40 in the morning of August 30 this swimming form had partly emerged through a rent in the dwelling.

This protruding anterior part of the animal swam violently, held tethered to the dying posterior half left within the dwelling.

At ten forty the free-swimming part settled down on the outside of the dwelling and carried out the normal series of acts in fabricating a new dwelling attached to the old one and almost completed at 12:40.

But at one P.M. the animal was destroyed and rhythmic alternation thus ended.

It is inferred that these alternations of form with differentiation and dedifferentiation are not directly dependent upon such external conditions as exposure to long stretches of water, feeding,



nor probably, upon direct concomitants of day and night successions.

The nature of the internal factors responsible for this apparent striving to complete the normal alternations of phase, and the causes underlying the omission of the usual making of a dwelling, which would in this case be redundant, remain to be found out. Were there a complex nervous system we might refer much of these activities to it.

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