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THE SIPHONOPHORES.

I.—THE ANATOMY AND DEVELOPMENT OF AGALMA.

BY J. WALTER FEWKES.

THE tubular jelly fishes present very interesting conditions of life, and so little has been written about them, except in special scientific memoirs, that a popular account of the anatomy and embryology of a few typical forms may be interesting to those who have not access to the literature. The scientific name of these animals is Siphonophoræ; they are all marine and found in almost every latitude, although most abundant in tropical oceans.

The best known example of the Siphonophoræ is by no means the best adapted to give a general idea of the structure of the order. The most common representative in our waters is called by sailors the "Portuguese man-of-war." Its scientific name is *Physalia*, and figures of it appear in almost every text book on zoölogy. The animal, however, is badly chosen to represent the order, for it is widely different in structure from the other tubular jelly fishes, and not only does not have a tube-like body, the characteristic which has suggested the name of the order, but also its anatomy and development, as far as known, are both abnormal and present many difficulties to one who wishes a knowledge of those jelly fishes with which it has a kinship.

If one should be asked to choose the genus best calculated to give a good idea of a tubular jelly fish, I think he would find one of the Agalmidæ the best choice. Two genera belonging to this family are found in our waters; these genera may be known as *Agalma*[1] and *Agalmopsis.*

A popular description of the latter of these animals was given by Mrs. Agassiz in the well-known "Seaside Studies in Natural History" under the name of *Nanomia*.[2]

The present article will be devoted to the anatomy of *Agalma*, as I consider it the most typical representative of the tubular jelly fishes which have a float. I hope to follow this paper with another on the embryology of the same genus. Both articles are outline sketches of the subjects of which they treat.

The word *Agalma* is of Greek derivation, and means simply an ornament. No doubt Eschscholtz, the pioneer in the study of jelly fishes had in mind an ornament for the neck when he gave this name to the animal. As it gracefully floats in the water with its long pendant tentacles hanging behind it, the likeness to a living necklace with rosy band and transparent beads is very great. It also resembles closely a long, transparent, crystalline prism through which passes a highly colored thread resembling a longitudinal axis, such as is often found in glass models of crystals used in the study of mineralogy.

It will be found immediately, if one tries to raise the *Agalma* out of the water by the hand, that the prism is not a simple crystalline body, but is formed of members which are joined together in such a fragile manner that an attempt of this kind detaches all the component parts, and the beautiful crystal falls back into its native element broken into a hundred fragments. The parts thus detached are commonly known as individuals, and the whole prism as a colony. The individuals or pieces which compose the colony are extremely transparent, so that one can with difficulty follow by means of the eye their bounding lines, and often times to convince himself where the outline is, the sense of touch must supplement that of sight; even then one only becomes conscious that he has touched the animal when it shrinks away from the finger or contracts itself as if alarmed.

[1] Our *Agalma*, which I think is the same as Sars' *Agalmopsis elegans*, was discovered by me while at work in the laboratory of Mr. Alex. Agassiz at Newport. My reasons for considering *Nanomia* a synonym of *Agalmopsis* and not *Halistemma* or *Stephanomia* were given in a paper published in the Bulletin of the Museum of Comparative Zoölogy at Cambridge.

[2] *Nanomia* was first described by Mr. Alexander Agassiz. Proc. Boston So. Nat. Hist., IX, p. 181, 1863. See also North American Acalephæ, p. 200.

To take the animal entire out of the water where it lives, it is

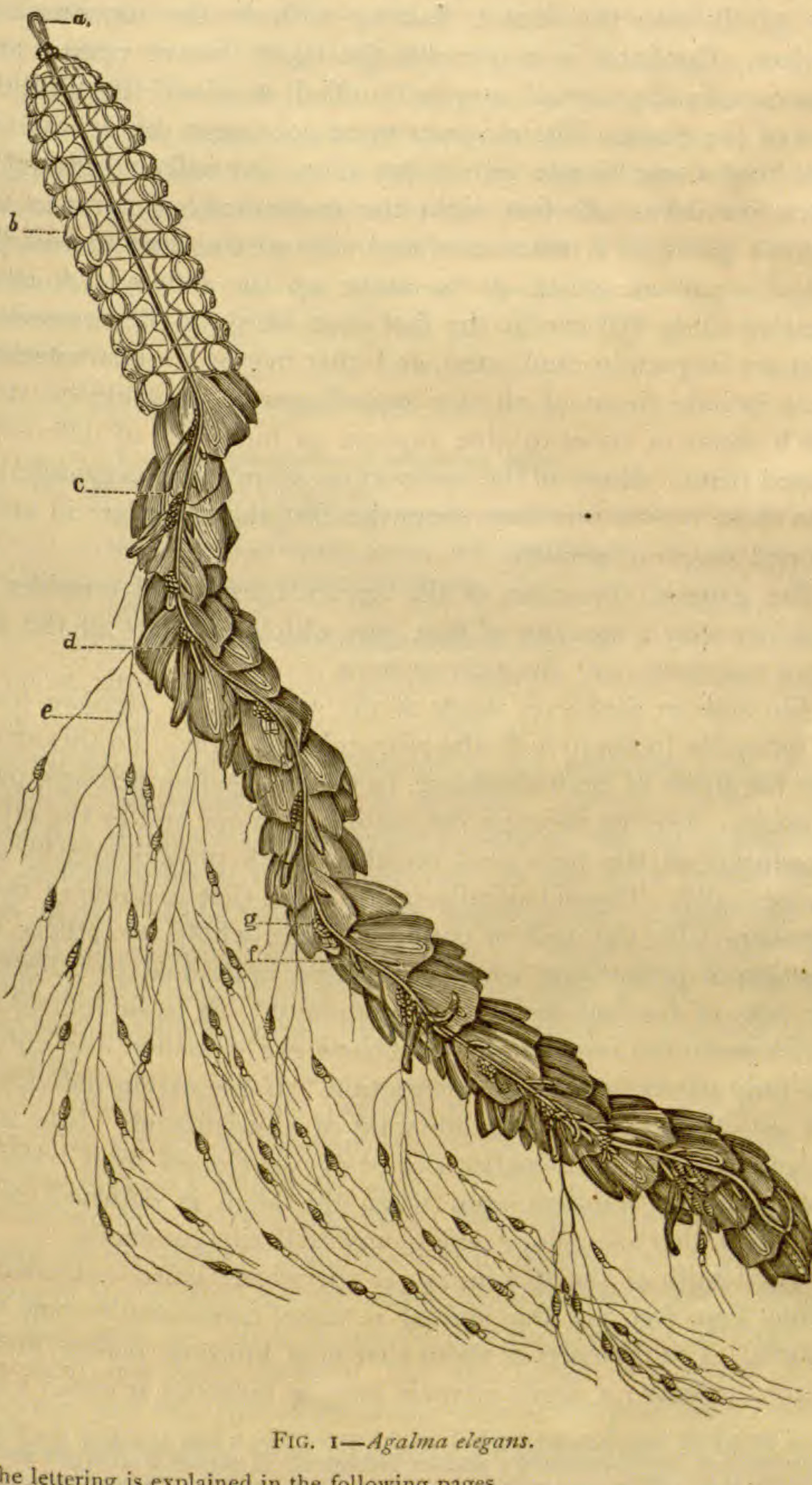

FIG. 1—*Agalma elegans.*

The lettering is explained in the following pages.

best to place under it a deep glass jar and then allow the water to flow gently into the vessel, floating with it the unconscious *Agalma.* Confined in a jar with the light thrown upon it at a proper angle, the animal may be studied at leisure through the sides of the glass. The observer must not forget that he can seldom keep these fragile jelly fishes alive, in confinement, longer than a few days. At first sight the multiplicity of parts in the *Agalma* gives us a rather confused idea of the structure of the several members which go to make up the colony. A more attentive study will reveal the fact that many of the component parts are frequently duplicated, and that five or six characteristic forms include those of all the appendages to an axis or stem which seems at times to give support to hundreds of differently shaped parts. Many of the appendages seem to be very different from these typical members, from the fact that they are in undeveloped stages of growth.

The general characters of the appendages I will consider in sequence after a mention of that part which connects all the different members, viz: the axis or stem.

The Axis or Stem.—A study of the anatomy of *Agalma* leads us naturally to begin with the rosy-colored axis. To this structure the order of Siphonophoræ, to which *Agalma* belongs, owes its name. Passing through the colony from one end to the other, it connects all the individual members both physiologically and anatomically. Physiologically in the sense that to some of these members falls the task of eating for the whole, to others the function of propulsion, while to a single individual is delegated the duty of floating the whole community.[1] If those individuals which serve the function of propulsion are detached, the colony has only passive means of locomotion. If the eating individuals are cut off, the colony dies for want of nourishment. New individuals, however, are continually being developed from buds, so that it seldom happens, even when the stem is deprived of its members, that the colony suffers any fatal consequences.

The length of the stem in larger specimens, when extended, is about four feet, yet the animal is often contracted to half that length. The diameter is about that of a knitting needle, and is nearly uniform ; a slight increase may be detected at either end.

[1] That which supports the animal in the water, and which is called the float, is considered by many naturalists a distinct individual. I regard it an organ and not an individual. My reasons will be given when I consider the development of this structure.

The different appendages or members, all arise from one side of this axis; this side has been called a ventral line. The fact that they appear to take their origin on all sides is brought about by a twisting of the stem itself There are two regions to be distinguished in the stem, which are known as the necto-stem and the polyp-stem. The former is known by appendages which act as means of propulsion, the latter by the polypites or feeding polyps. *Agalma* is said to be polymorphic because it bears on the stem individuals which assume different forms according to their functions. These individuals are as follows (Fig. 1, letters as below):

I. Appended to the necto-stem:
   a. The float.
   b. The necto-calyxes or swimming bells.
II. Appended to the polyp-stem:
   c. The covering scales or bracts.
   d. Polypites or feeding polyps, from which hang
   e. Tentacles and tentacular knobs.
   f. Tasters.
   g. Sexual bells of two kinds, male and female.

Those who believe with Leuckart that every bud on the animal is an individual, must regard the tentacular knobs also as separate individuals. The float, necto-calyx and covering scale are of jelly-like consistency, and are modified "medusa bells." The polypites and tasters are modified probosces, and the sexual bells are combinations of both. The last are the most perfect members of the whole colony. The tentacles are organs and not individuals, although so looked upon by many naturalists. The same remark also applies to the tentacular knobs. The first structure to be noticed is a little sac filled with air, which is called the float.

The Float.—The only appendage to the stem which is not duplicated except in monstrosities is the air-bladder or float. In *Agalma* it is very small and seems hardly large enough to buoy the animal up. It is supposed to keep the colony upright as it swims in the water. Many naturalists regard the float as the enlarged end of the axis in which, from its upper walls, hangs a sac filled with air. It is supposed by them that the extremity of the stem has been infolded like the finger of a glove when reversed, and that the edges of the stem at the position of infolding had approached so as to leave a small opening leading from the reëntering part into the surrounding water. This opening can be seen in *Agalma*, but is not so well marked as in certain allied genera. Another suggestion for the homology of the float of *Agalma* is that it is a bud the same as certain of the other structures along the axis. This view was first published by Metschnikoff. I shall consider it at length when I speak of the development of this part.

The air sac in *Agalma* contains air or gas, and it opens into the cavity of the stem by an aperture opposite that into the surrounding water. The opening from the float into the water is surrounded by a sphincter muscle and dark crimson pigment spots of unknown function.

The Necto-calyxes.—The individual which performs the function of moving the colony through the water is called the necto-calyx or swimming bell. These are found occupying about one-third of the whole axis of the animal, and are arranged in two rows. They are transparent, bell-shaped and easily detached. Each row contains from ten to fifteen members. All the buds which later develop into necto-calyxes are grouped together in a botryoidal cluster just below the float. No necto-calyxes are developed from any part of the stem except this cluster of immature buds just under the float. The growth of an adult necto-calyx from a bud is very complicated, and there is no uniformity of opinion among naturalists as to its method.

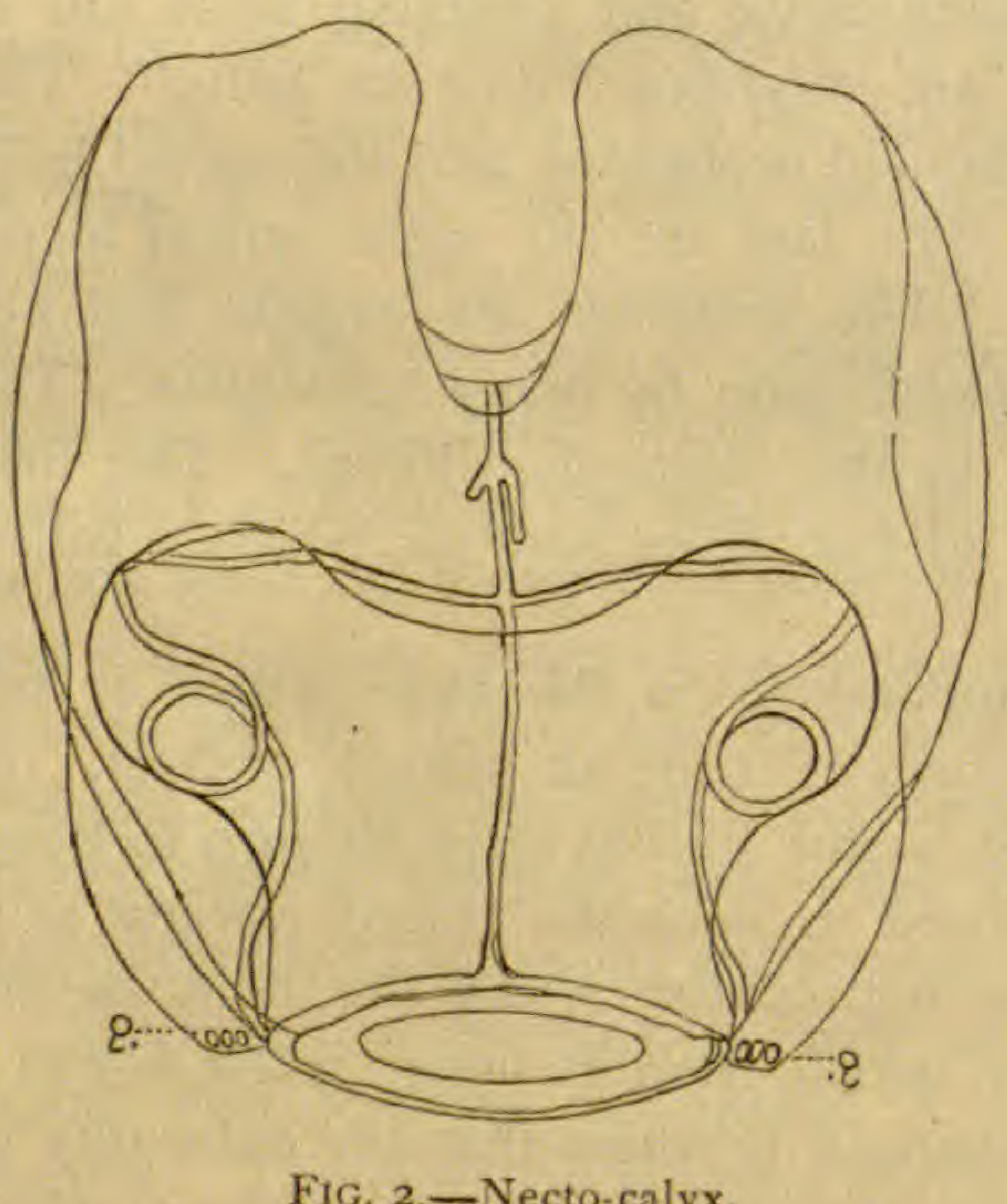

FIG. 2.—Necto-calyx.

A necto-calyx is simply the locomotive part of an ordinary hydroid Medusa. It is the bell, and the proboscis and tentacles are wanting, as would naturally be expected in consideration of their function.

Each necto-calyx is united to the stem at a point diametrically opposite the entrance into the cavity of the bell, and the approximating sides of consecutive necto-calyxes fit closely together.

Two opposite sides of the bell walls rise as horn-shaped projections which embrace the axis and fit closely into certain spaces left between similar projections on bells of the opposite series. By a dovetailed arrangement of this kind rigidity is given to both series, and loss of energy in muscular action reduced. The action of the bell is as follows: Water is taken into the cavity and by muscular contraction of the walls is violently returned through the opening by which it entered. The resistance which the water thus forced out encounters from the surrounding medium, determines the amount of motion given to the colony. The direction which the animal takes depends upon the angle which water passing out of the necto-calyx makes with the line of the axis. This final condition depends in turn upon the position of the mouth of the bell as referred to the stem, and is regulated by the animal. When, for instance, the openings of all the bells on one side are at right angles to the line of the stem, and water is forced through them, lateral motion is given to the animal. In such a case the muscular contraction of the walls of the bells in a series must be simultaneous. Solitary action of necto-calyxes at either end of the series would alter the inclination of the stem in the water. When the bell mouths point downwards, *i. e.*, towards the end of the axis opposite the float, resistance would be exerted at an angle less than a right angle, and as a consequence a motion in the direction of the axis is a result. Combinations in the action of different bells might be made to impart almost any motion to the colony. The motion in *Agalma* is seldom rapid but very graceful.

What has been said would seem to indicate the existence of a nervous system, but in *Agalma* no nervous elements have yet been made out satisfactorily. Pigment spots found on the rim of the necto-calyx may be regarded as organs of sense, but that they are such is only probable. *Agalma* is sensitive to the touch of the finger on almost any part of the body.

Nourishment is brought to a swimming bell by means of the stem, and is distributed in the bell by what are known as the chymiferous tubes. These are radially situated and are four in number, to which may be added a tube running around the rim of the bell, and a medially placed vessel which unites the radial system with the stem cavity.

In the earlier conditions of the necto-calyx the four radial tubes resemble each other very closely, and are straight vessels passing from a common junction directly to a circular tube. In the fully grown bell, however, two of these tubes diametrically opposite differ considerably from the other pair, and take, in their course from common junction to the rim of the necto-calyx, a peculiar turn or twist which I have represented in my drawing. At their junction with the "circular tube" in the rim of the bell lie two or three large lasso or stinging cells, which do not appear in a corresponding position in the other tubes; these cells have been regarded by some naturalists as the remnants of tentacles which never are found fully developed on the necto-calyxes. The portions of the bell in which the tubes with an abnormal course lie, are the same which send out the projections embracing the axis, and interlocking in the dovetailed manner I have described above.

I should not regard even a popular account of the necto-calyx complete, if it did not include a mention of two tubes ending blindly in the substance of the bell; these arise from the medial tube connecting the radial system with the stem cavity, and are known as the "mantle vessels." They lie in the same plane as those two radial tubes which do not have any variation in their direct course to the circular vessel. One of these tubes may be the same as the tubular cavity of the covering scale. Many naturalists have supposed that the structure last mentioned corresponds with one of the radial tubes of a swimming bell. I think that homology not a good one, but I consider the cavity of the covering scale is homologous with one of the "mantle tubes."

The necto-calyxes never voluntarily separate from the stem, but when by any mishap they are broken off, they still retain power of motion and move aimlessly about in irregular circles, keeping up muscular action for a considerable time. Their independent life, however, is very short, for since they are separated from the axis no nourishment can be supplied them. They are locomotive in their function, but rely upon the fluid which circulates in the stem for their support. When such is not supplied them they die.

c. The Covering Scale.—All of the stem except that upon which the necto-calyxes are fastened, is protected, in *Agalma*, by structures known as covering scales or bracts. The German designation of these parts "*Deckstücke*," is used by some English and American naturalists. The covering scales are gelatinous, resembling in that respect the necto-calyxes, and are so closely approximated, as to overlap each other and apparently to form a single unjointed prism. They have an irregular triangular outline, and a flat leaf-like shape. In *Agalma* they seem to serve simply the function of protecting the structure beneath them. They are traversed throughout by a medially placed canal or tube, which terminates blindly at the distal end, and opens at the other extremity into the cavity of the stem. The junction with the stem is by means of a pedicel, which is appended to one angle of the bract and has muscular fibers on its under side.

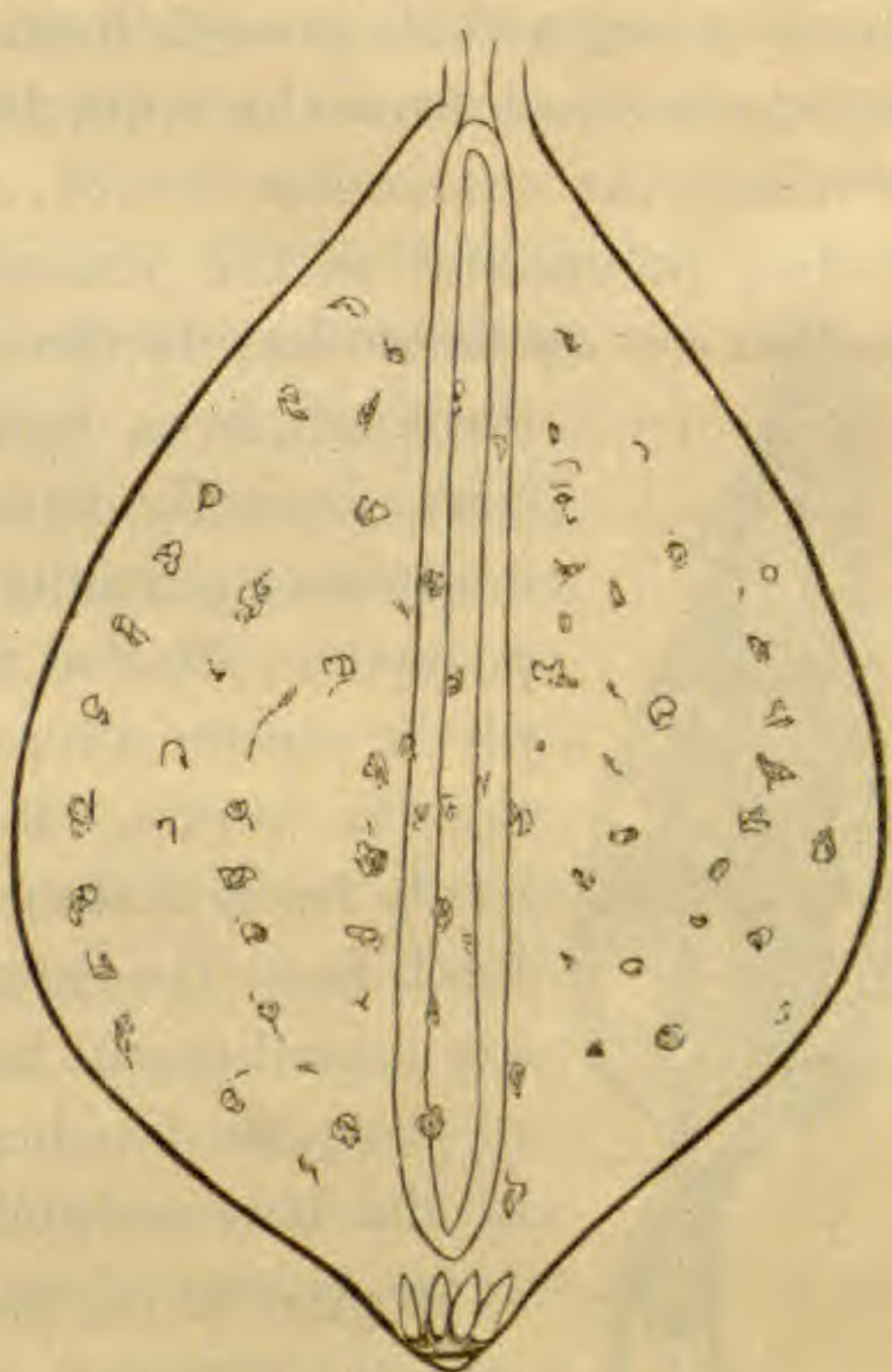

FIG. 3.—Covering scale.

At the very tip of the covering scale there is a cluster of cells which have been supposed to indicate the homologies of the scale with a portion of the necto-calyx. These cells are looked upon as rudimentary tentacles, and are relatively much larger in the young scale than in the adult.

Agalma has, in addition to those described, two kinds of covering scales, which are embryonic and provisional. These will be mentioned under the embryology, for they are confined to early stages in the development of the animal.

The feeding polyps which lie under the covering scales and which are protected by these modified medusa bells, next claim a description. They are known as the polypites.

d. Polypites.—Certain flask-shaped bodies, more highly colored than those yet described, are appended to the polyp-stem, and their distal extremities extend out between the covering scales. They are supposed to be stomachs and to eat for the whole colony. A mouth at one end takes the food, hepatic cells arranged in rows along the inside of the polyp assist to digest it, and after being digested the nutritive fluid is passed into the stem cavity through which it is distributed to every member of the community. From the base of the polypite on the upper side arise the tentacle and tentacular knobs. The tentacle is jointed, very contractile, and histologically differs in no respect from the stem. Each tentacle can be drawn up to the base of its polypite, where it may be snugly packed away under a protecting scale, or it can be extended and allowed to project beyond the body of the *Agalma* to the distance of a foot or a foot and a-half. When thus extended the tentacular knobs are best seen and studied.

e. The Tentacular Knobs.—Each genus of the tubular jelly fishes seems to have a characteristic tentacular knob. *Agalma* is not an exception. Although in the adult appended to the tentacle, they begin their growth from the ciliated base of the polypite, and do not bud from the tentacle itself. New buds which are to develop into tentacular knobs, are continually forming on the feeding polyp, and as the tentacle grows are being continually pushed out on its walls. In the earliest history of the growth of the knob, even before the polypite on which it is borne is fully developed, we find it with others in a cluster, partially coiled up at the base of the polypite. At that time there is no tentacle, but simply a cluster of partially coiled undeveloped tentacular knobs. In such a condition they might easily be mistaken for a wholly different kind of knob from the adult, and the polyps to which they are joined might be looked upon as a different kind of polypite. I believe them only undeveloped forms of the true polypite with tentacular knobs.

FIG. 4.—Tentacular knob.

In general outline the adult tentacular knob preserves a likeness to a Medusa. One portion of it may be likened to a bell and another to a proboscis. The bell is represented by an envelope surrounding the knob, and we might find the homologue of the proboscis in the coiled structure within this envelope. The bell portion is called the involucrum; the coiled proboscis, the sacculus. The sacculus is of dark crimson color, and ends in two filaments, or threads, and a sac supposed to be contracti e. The sac lies between the two filaments at their point of junction with the sacculus. It has been called a food reservoir, or "*Saft-behälter.*" This last term has been also applied to other structures in the *Agalma.*

According to Keferstein and Ehlers, the tentacular knob of

Agalma is still more complicated. According to these naturalists there are two elastic bands or threads, which arise from the inside of the involucrum and are fastened to the extremity of the coiled sacculus. Their figures of a knob where the sacculus has been uncoiled, show these bands very plainly. When the sacculus is withdrawn into the involucrum it is wound around a style which passes directly from the fundus of the involucrum to the contractile sac. I have seen portions of the elastic bands, and figure them in my drawing. Provisional embryonic knobs exist in larval stages: they will be described later.

f. The Tasters.—The word taster,[1] by which organs now to be described have been designated by the Germans, is one of the best which has been suggested. The tasters have also been called "hydrocysts" and "*Saft-behältern.*" These bodies are easily to be mistaken for undeveloped feeding polyps, but a more intimate study of them shows the error of so doing. They differ from the adult polypite in that they have no mouth, are destitute of hepatic cells, and their tentacles have no tentacular knobs. They never, in *Agalma*, drop off, and it is extremely doubtful that they ever separate from the colony and form new communities similar to those from which they are themselves buds. Large lasso cells are sometimes found near their base, at the proximal end, one of which was erroneously mistaken for a float. Claus has made some very beautiful researches on the histology of the taster. I believe the taster is homologous to a polypite, and that its function has, in certain respects, changed its form.

FIG. 5.—Taster.

g. The Sexual Bells.—There remains yet to be mentioned the sexual members of the "colony." They assume the most perfect medusa form, and are found in clusters along the whole polyp stem. *Agalma* is monœcious; the male and female bells are separated from each other on the same stem, and arise on special pedicels from the axis. The female bells form botryoidal clusters and lie about midway between two polypites, but are never joined to the tasters as in some other genera. Each

[1] From "*tasten,*" to touch.

female bell carries one egg, which will be described in the next article. Its growth and development will be found in the same place. The eggs are dropped in the water and there fertilized. Male and female bells ripen their products at different times. When the egg has left the animal, the sexual bell shrinks up on the stem and is finally absorbed or dropped; a scar on the stem alone tells of its former existence.

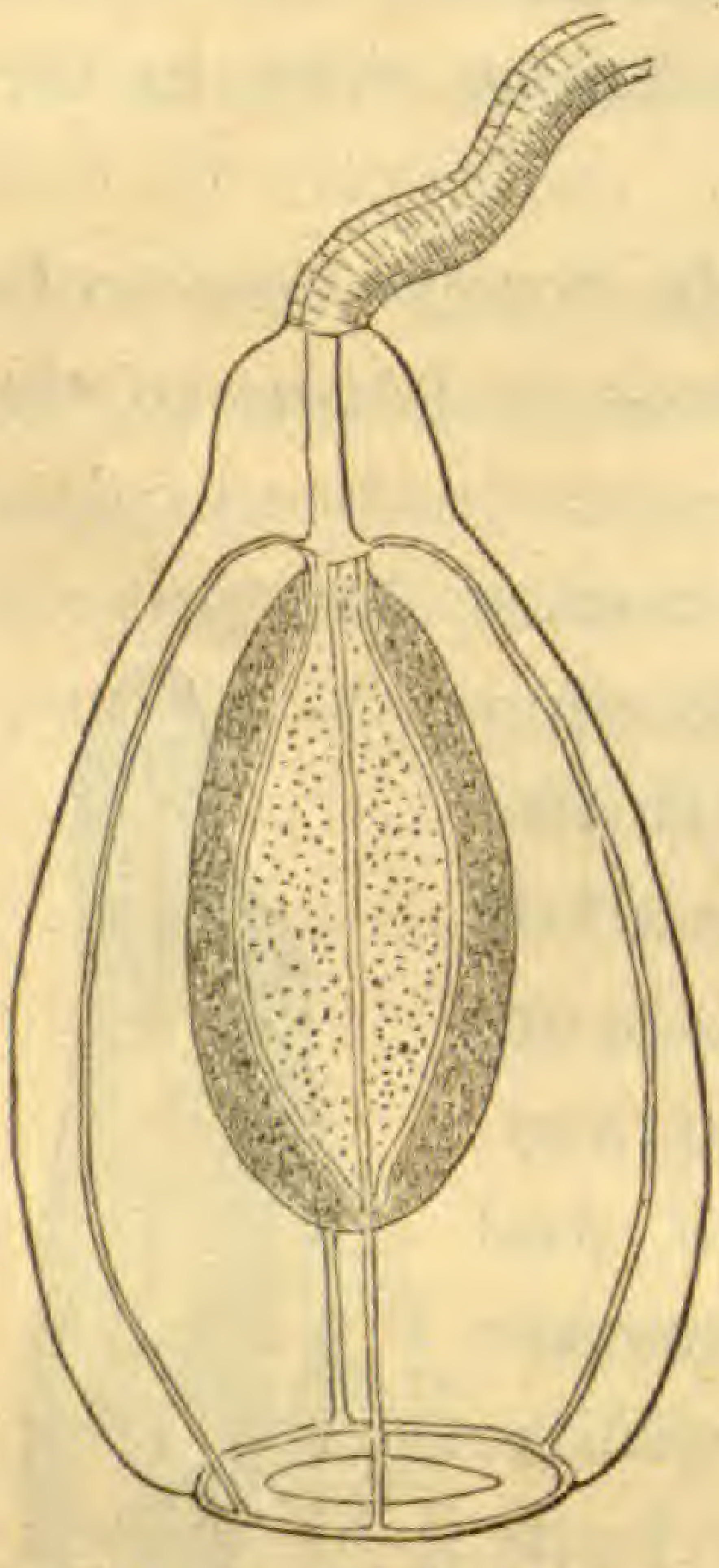

FIG. 6.—Male bell.

The male bells have more elongated pedicels than the female, but in both cases the sexual products are borne on the proboscis between the ectoderm, or superficial layers, and the endoderm. They probably originate from the intermediate layers, or mesoderm (?).

Agalma becomes sexually mature while yet retaining embryonic features. A young form of the most common species in the Mediterranean *(Agalma sarsii)* has been called another animal *(Agalma clavatum)*. It is, however, only an immature form arrived at sexual maturity. I believe *Nanonia cara* is the sexually mature young of the genus *Agalmopsis*. *Nanomia* was found at Newport and Nahant.

A few theoretical questions suggest themselves after this fragmentary account of the anatomy of *Agalma*. The first question which arises is, to what great groups in the animal kingdom is it allied? From the study of the anatomy naturalists were led to believe that *Agalma* was a free swimming hydroid. This theory was simultaneously and independently brought out twenty years ago by several naturalists. The Siphonophoræ were regarded as hydroids which instead of being fastened to the bottom of the ocean, were detached or free swimming, and the point of attachment of the fixed form was supposed to be represented in a float to support the animal in the water. Many bitter personalities, happily now forgotten, were indulged in by those who claimed to have originated the theory, and it was defended with great zeal by its advocates. Embryology teaches another answer to the question of what *Agalma* is, and it is my purpose to speak of that answer after a consideration of the development of the animal.

Another question no less significant than the first is, as to how we know that the different appendages along the axis are individuals and not organs. Why not look upon them simply as organs? To answer this question we get some light from a study of animals allied to *Agalma.* There are tubular jelly fishes in which the appendages to the stem are not so numerous as in *Agalma*, and where there are clusters of appendages at intervals along the stem. Each one of these clusters, however, is composed of all essential members to fit it to lead a separated existence. We have in each a necto-calyx, a covering scale, feeding polyps with tentacle, and sexual organs. These clusters are bound together by the stem, and at a certain age in the life of the colony the stem breaks midway between two clusters, which swim about as separated individuals which live long enough to change their general form. In these genera we certainly have a composite animal composed of smaller clusters, each one of which is a colony. In *Agalma* that fact is masked, since the different component parts are pressed so closely together on the axis, but it seems none the less certain that the *Agalma* is composite. If we take the different parts which compose one of these colonies, many of which joined together form the *Agalma*, we find a resemblance to a typical hydroid medusa in each of its component parts. In the necto-calyx we have a hydroid medusa where tentacles and proboscis are wanting; in the sexual bells we find the same likeness where bell and proboscis are present and tentacles fail. The covering scale, polypite and tentacle together make up another, and so on. All closely resemble a common type of hydroid medusa. Embryology will shed much light upon this question, which I shall again discuss.

From what the anatomy of *Agalma* teaches, we may conclude that we have in this animal the following polymorphic individuals whose homologous parts "*inter se*" and with a common *Lizzia* are given below:

LIZZIA,	Bell.	Tubes of the bell.	Proboscis.	Tentacles.	
AGALMA,					
1st individual,	Float.	————	Stem.	————	
2d "	Necto-calyx.	Present.	————	——repres'd by lasso cells	(*b.*)
3d "	Covering scale.	Cavity of scale.	Polypite.	Tentacles.	(*c.d.*) (*e.*)
4th "	Covering scale.	Cavity of scale.	Taster.	Thread-like tentacles	(*c.f.*) (*e.*)
5th "	Bell.	Present.	Proboscis with ova.	————	(*g.*)
6th "	Bell.	Present.	Proboscis with sperm.	————	(*g.*)
Doubtfully I add to those given					
7th individual,	Involucrum.	————	Sacculus.	————	

The first individual is never duplicated; the remaining are numerous along the stem. A dash shows that the organs of the typical medusa are wanting.

It will be seen that I do not homologize the stem of *Agalma* with the stem of a fixed hydroid, but with the proboscis of a medusa. The Siphonophoræ are not free swimming hydroids, but medusæ with polymorphic individuals budding from it similarly to the condition in *Lizzia*. These buds are not zoöids but physiological and morphological individuals. I cannot follow Leuckart when he considers, however, that every bud is an individual. Three buds, the scale, the polypite and the tentacle together make one individual. Upon this subject we must look to embryology for light.

——:o:——

DESTRUCTION OF OBNOXIOUS INSECTS BY MEANS OF FUNGOID GROWTHS.

BY PROF. A. N. PRENTISS.

[*Concluded.*]

Experiment No. 3.—May 10—A calla lily has become infested with aphides and red spider. The whole plant is carefully washed with a sponge except a small spot on one leaf where twenty-seven aphides are left, and a similar spot on another leaf where about twenty red spiders are left. The whole plant is sprinkled with domestic yeast, care being taken to thoroughly drench both the aphides and red spiders. The plant is covered by a bell jar which rests upon a ring of cotton batting, so as to shut the plant off from the approach of insects or spores from without, and prevent the escape of those within. Under the bell jar are placed two cups of actively fermenting yeast.

May 14.—The plant carefully examined. No dead aphides to be found. A number of cast-off skins are seen. The aphides are well scattered over the plant, but more than the original twenty-seven can be counted. The red spiders are also scattered so that the number cannot be ascertained. Several living but no dead ones are seen. That the spiders should have decreased in numbers might be expected from the moisture of the yeast independent of the Torulæ.

Experiment No. 4.—April 8.—Selected a thrifty rose geranium, about ten inches high, that had by count seventy aphides upon it, collected mainly upon the tender shoots.

The yeast is prepared by dropping pieces of compressed yeast-cake, bought at the grocer's, into Pasteur's fluid with sugar. In