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# PROCEEDINGS

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Geological Survey of New Hampshire for the year 1871 I made the following observation:

“As the ore here occurs in vertical segregations, there is more uncertainty as to its extending to a great depth than if the ore occurred in lodes in a stratified rock; but this uncertainty is in a measure counterbalanced by the large masses in which it occurs.” The locality is easiest reached from Glen Station, on the Portland & Ogdensburg railroad.

NOTE ON THE STRUCTURE OF RHIZOPHYSA FILIFORMIS.

BY J. W. FEWKES. (With Plate 2.)

The interesting Siphonophore *Rhizophysa filiformis* was discovered and first described by Forskål. He gave it the name *Physophora* and does not seem to have separated it from *Athorybia* nor from that animal which is now known as *Physophora hydrostatica*. Many subsequent naturalists have confounded it with other genera, or considered it a mutilated stem of another physophorid whose swimming bells and covering scales had fallen off. Chamisso found a *Rhizophysa* in the northern Pacific, and Eysenhardt described it as a new species. In the classical work of Eschscholtz a third species is mentioned and referred to the genus *Epibulia*.

Brandt divides the genus into the two forms, *Rhizophysa* and *Brachysoma*, which differ only in the length of the body. As Gegenbaur rightly says, the latter genus may be simply a form of *Rhizophysa* with contracted stem.

Lesson, in his *Acalèphes*, gives a short description and drawing of *Rhizophysa*, between which in certain respects, as Huxley says, there is a lack of consistency. His so-called “paquets d’ovaries,” which must be the reproductive organs described by Gegenbaur, as Huxley well comments, are described as “jaunês,” and figured as bright pink. The imperfection of his knowledge of the genus, as we now understand it, is clearly brought out by the praise which he gives Delle Chiaje’s description of another animal which was thought to be his own *Rhizophysa*.

Still another example of this animal was described by Huxley in his work on the Oceanic Hydrozoa.

Huxley evidently had the species of *Rhizophysa* called *R. Eysenhardtii* in the single specimen which he found in the Indian Ocean. The peculiar unbranched organs from the tentacles, the existence



of the so-called sexual clusters at the base of the polypite, and the entire absence of any of the three kinds of tentacular knobs, seem to point this out very evidently. It rarely happens in *Rhizophysa* that the tentacular knobs are dropped by long confinement in a glass vessel, so that one could hardly believe the specimen which he had was mutilated. The thread-like character of the secondary appendage to the tentacle would seem to indicate the truth of the theory that they were only pedicles of secondary appendages whose sacculus had dropped off.

Huxley figures and describes the coeca-like appendages which are so well marked in the float of *R. filiformis*, and he declares himself unable to find the small rounded cells between the endoderm and the air sac. I was also unable to find these in my own specimens, a failure, I think, as such structures have been redescribed. Considering the problematic position of *Velella* and *Porpita* these bodies have more or less theoretical importance. If one should push the comparison of a *Velella* to a physophorid as far as Leuckart has in his schematic figure, one could better compare that dark mass which has been likened to a liver in the case of *Velella* with the finger-like, often bifurcated appendages of the float in *Rhizophysa*.

One of the best descriptions which we have of this animal is that by Gegenbaur. He observed it frequently in quiet weather in the neighborhood of Messina. I shall frequently have occasion to speak of his account.

Kölliker does not appear to have studied the form. No mention of it occurs in his work on the Siphonophorae of Messina. Leuckart and Vogt did not find *Rhizophysa* in the bays near Nice. The former of these authors declares in a note that the *Rhizophysa filiformis* of Risso is the same thing as the animal which he calls *Galeolaria filiformis*. Keferstein and Ehlers give a casual mention of it, supporting Sars's view in regard to the tentacular knobs. One of the last additions to our knowledge of the different Rhizophysidae, is a paper by Studer (*Zeitschrift für wiss. Zööl.*, Bd. xxiv) on the Siphonophorae of the deep sea. I am inclined to question the validity of the new genus and species which he proposes. That these animals were brought up from the depths which he gives is also, as Mr. Agassiz shows, not conclusive. Among the few forms as yet described as belonging to the Siphonophorae from North American waters, no mention has been made of *Rhizophysa*. There is hardly a doubt that it will later be added to the number already known,



especially when the waters of our southern bays have been more carefully studied.<sup>1</sup>

In the course of my work in Villefranche sur Mer, my fisherman brought me five or six specimens of *Rhizophysa filiformis*. I think the form is not common there, at least in the winter months. My specimens were taken in February and March. On account of its apparently mutilated condition, Rhizophysa is one of the most bizarre of the Siphonophores. This is mainly due to the fact that the bells, which fail among related forms in Physalia, are here completely wanting. They neither appear as swimming organs, covering scales, nor in the so-called sexual parts.

The float alone, that strangely modified structure which Metschnikoff has homologized to a bell, and whose form is so varied, is the only thing which we find in Rhizophysa representing a medusa bell.<sup>2</sup> Except the most limited movements of contracting the axis, the animal is wholly devoid of means of progression. The contrast

<sup>1</sup> Up to the present time, there have been described from New England waters only three forms of Siphonophorae. *Nanomia cara*, the only known Physophorid except Physalia, was studied by Mr. Agassiz. It was found by him at Newport and Nahant. In the summer of 1876, while at work in his laboratory at Newport, I found a second physophorous Acaleph, *Agalma elegans*, as yet neither described nor figured. Of Calycophoridae none have yet been found in New England waters by others. To this fauna I can add *Eudoxia Lessonii* and *Diplophysa inermis*. Velella is sometimes washed up on our coasts, and Physalia is by no means so rarely met with in Vineyard Sound as in Villafranca, Naples or Messina.

<sup>2</sup> The origin of the float has of late been studied in other Physophoridae by Haeckel, Kowalewsky and Metschnikoff. The opinion of the former that it is simply one end of the primitive cavity seems, after the investigations of the two last, to be erroneous, Metschnikoff and Kowalewsky both showing that it first appears as a simple bud, independent of the cavity itself. Kowalewsky believes that the float is first formed as an invagination. In Metschnikoff's figures of *Agalmopsis Sarsii* the float is represented as of ectoderm alone. Both ectoderm and entoderm enter into the formation of the bud, which is at first an invagination, as many of my own preparations show is the case in *Physophora hydrostatica*. The earliest stage of the young of Physophora is a true gastrula of the invaginate kind. The theory of the relation of the Siphonophorae to a budding Medusa and not to a free swimming hydroid was first suggested by McCrady. In late years it has been urged on embryological grounds by Metschnikoff and P. E. Müller. This theory is directly connected with the homology of the float. Homologically speaking there is very little difference between a free swimming hydroid and a medusa with attached and highly differentiated buds such as one finds them in the Siphonophorae. While Haeckel was the first to discover the resemblance of the larva of the Physophoridae to a young medusa and to homologize the provisional "deckstück" with the bell of a medusa, he looks upon the other later formed bracts as individuals after Leuckart's conception. It is a strange inconsistency.



between this and the rapid motion of a *Galeolaria*, darting through the water almost with the velocity of a *Doliolum*, is very great. The lower Siphonophorae, as *Physalia*, have some means, passive as they are, of progression, but *Rhizophysa* seems to stand alone among the Siphonophorae in its helplessness. The animal, however, has a certain prehensile power in its polyps not unknown among other Siphonophores. *Physophora hydrostatica*, which manifests phenomena of sensation more quickly than the other Siphonophores, will grasp a pencil in its so-called tasters, and cling to it with great tenacity.

That power is also, though in a less degree, possessed by the feeding polyps of *Rhizophysa*. The sensation however, in the whole body is very marked, as exhibited by the responsive contraction of the stem. When excited, the ability of the tentacles and their complicated tentacular knobs to grasp, is an additional element in the propulsive power of animals so helpless as *Rhizophysa*. Firmly seizing a floating weed, piece of wood, or even another living body (for I think at times even a large animal is fastened upon), it is thus moved from place to place by a foreign agent.<sup>1</sup> The *Rhizophysa* makes up in this way those means of progression of which it is destitute, but which even its own relations possess in such a highly developed form. The peculiar problematical organs, which since Leuckart's investigations have been commonly known as "tasters," are also wanting in *Rhizophysa*. Three or four of those feeding polyps nearest the float, bear a very great resemblance to these structures in other Siphonophores. They have the same simple tentacles, and mouthless stomachs, but are evidently only the undeveloped stages of true feeding polyps. Farther down on the stem we find them passing into tentacles with tentacular knobs, and true polyps with mouths.

The slender, needle-like shape of *Rhizophysa*, caused by its destitution of swimming bells, renders it a most inconspicuous object in the water. The long tentacles hang gracefully down far below the extremity of the animal, at times contracting at the very base of

<sup>1</sup> I have never seen it grasp the sides of a glass dish in which it was confined, and pull its float under water as Huxley says. Still the anastomosing tentacular knobs have the power of firmly fastening themselves to a foreign object. These structures, however, it must be remembered, were not found in the species which Huxley had. Whenever I have found it attached, its whole body was coiled around the object very much in the manner in which it was found by Mr. Agassiz on the lines used by him in deep sea fishing.



their polyps, and then leisurely dropping into their extended position with great facility. The highly contractile stem of the *Rhizophysa* shortens itself into a shapeless snarl, bringing with it feeding polyps and tentacles into a tightly coiled mass. In this condition, however, it remains but an instant, and the closely drawn spiral is gently uncoiled, and one after another of the tentacles gracefully extend to their normal condition. Gegenbaur gives the length of the stem of the animal as  $1\frac{1}{4}$  ft.; certain individuals, however, reach much greater lengths, and some of the specimens I have studied measured three feet at least. The diameter varies in different positions along the axis. Directly under the float the stem is very small, and it increases gradually to the very distal extremity. For a Siphonophore of its size, the diameter directly under the float is very small as compared with other Physophoridae. A slight stem of the character found in *Rhizophysa* could not support swimming bells and covering scales so much developed as in *Agalmatopsis* or *Halistemma*.

The air-bladder or float of the *Rhizophysa* differs in one respect from that of any other Siphonophore. Enclosed in an enlargement of the stem, as that of the others, it has, from its under portion, branched and simple saccular appendages, which hang down from its lower surface. That into which they open is a very peculiar supplemental float, surrounding its lower hemisphere. As far as I am acquainted with the Physophoridae, these sacs are a peculiarity of *Rhizophysa*. Their function is unknown. They are wanting in certain *Rhizophysidae* described by Studer. The float has an opening into the surrounding medium, and the air can be expelled at the will of the animal. Gegenbaur saw the escape of air from the float when pressed, notwithstanding his previous declaration of its impossibility. This was first seen by Huxley. I have observed the float contracted, the air expelled in bubbles, the walls of the opening being at the same time protruded in a funnel-like structure. The opening is surrounded by dark crimson pigment spots, arranged with some regularity, and of polyhedral shape. I think they belong to the air-bladder, and are not on the external envelope. There is no opening from the float into the cavity of the stem. The float on the surface of the water always lies at right angles to the stem, as is shown in figure 2 of the plate. In this way the opening into the cavity does not lie at the apex of the animal, but at one end of the float. When we compare the float of *Physalia* with that of *Rhizophysa*, we find the opening in an homologous position at one end of



the bladder-like float. It is therefore evident that the place of origin of the different parts along the under side of *Physalia* correspond more or less with the side of the float of *Rhizophysa*, and not with the point of attachment of the stem. We should expect the earliest developed oldest parts of a *Physalia* to take an origin at a point or pole opposite the opening corresponding with the point of origin of the stem of a *Rhizophysa*. Such is the case with certain younger stages of *Physalia* which have been figured as new species.

The peculiar suspensoria which are so well marked in certain species of *Agalmatopsis*, are not present in *Rhizophysa*. The shape of the float itself is that of a prolate spheroid; the outline of the extremity of the stem which forms its envelope is pyriform. Both parts consist of two well defined layers. These layers fit closely together except on the lower hemisphere of the float, where they are separated to such an extent as to create a cavity into which the peculiar "coeca" like bodies open. This cavity, formed simply by a separation of the two component layers, can be voluntarily inflated in such a way as to be easily distinguished from the upper half.

In none of the Siphonophores have we a better opportunity to trace the development of the feeding polyps and tentacles than in *Rhizophysa*. Directly under the float the least developed polyps appear as simple buds from the stem, with no differentiation into stomach and tentacle. A more developed bud shows the origin of the tentacle as a supplementary extension of the wall of the polyp on its upper and basal surface. The secondary bud differs in no respect from the first, nor has it any differences from the polyp part itself. Indeed, both together form a bifid appendage whose component parts differ only in size. The subsequent growth has been very often described. It is nearly the same in *Rhizophysa* as in other *Physophoridae*. Only when we come to study the tentacular knobs and their development can we detect any marked variations from a common type of growth among the Siphonophores. For that reason these structures have always played a great part in the classification of the Siphonophore. We fail to find in *Rhizophysa* those characteristic pigment spots so well marked at the base of the feeding polyps of *Agalmatopsis* and *Agalma*. The polyps are of a uniform flesh color throughout, with little or no variations either at base or apex.



The tentacles do not differ from other tentacles as found among the Siphonophorae. They are composed of the same two layers, and arise from the base of the polyps. When the polyp is detached the tentacle never remains on the stem, but continues united to the base of the polyp.

The motion of the tentacles is for the most part a simple contraction and extension. The festoon-like position into which, according to Mr. Agassiz, the tentacles of *Nanomia* are thrown, is rarely seen in the tentacles of *Rhizophysa*. They hang listlessly down by the side of the stem, and, except when the animal is alarmed, are never moved. Their length, as compared with the distance between the polyps, is much greater than that represented by Gegenbaur.

The appendages to the tentacle are the most unusual structures in the organization of this curious Siphonophore. Nowhere do we find a similar complication of structure, nor so many different forms. Other Siphonophorae have as complicated types of tentacular knobs, but no adult more than one kind, nor do they serve for more than one purpose. *Rhizophysa* has three kinds of appendages attached to the tentacle, and I think these have three functions; each one of these parts passes through a distinct and more or less characteristic development.

Gegenbaur pointed out these three kinds of knobs, but did not trace the first to its adult condition. The figure which he gives corresponds with the undeveloped stage which I have figured in my plate. (Plate 2, fig. 5.) This form is immature, and passes into the more advanced condition, fig. 6.

Keferstein and Ehlers follow Sars in regarding the second kind of tentacular knob as developed from the first. That view is, I think, a wrong one, for the second kind of knob has a very different mode of development from the first, and has early formed structures which never appear in the former.

There seems little doubt that Gegenbaur was right in considering that there are three kinds of tentacular knobs, although he studied only the undeveloped form of the first.

The first and most numerous kind of tentacular knobs is found by hundreds along the tentacle, extending to its very extremity. As would be naturally expected, they are found in all stages of development, with the most distal the most complicated in structure. When fully grown, they are united to the tentacle by a secondary stem, which is highly contractile, and in structural character differs in no



respect from the tentacle itself. They arise as simple buds from the tentacles, and in early conditions are sessile. It is only when more developed that the secondary stems are formed. In the first stages we have a club-like body, slightly constricted at its base and position of union with the tentacle. In this primitive knob there are many large lasso cells, always imbedded in the surface layer. These cells are described by Gegenbaur.

The first differentiation in the development, which up to this time presents no variation from that of other Siphonophores, is the aggregation of these cells at one pole, which is the distal extremity of the knob, and the formation of a finger-like extension, tipped by a cluster of smaller cells; this cluster of smaller cells is never lost, and forms one of the characteristics of the first kind of tentacular knobs. They may be seen in fig. 4, where the prolongation is greater than in subsequent stages.

From both sides of the under hemisphere of the knob a bud now forms, which is simply a proliferation of the walls of the appendage; fig. 5 gives an idea of the appearance of the knob at this stage. Lasso cells are scattered irregularly through these parts, which are smaller than the first formed, although larger than the cluster mentioned as existing at the apex. This is very near the stage which Gegenbaur regarded as the first form of tentacular knob; its development, however, is not yet finished.

The two side appendages lengthen, become more slender; the median portion becomes more spherical, and a well-defined neck forms at its base. The lasso cells, which were formerly irregularly scattered over the whole surface, aggregate into two clusters, one terminal and the other about midway down the arm. Various drawings were made of this stage, of which figs. 5, 6, 8 give a good idea. This is the most developed condition in which I have found the first kind of tentacular knob.

There is a remote resemblance between this knob and that of the genus *Agalma*. The envelope so well known in this genus is, however, wanting. It would be very hard, in the present stage of our knowledge, to carry out such an homology, which may be only superficial, but it would be a convenient way to designate this kind of an appendage, from others yet to be mentioned, if it were known as the *Agalma*-like knob.

Very different in the method of development from that of those already mentioned is the history of the second kind of tentacular



knobs of *Rhizophysa*. Like the former structures they also arise as simple buds, but their subsequent growth is very different. Their developed form is characteristic of the genus under consideration, and does not bear even a superficial resemblance to the tentacular knobs of other Siphonophorae. They are larger and less numerous than the former. The adult form is well described by Gegenbaur, to whose account I refer the reader. He does not mention the power of progression which one of these has when separated from its stem, nor the grasping power possessed by the different branches. Both of these characteristics I have often watched under a glass of low power.

The first stage of this tentacular knob is also a simple bud, but of very different natures are the subsequent forms of the two. Fig. 9 represents the simple spatulate outline in the youngest stage; it is devoid of lasso cells, and larger than the younger stages of the other. In the former case one of the earliest differentiations was the formation of a median or apical cluster of smaller cells; here, however, we find an apical depression, as shown in fig. 10. Scattered lasso cells have appeared, but in a different position from what we found them in the former case. Fig. 11 gives us a view where the depression has grown still deeper.

A new and secondary division now appears, so that, as in fig. 12, we have the knob divided into four parts; one large and two smaller depressions forming four bifurcations. The lasso cells have clustered upon these projections as represented in the figures. The tentacular knob now differs little from the completely developed, and subsequent growth is simply a bifurcation and prolongation of these four parts into branches, at the extremity of which is always a black spot, as represented in fig. 12.

There is in this stage a peculiar cell, larger than the rest, which I have sometimes thought was an opening, and connected with higher organs of excretion or sensation; this peculiar structure appears in the angle of the larger branches at the point (A). In the adult it is a cluster of pigmentary bodies of dark yellow color, surrounded by a wall, or enclosed very much as an otolith. Gegenbaur mentions it in his text, but does not figure it. In no fully grown *Rhizophysa* is this structure absent, and in the youngest stages it can be seen as a simple, prominent cell.

I have nothing of importance to add to Gegenbaur's description of the third kind of tentacular knob, except that it does not follow the



type of development of either of the two mentioned above. It seems to resemble more the tentacular knob of a Calycophore, as a Galeolaria or Diphyes, than the same structure in the Physophore.

Between the polyps are curious organs of botryoidal appearance, which are commonly called the sexual organs. They have never been found with any structure which can be likened to a germinative dot or vesicle, nor have the male been distinguished from the female elements; indeed, they differ so greatly from sexual parts as generally met with among Siphonophorae, that one is almost in doubt whether they are really parts of this system or not. The interior has a ciliated surface, as Huxley pointed out. Situated on the stem between every pair of polyps, except those in close proximity to the float, we find from one to five of these clusters, wholly isolated from the remaining parts of the animal. Like the other organs of the body, these parts develop also as simple buds, of two layers, in the form of a small bladder, smooth in outline and destitute of lasso cells.

The first change in the growth is the formation of irregularities on the whole surface, as shown in fig. 14. These irregularities originate in wart-like projections on the surface, and present an appearance whose outline is given in fig. 15.

The structure resembles, as Gegenbaur says, a "Morgenstern", one of those mediaeval weapons in use before the introduction of fire-arms. The whole organ, in its histological structure, is composed of two layers: an outer layer, composed of transparent fibres with an intermixture of lasso cells; and an inner, sharply defined from the former, and clearer, destitute of cells, and apparently lined with cilia. I do not know certainly whether cilia exist, although both Huxley and Gegenbaur declare that the innermost surface, or the wall of the cavity, is ciliated. The different prominences of the botryoidal structure become more irregular in outline; the single elevations, instead of being spherical, take the irregular triangular form shown in fig. 17. That condition is followed by a specialization of growth at one angle, as shown in fig. 19. When the growth has proceeded still more, as in fig. 20, we notice near the apex of the prolonged portion a singularly large lasso cell, which remains constant in the more developed forms. Other adjoining cells of like nature make their appearance later, as seen in figs. 21, 22; the whole cluster is united, as seen in fig. 16. It sways to and fro independently, and can be contracted or expanded, as is the case with similar organs among other Siphonophores.



The peculiar cells which I have mentioned are not germinative vesicles as their number and variations plainly indicate, but more especially as seen in the absence of the germinal dot. I am inclined to think these so-called sexual organs are unisexual, and that we have in these animals a case unlike Gegenbaur's *R. Eysenhardtii*.

Mr. Alex. Agassiz mentions and figures in his account of *Nanomia* a most wonderful and unique form of development of the young *Nanomia* from a bud, as well as from the egg; he considers an egg development also to be present, but apparently did not find the very early stage of the egg.<sup>1</sup> Such a method of development by a bud has only been observed in this single case, and by him alone. Rhizophysa may have a similar form of development in these botryoidal structures. Certainly there is very little resemblance between the oldest observed stage, which I have figured, and the egg or male organ as found among the Siphonophorae.

*Note.* The following is not a complete list of the literature of the Siphonophorae but of works mentioned in this paper.

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<sup>1</sup> According to Metschnikoff, *Nanomia cara* is simply a member of the old genus *Stephanomia*. He does not seem to give importance enough to this peculiar budding development. Its existence in one and not in the other, would be sufficient cause for a generic difference, yet it remains to be seen whether such a method of reproduction does occur in *Stephanomia*; further study of the history of the young of *Nanomia* is also needed.



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## EXPLANATION OF PLATE 2.

1. *Rhizophysa filiformis*. *a*. Float. *b*. Stem. *c*. Feeding polyps. *d*. Tentacle. *e*. Grape-like clusters.
  2. Customary position of the float on surface of water.
  - 3-8. Tentacular knobs of the first kind.
  - 9-13. Tentacular knobs of the second kind.
  - 14-22. Botryoidal clusters found between the polyps, and known as sexual organs.
  - 23-29. Early stages of development of the first kind of tentacular knob. View from the side.
- All the figures are optical sections except fig. 1.

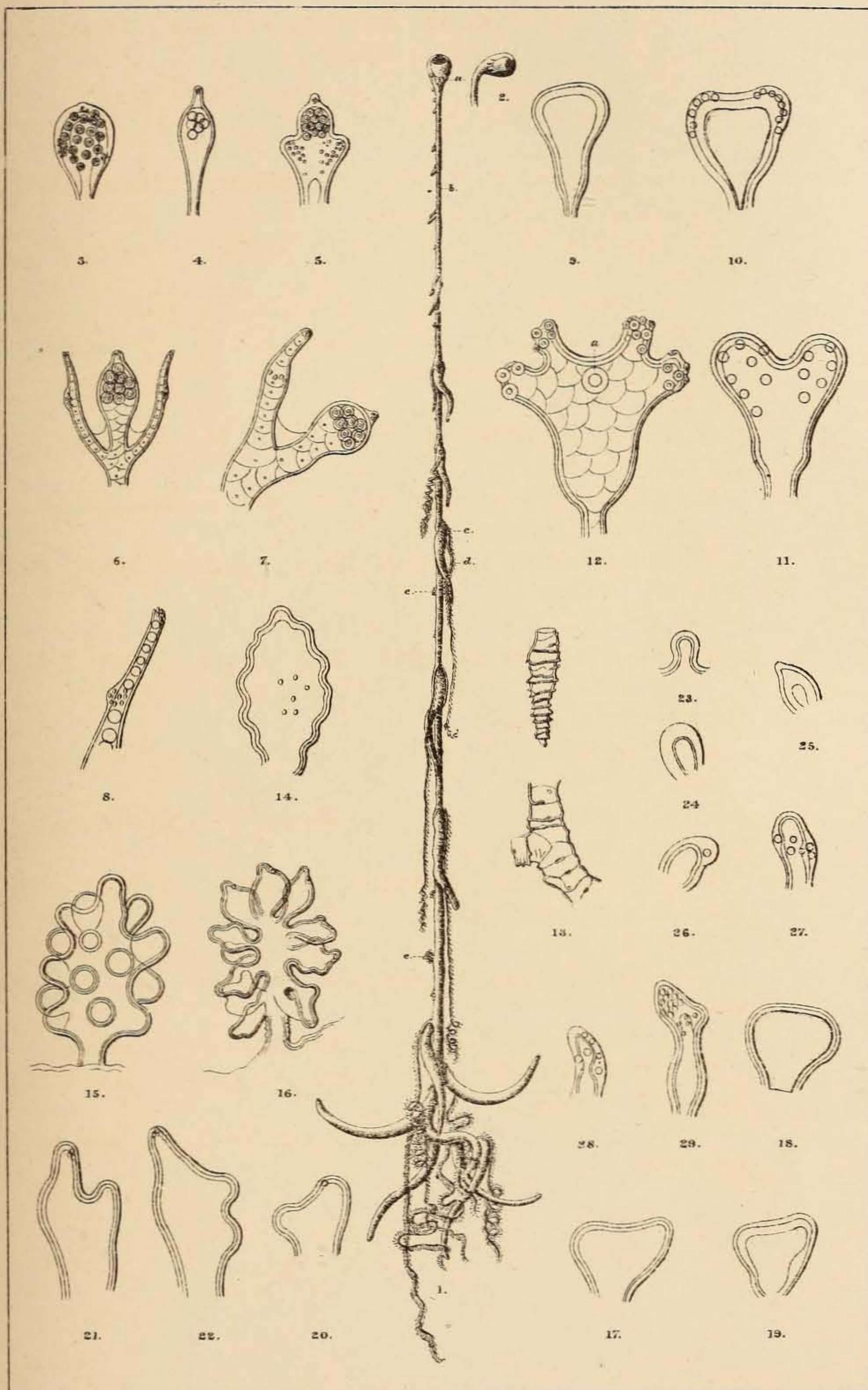
In response to a request from the chair, Dr. M. E. Wadsworth gave a brief sketch of some results of his studies in the Lake Superior region during the past summer, of which he proposed to give a fuller account in a paper to be read before the Society at a future meeting.

Mr. L. S. Burbank, Prof. W. H. Niles, the President, and others, remarked on some of the points referred to by Dr. Wadsworth.

Dr. Thos. M. Brewer announced the gift of a specimen of the Shearwater, *Rhyncops nigra*, taken at Wood's Holl, by Mr. J. F. Carleton, to whom the thanks of the Society were voted.

A vote of thanks was also passed to Mrs. S. B. Cragin for gifts to the Museum.





E. S. S. del.

J. W. T. ad. nat.

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