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THE SIPHONOPHORES.

BY J. WALTER FEWKES.

(*Continued from October number, 1881.*)

IV.—ANATOMY AND DEVELOPMENT OF DIPHYES.

THE Siphonophores which we have thus far considered all agree in this particular, that they have a float attached at one end of the stem to buoy it up in the water. It may, in some genera, be doubtful how far this structure is necessary, or to what extent it is functional, but it is never without representation in any of the Physophoridæ. We come now to consider tubular jelly-fishes, which may be looked upon as in many respects the highest[1] of the Siphonophores. In no member of the group is there a float such as is to be found in Agalma and its allies, while in details of structure their organization is very characteristic, and different from the tubular Medusæ already studied. A good representative of these Medusæ, whose several genera make up the Diphyidæ,[2] is the beautiful genus Diphyes, represented in our waters, as far as explored, by a single species. An account of the anatomy and development of this genus seems a fitting introduction to a more extended acquaintance with the remaining Siphonophores, which embrace some of the most beautiful animals with which the student of marine life is familiar.

The differences between Diphyes and Agalma seem so great

[1] If we consider, however, their anatomy, and the likeness of some of the Diphyidæ to the primitive medusa of Agalma, we may place them, as a whole, below the Physophoridæ. My reasons for placing them higher will be given later in this paper.

[2] The designation Diphyidæ seems to me preferable to Leuckart's term, Calycophoridæ. The very aberrant genus Hippopodius is the type of a family between the Physophoridæ and Diphyidæ.

that, at first sight, it is almost impossible to recognize anything in common between them both. A more intimate study, however,

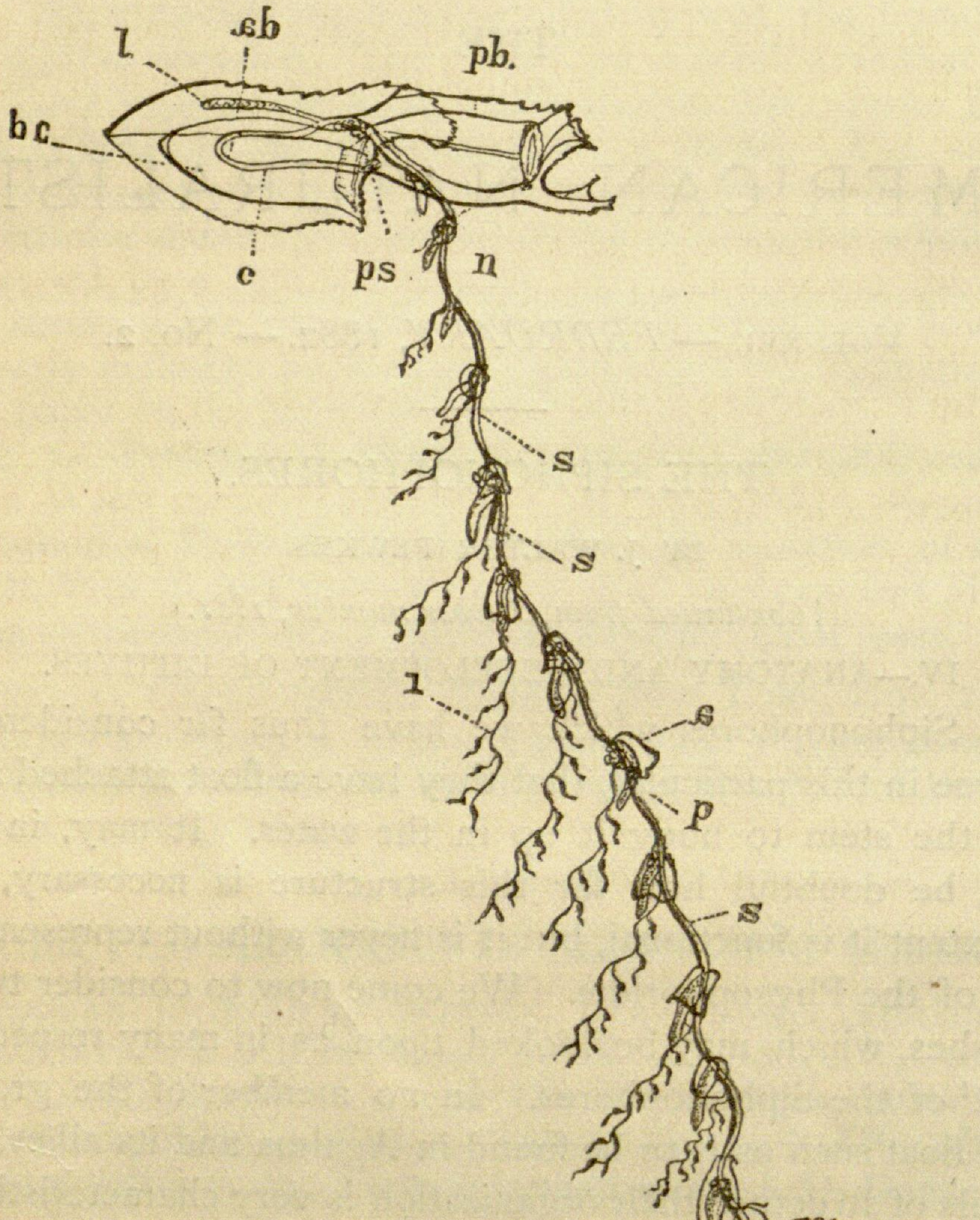

FIG. 1.—*Diphyes formosa*, sp. nov. *a*, covering scale; *ab*, anterior bell; *bc*, bell cavity; *pb*, posterior bell; *ps*, pigment spot (ocellus?); *c*, long tube of anterior bell; *l*, somatocyst; *n*, ridges on lower side of posterior bell; *s*, stem; *a* covering-scale; *p*, polypite; *i*, tentacle.

brings out very many resemblances which a casual observation had overlooked.

Prominent among all the structures which characterize the Siphonophores, is the axis or stem from which the group is named. In Diphyes this part *(s)* is very well developed, and in live specimens may be seen trailing behind to a great distance in the water, just as we have seen was the case in the genera of Physophoridæ already mentioned. Along its whole extent we find appendages so fastened that they do not incommode in the least possible manner the direct motion of the animal through the water. In the genus Diphyes it will be noticed that all the organs are especially adapted for rapid motion, and as one watches these graceful tubes, with their appendages, shooting through the sea, the adaptation for this mode of life seems complete. With this thought in mind, one can almost predict the organs of the Physophores which should be missed in Diphyes, and the modifications of their form which would be expected.

A float would, if of any size, be a great impediment to the free motion of the jelly-fish. In Diphyes, consequently, it is altogether wanting, and other methods are resorted to in order to diminish the specific gravity of the colony.

No organ of Diphyes better illustrates the modification and adaptation which has taken place to bring about rapid motion, than those which move the colony, which are here, as in all Siphonophores, the nectocalyces. There are only two of these swimming-bells, as they are called, and they are very different in outline and general appearance from the swimming-bells of any of the animals which we have yet considered. These bells differ also one from the other, in size, shape and anatomy.

At one end of the axis of Diphyes, as it floats gracefully extended in the water, there are two gelatinous, transparent bodies of somewhat conical shape *(ab, pb)*; these are the two nectocalyces which, with the exception of one genus, Hippopodius, are double throughout all the members of the Diphyidæ.[1] The connection between the two bells at the extremity of the axis is so strong, that when they are raised from the water they are not broken apart, but the axis, by contraction, is simply drawn up into a deep groove in the under side of the bell, while the appendages, even when the colony is lifted out of water, remain attached

[1] In the genus Monophyes there is but a single nectocalyx. This genus is, in this respect as well as in other details of structure, very peculiar. I shall speak of it more at length in considering the different genera of Diphyidæ. Hippopodius has many nectocalyces.

much more strongly than corresponding structures of Agalma and kindred forms. In this retracted position they are often carried, as the animal darts forward in its course through the water. To facilitate that motion by diminishing the resistance of the surrounding medium, the method of attachment no less than the form of the bells, contributes.

In Agalma the nectocalyces, as we have seen, seem to arise in two rows, with bell openings looking in opposite directions. They are capable of a very limited change of position, and most of the variety of motion which the colony has, is brought about by combination in the action of nectocalyces situated in different regions of the stem, or in a muscular twisting of the axis upon which they are fastened, by which their openings are made to face in different directions. The method is too simple if rapid motion be desired, and ill adapted to that purpose in Diphyes. In Stephanomia variety and rapidity of movement are brought about by multiplication of nectocalyces. Even in this genus the means are inferior to those which we find in Diphyes.[1]

The swimming-bells of Diphyes are placed one behind the other, so that their longer axes lie in a straight line which falls in the direction of motion. Both bell cavities open in the same way, facing backward as they float in the water. When they act simultaneously the fluid ejected from their cavities by the contraction of the bell walls, presses together on the surrounding medium and reinforces each other. There is no action of one bell in opposition to another, as may happen in Agalma. The volume of ejected water is comparatively much larger than in any of the Physophoridæ.

The anterior bell *(ab)* of the two nectocalyces has a pyramidal shape, and is pointed at the apex opposite the bell opening. If this bell were attached by the same region as the nectocalyx of Agalma, it would seem as if this apical prolongation should also indicate the place of attachment of the stem. In Diphyes, however, this is not the case. The apex of the first bell is not homologous to the apex of the bell of other Medusæ, nor does it correspond to the point of attachment of the nectocalyx to the stem

[1] The motion of the Diphyes is sometimes so rapid that the eye cannot follow the animal. The water is driven out of the bell cavity by a single muscular contraction of the bell walls and when the impetus is lost a new contraction follows. The movement of the two nectocalyces is simultaneous.

of Agalma. The apex of the anterior bell is in reality the prolongation of the side of the bell, while the true apex has been abnormally twisted out of position, and is found just above the bell opening, near the origin of the stem which seems to hang down between the two nectocalyces.

Nowhere in its structure is the modification, which takes place in the organs of the bell as a result of this abnormal twisting, better shown than in the course of the chymiferous tubes upon the inner walls of the bell cavity. The radial tubes are especially modified in their course by the change in external form which the bell has undergone.

The chymiferous tubes of the anterior nectocalyx in Diphyes, consist of a system of four radial vessels placed upon the inner walls of the bell cavity, and a single large tube or cavity extending into one side of the bell walls parallel to the outer surface. The former tubes start from a common junction, and pass radially to the bell margin, while the latter ends blindly about two-thirds the distance between the bell rim and the pointed extremity of the nectocalyx. Both open into the cavity of the stem; the former by a vessel passing from their junction to the stem; the latter more directly through the same tube.

The length of the four radial tubes is very unequal, as would naturally be expected if the distortion which we have suggested as having taken place in the anterior bell, has in reality occurred. The two tubes *(c)* which lie in those parts of the bell which have been enlarged, are therefore naturally much longer than those in the remaining portions of the bell. So small indeed has that side of the nectocalyx which adjoins the posterior bell become, and so enormously has the opposite half been enlarged, that the tubes of one are inconspicuous and with difficulty traced, while those of the other are very prominent on the inner bell walls. At first sight then, we might suppose that there were but two radial vessels, while a closer study shows that there are four such tubes as we have seen exists in the nectocalyces of all Siphonophores. At the common junction of these tubes, we must look for the apex of the bell cavity. At that point, about midway in the length of the two bells, the vessels communicate with the stem cavity by means of a short tube, similarly placed to a like vessel in the nectocalyx of Agalma.

There is, however, in the anterior nectocalyx a tube *(l)* which

has the form of a cavity filled with a spongy mass[1] of cells, and which seems without representation in the bell of Agalma. This cavity starts from the union of the vessel last mentioned with the stem cavity, and extends through the substance of the bell walls, ending blindly a short distance from its union with the stem. If we look for its homologue in the bells of Agalma, it will be found to exactly correspond in position with the mantel tubes, which are diminutive branches from the vessel which in Agalma connects the radial system with the cavity of the axis. This greatly developed mantel tube in the anterior nectocalyx of Diphyes has been called the somatocyst. It is not a float, as far as its homology goes, although it may, at times, contain globules of oil, which serve to diminish the specific gravity of the animal. The existence of the somatocyst in the bell walls on one side, and not on the other, necessitates a thickening of those lateral walls, which are usually placed uppermost as the medusa floats in the water. The walls on the opposite or lower side are very thin. The thickened upper bell walls, from which the axis hangs, are continued beyond the margin of the bell in order to give a basis of attachment to the stem. This elongation extends over and protects[2] a portion of the posterior nectocalyx, as shown in the figure. It often happens that the posterior bell is ruptured from its connection with the anterior, and but one nectocalyx, with its attached stem, is found. Such a find is liable to deceive a novice in the study of the tubular medusa. It can be laid down as a law to which there is but one exception as yet known, that all the adult Diphyidæ have two nectocalyces in their normal condition.

The second or posterior nectocalyx *(pb)* differs widely from the anterior in shape and in the character of its chymiferous vessels, more particularly in their course through the bell walls. While it has the elongated form of the anterior, the course of the

[1] The appearance of a "spongy mass," which seems to fill the somatocyst of Diphyes, is due to an enlargement of the walls so that the cells seem to fill the whole cavity. *D. turgida*, described by Gegenbaur, has no somatocyst. (Gegenbaur, Zeit. f. Wiss. Zool., v, 1854, p. 442–448, Taf. 23. Keferstein and Ehlers, Zoologische Beiträge, p. 16.

[2] It is to be noticed that the projection of the prolongation of the anterior nectocalyx over the posterior, strengthens the union of these two structures. A firm union is necessary in order that in their simultaneous action no movement of one bell on the other should take place. If such a motion occurs a part of the forward impetus would be lost. Rigidity of the nectocalyces is here very necessary, and hence the close soldering together of these parts.

radial tubes as well as the point of attachment of the bell to the stem, shows that one side of the bell is not abnormally developed at the expense of the other. Its general form is exactly what would take place if an Agalma bell were much elongated in the line of its height, in order to secure a greater capacity for the cavity.

The most important variation in shape from the anterior bell, is the formation of two ridges extending the whole length of the under side of the posterior nectocalyx on the side which is opposite that part of the anterior bell which is thickened and bears the somatocyst. These ridges are continued into two prominences beyond the bell opening.[1] In the interval between these two ridges there is a groove in which is lodged the stem when retracted. In some genera, as Abyla, still further means of covering the stem when thus retracted are found, but in Diphyes the groove is without covering. The posterior bell is smaller than the anterior, and is easily detached. Its radial system of vessels communicates with the stem cavity by a small vessel which is destitute of mantel tubes or somatocyst. While the two nectocalyces of Diphyes are the most prominent structures in the animal when alive, and the only organs to be studied in alcoholic specimens, they are by no means the most important. The active habits of Diphyes has given them this predominance in size. There remain many other appendages to the stem yet to be mentioned.

These parts of the colony are fastened regularly along the whole length of the stem to its very extremity. They consist of covering-scales, polypites to which are appended tentacles dotted along their length with tentacular pendants, and clusters of sexual bells. Representatives of the bodies called tasters in my account of Agalma do not exist, as far as known, in the Diphyidæ. The appendages are not placed irregularly upon the stem, a polypite in one place and a cluster of sexual bells in another, but are found in clusters, separated by short intervals of the stem. Each cluster consists of a covering-scale, a polypite with its ten-

[1] The projections formed by the continuation of the ridges on the under side of the posterior nectocalyx probably act as rudders to determine the direction which the animal takes as it moves, or to regulate the angle at which the water leaves the bell cavity. In some genera of Diphyidæ, similar structures undoubtedly have this function, and it seems highly probable that the same is true in the projections under the opening of the posterior bell in Diphyes.

tacle and a cluster of sexual bells. In Apolemia we find a like clustering of homologous parts, and the same law goes through all the Diphyidæ with the exception of the single genus Hippopodius.

The clusters which were described in the genus Apolemia, separate from the remainder of the colony and lead an independent life. This is also true in a more complete form in the clusters of the Diphyes colony. For a long time these separated fragments were thought to be new genera, that from a Diphyes had been called Eudoxia, until it was shown by Leuckart that it was in reality only a fragment dropped from the stem of a Diphyes.

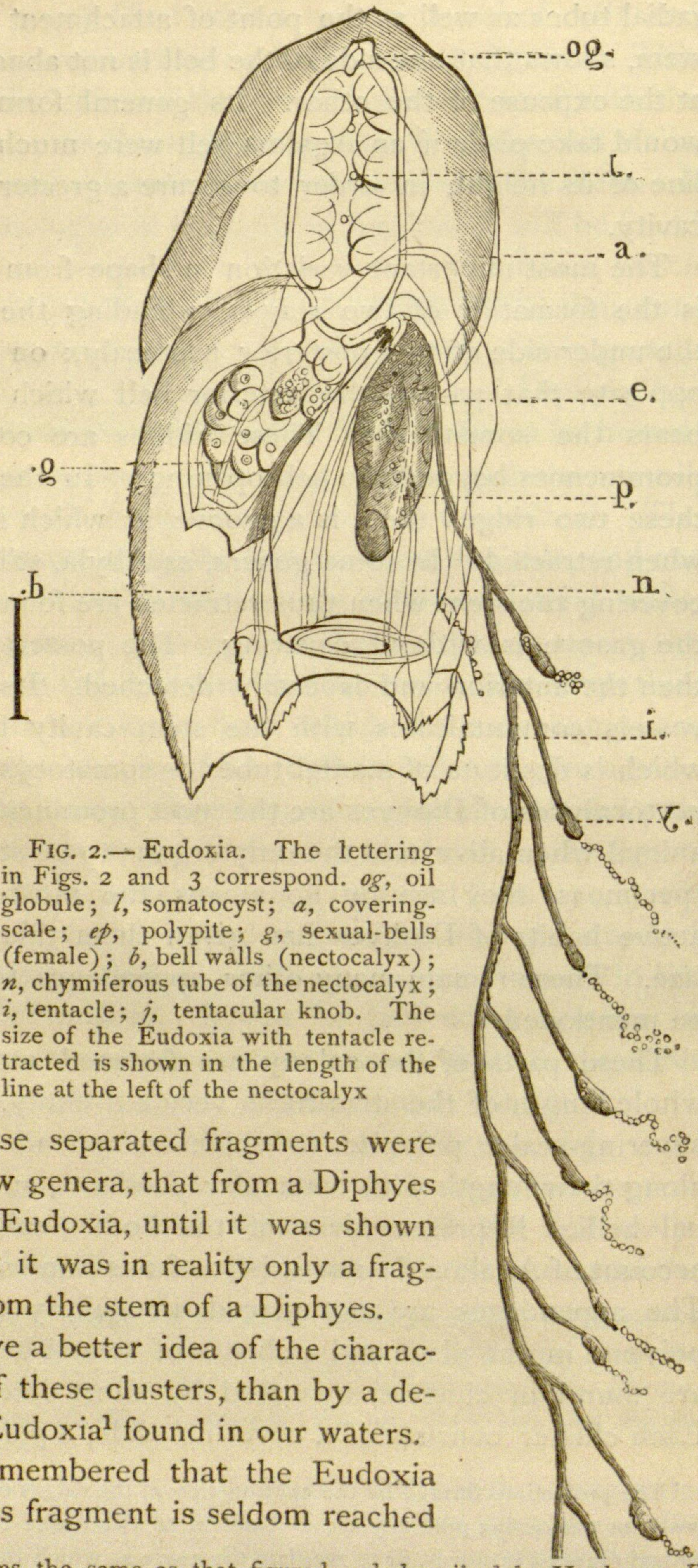

FIG. 2.— Eudoxia. The lettering in Figs. 2 and 3 correspond. *og*, oil globule; *l*, somatocyst; *a*, covering-scale; *ep*, polypite; *g*, sexual-bells (female); *b*, bell walls (nectocalyx); *n*, chymiferous tube of the nectocalyx; *i*, tentacle; *j*, tentacular knob. The size of the Eudoxia with tentacle retracted is shown in the length of the line at the left of the nectocalyx

We cannot give a better idea of the characteristics of one of these clusters, than by a description of the Eudoxia[1] found in our waters.

It must be remembered that the Eudoxia form of a Diphyes fragment is seldom reached

[1] This Eudoxia seems the same as that figured and described by Huxley as *E. Lessonii.* It is here supposed that this Eudoxia is the diphyizoid of *Diphyes acuminata.* The form of the appendages extending backward on the lower surface of the posterior nectocalyx are so different in shape in this species and *D. acuminata*, that the species here figured may be as yet undescribed.

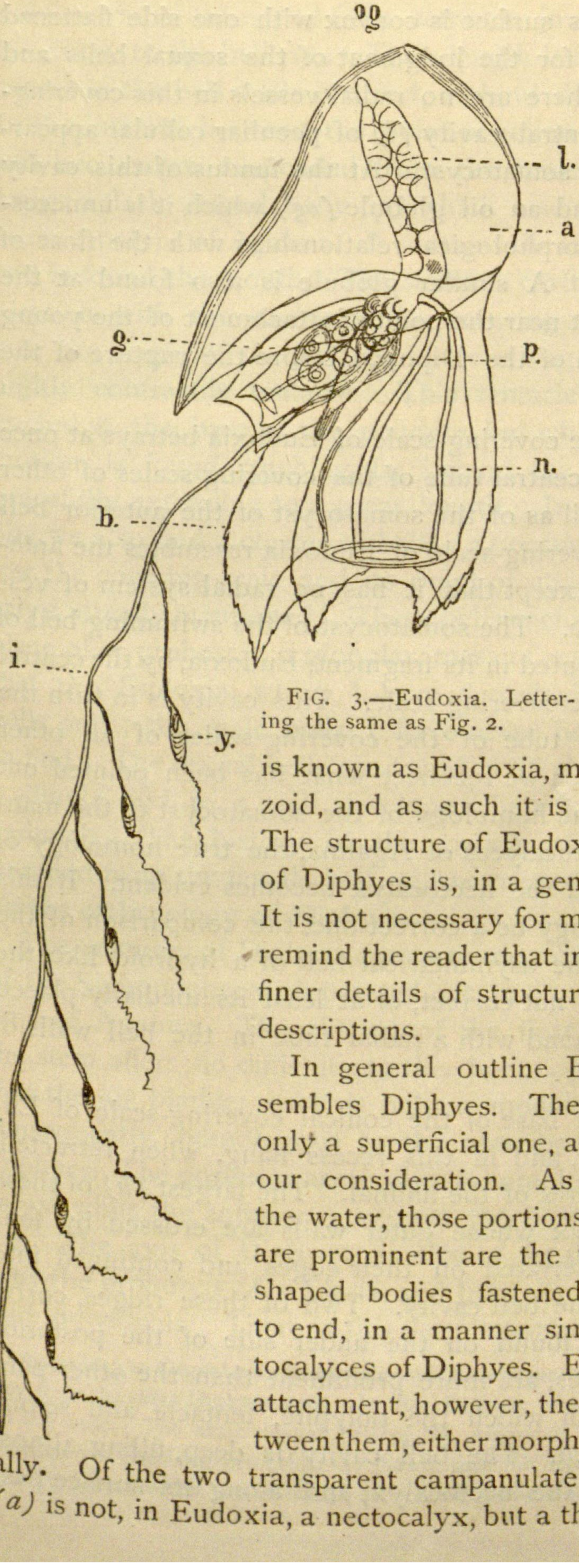

FIG. 3.—Eudoxia. Lettering the same as Fig. 2.

while attached to the axis. It is only after separation that the appendages grow to a form like that which we are about to describe. The Eudoxia discovered by us at Newport, R. I., although probably the same species as that mentioned by Huxley and others, was found one or two seasons before its Diphyes was taken.

A separated fragment of one of the Diphyidæ, which in the case of Diphyes is known as Eudoxia, may be called a Diphyizoid, and as such it is commonly described. The structure of Eudoxia, or the Diphyizoid of Diphyes is, in a general way, as follows. It is not necessary for me again to more than remind the reader that in these popular papers finer details of structure are omitted in my descriptions.

In general outline Eudoxia (Fig. 2) resembles Diphyes. The likeness, however, is only a superficial one, as will be seen later in our consideration. As it floats or swims in the water, those portions of the colony which are prominent are the two gelatinous bell-shaped bodies fastened to each other, end to end, in a manner similar to the two nectocalyces of Diphyes. Except in the mode of attachment, however, there is little likeness between them, either morphologically or functionally. Of the two transparent campanulate bodies, the anterior *(a)* is not, in Eudoxia, a nectocalyx, but a thickened, almost con-

ical covering-scale; its surface is convex with one side flattened and the base concave for the lodgment of the sexual bells and retracted tentacle. There are no radial vessels in this covering-scale, and only the central cavity *(l)* of peculiar cellular appearance, representing the somatocyst. At the fundus of this cavity there is generally found an oil globule *(og)* which it is unnecessary to say has no morphological relationships with the float of Agalma and its allies. A similar globule is also found at the base of the somatocyst near the point of attachment of the young Eudoxia to the stem of the Diphyes, before the rupture of the fragment took place.

The structure of the covering-scale of Eudoxia betrays at once the homology of the central tube of the covering-scales of other Siphonophores, as well as of the somatocyst of the anterior bell of Diphyes. The covering-scale of Eudoxia resembles the anterior bell of Diphyes except that it has no radial system of vessels and no bell cavity. The somatocyst of the swimming-bell of the Diphyes is represented in its fragment, Eudoxia, by the central cavity *(l)* of the large covering-scale. This cavity is in turn the same as the central tube of the covering-scales of all other Siphonophores. When we recollect what has been pointed out above in relation to the homology of the somatocyst to the mantle vessels in the nectocalyces of Agalma, the true homology of the covering scale and the nectocalyx becomes evident. If this view of the morphology be a correct one, the comparison of the covering-scale with the asymmetrical bell of a hydroid like the genus Hybocodon, is not correct, or at least its medially-placed tube does not correspond with a radial tube in the bell walls of the hydroid medusa.

The under side or base of the conical covering-scale of Eudoxia is very concave, and in this recess hang, when retracted, the remaining structures of the animal. The largest *(b)* of these bodies is a nectocalyx whose outer walls are crossed by four longitudinal ridges, serrated on their edges and continued into projections beyond the bell cavity. Two of these ridges, corresponding with those found on the under side of the posterior nectocalyx of Diphyes, are more prominent than the other pair, and enclose a canal in which the polypite, tentacle and sexual bell, lie when retracted. The bell cavity is deep, filling almost the whole interior of the nectocalyx, and along its surface pass

the four radial tubes *(n)* from common junction at the apex of the cavity to the bell rim. Their length is about equal, and their course in the bell walls is direct, without division or bifurcation. In the interval between the point of union of the covering-scale and nectocalyx, suspended from the under side of the former, hangs a flask-shaped body *(p)* which resembles very closely the feeding polyps of Agalma. It contains the stomach, and at its free end is found the mouth. The stomach cavity is in direct communication with the cavity of the covering-scale. From a point near the origin of the polypite there is suspended a long flexible highly contractile tentacle. This tentacle can be wholly retracted at the base of the polypite, but when the Eudoxia is in motion, is found reaching far behind the point of suspension, gracefully extending to a great length. In addition to the polypite we also find a cluster of bells *(g)* occupying the interval below the covering-scale and its point of attachment to the nectocalyx already mentioned. These bells enclose in their cavities, in place of a proboscis, a globular mass of eggs. It will be seen that the Eudoxia, which I have described, has female[1] sexual bells only; the male bells I have never been fortunate enough to find. The sexual bells are found in all stages of growth, from a simple bud to a well developed bell hanging from a stout peduncle. The history of the growth of the egg after it is dropped from the female bell, will be treated of in a special paper on the embryology of Diphyes.

The anatomy of Diphyes seems to me to sustain the homology of the Siphonophores as pointed out in our account of the anatomy of Agalma. The absence of the float at the extremity of the stem offers no difficulty to this homology when we recollect that the air bladder itself is only a modified medusa bell, and consequently homologous to the anterior of the two bells of Diphyes. The posterior nectocalyx is homologous to a true nectocalyx, while the anterior represents the float of the Physophoridæ. The axis of Diphyes, as that of Agalma, is homologous with the proboscis of a Lizzia, and from its sides bud the medusoid individuals. There is this very important difference between

[1] According to Gegenbaur, Keferstein and Ehlers, male and female sexual organs coexist on the same Diphyes stem. In the Diphyes which I have studied, that is not the case. The male sexual bell of the American form is unknown to me. Leuckart has also long ago (1853–4) shown that the European Diphyidæ are diœcious (Siphonophoren von Nizza, p. 28. Zoologische Untersuchungen, p. 36).

the proboscis of Lizzia and the stem of Diphyes, that while the buds from the former separate without absorption of the stomach walls, the Eudoxia appropriates a section of the Diphyes axis to form essential parts of its body.

To my mind there is no difficulty in a comparison of the Eudoxia with Lizzia[1] and with the Physophoridæ. Eudoxia is the adult form of which the Diphyes is the "nurse stage," so that we have here a true alternation of generation as in other medusæ. It is natural, therefore, that the likeness between Eudoxia and Agalma should be a distant one, since the latter genus never passes out of the Diphyes form, or the "nurse" from which the Eudoxia buds. On this account I consider the Physophoridæ as lower, anatomically and embryologically, than the Diphyidæ. Like those forms of fixed hydroids, which never drop medusa-shaped buds, and never, therefore, advance out of the fixed "nurse stage," the Physophoridæ never attain as completely developed a form as the Diphyidæ. They never bud off a gonophore as the medusoid bud is sometimes called, but always remain in the embryonic form. As the Diphyes stage is comparable with a strobila or a budding Lizzia, the Eudoxia is the completed generation comparable with the adult Lizzia which drops the eggs, or the sexual form.

The following table exhibits the corresponding parts of Lizzia and Eudoxia:

Lizzia.	Eudoxia.
Bell.	Covering scale (*a*).
Manubrium (proboscis).	Feeding polyp (polypite) (*p*).
Tentacle of a bud from the proboscis, the bell of which is aborted.	Tentacle (*i*).
Modified medusa bud from the proboscis, the proboscis and tentacle of which are lost (aborted).	Swimming-bell (*b*).
Several buds from the proboscis (young Lizziæ).	Sexual-bells (*g*).

[1] The comparison of Eudoxia to a "budding Lizzia" was set first forth, substantially as given in this article, by Professor McCrady in 1857 (Gymophthalmata of Charleston Harbor, p. 67). Since that date the theory has been urged on embryological grounds, without a mention of McCrady's suggestion, by Haeckel, Metschnikoff and P. E. Müller. (Haeckel. Zur Entwick. der Siphonophoren, 1869. Metschnikoff, Stud. uber Entwick. d. Medusen u. s.w., Zeit. f. Wiss. Zool., Bd. XXIV. P. E. Müller, Iag. over Nogle Siphonophorer, Nat. Tidsskrift 3. R. 7. B. Resumé in French). I am indebted to my friend, the late Mr. G. Winther, for a written MS. translation of portions of Müller's work.

If we were to follow precedent in our studies of the Siphonophores, we must apply to the adult the name Eudoxia instead of the almost universally used Diphyes. It is just as absurd to retain the name Diphyes to designate anything but a younger stage in the growth of Eudoxia, as it would be to designate the adult sea-urchin a pluteus, or to retain the word auricularia for the adult starfish. The monogastric form, or the Eudoxia, is the adult; the polygastric, or Diphyes, the larva.

There is another point to be considered. If from the embryonic feature of possessing a long axis, or stem, the relatives of Diphyes are referred to the Siphonophores, is that reference a good one, and would the characters as assigned to the group to which Agalma belongs (Siphonophoræ) hold in descriptions of the adult Diphyid? The Eudoxia has no stem-like structure, which gave the name to the group, although it is a true relative.

The comparison of Eudoxia with Agalma, or the adult stage of Diphyes with the corresponding larval condition, Agalma, is evidently legitimate, as the comparison of the developed bud of Lizzia with a genus similar to the Lizzia from which it budded. Although we have in Eudoxia an alternation of generation, it is unlike that condition in some other animals, as in the echinoderms, where the nurse cannot be homologized with the adult. In some respects it resembles most closely that process of growth which we are familiar with under the name of strobilation. The Eudoxia is the separated Ephyra, and the Diphyes is a free-swimming scyphistoma, as far as the relation of the nurse to the adult goes. Here however the parallelism ends. The same holds true also in a comparison of genera of Diphyidæ with the free-living proglottids of the tape worms (Leuckart, Siphonophoren von Nizza, p. 29). As McCrady has already pointed out (Lectures), there is a close resemblance between a Tænia and the Scyphistoma in mode of strobilation, but as there is no homology between the proglottids and the Ephyra, so there is little in common in the structure of the Diphyizoid and Ephyra. They resemble each other simply in the mode of strobilation.

The corresponding parts of an Agalma and an Eudoxia are given in the table below:

Agalma.	Eudoxia.
Float.	Covering-scale.
Nectocalyx.	Nectocalyx.
Polypite and tentacle.	Polypite and tentacle.
Covering-scale.	Covering-scale.
Taster and filament.	Wanting.
Sexual bells.	Sexual bells.

The axis or stem of Agalma is reduced in Eudoxia to the polypite condition, and is not distinguishable from this structure.