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XX.—*On the Cyclical Development and the Relationships of the Siphonophora.* By Dr. Carl Chun *.

[Plate V.]

I. *The Cyclical Development of* Monophyes primordialis, *Chun.*

In the year 1853 Leuckart † ascertained the remarkable fact that the appendages united in groups on the stem of the Diphyidæ break loose from each other, and lead a free existence separated from the colony. A whole series of supposed distinct species distributed under the genera *Eudoxia* and *Ersœa* (the "monogastric Diphyidæ") thus proved to belong to the developmental cycle of the Diphyidæ. When afterwards attention was called by Huxley ‡, Pagenstecher §, and Claus ‖ to certain very simply constructed small Siphonophora with only one nectocalyx, which, following Claus, we

* Translated by W. S. Dallas, F.L.S., from the 'Sitzungsberichte der k. preuss. Akademie der Wissenschaften,' 1882, pp. 1155–1172, Taf. xvii.

† 'Die Siphonophoren. Eine zoologische Untersuchung,' 1853, p. 56.

‡ 'The Oceanic Hydrozoa,' (Ray Society) 1859, p. 50, pl. iii. fig. 4.

§ "Eine neue Entwicklungsweise bei Siphonophoren," Zeitschr. f. wiss. Zool. xix. p. 244.

‖ 'Schriften zoologischer Inhalts. II. Die Gattung *Monophyes*, Claus, und ihr Abkömmling *Diplophysa*, Gegenb.,' Taf. iv.

may designate Monophyidæ, and the same clustered arrangement of the polymorphous individuals was detected upon their stems, it seemed probable that in these also the groups would separate. Claus demonstrated in his interesting memoir that the monogastric colonies described by Gegenbaur under the name of *Diplophysa* really represent the freed sexually mature offspring of *Monophyes*.

Consequently, so far as our knowledge of the cyclical process of development of the Monophyidæ and Diphyidæ on the one hand, and on the other of the highest Siphonophora, namely the Velellidæ, extends, we were justified in assuming that the brood of the *Eudoxiæ* and *Diplophysæ*, like the Medusæ budding and separating from the Velellidæ, namely the *Chrysomitræ*, in their turn furnish the polymorphous nurse-generation.

To my astonishment, however, the study of a new species of *Monophyes* showed me that the cyclical development of the Siphonophora manifests still further complications.

In briefly describing now the structure and development of *Monophyes primordialis*, which is the name I give to this new species, I only follow the course which my investigation took.

Among the rich pelagic fauna of Malaga with which the use of the surface-net furnished me I often remarked a small Siphonophoran stock which looked remarkably like a *Diphyes*. It is true that in all the specimens a second lower nectocalyx was wanting, a circumstance which, however, did not much strike one at first, seeing that, when at all roughly treated, both nectocalyces of the Diphyidæ easily become detached. But although I proceeded most carefully in their capture, I never succeeded in detecting a colony with the missing second nectocalyx. As, further, it was impossible to discover any point of insertion for the latter, I arrived at the conclusion, which was afterwards confirmed, that I had to do with a Monophyid of very aberrant structure. At first I regarded it as new, but subsequently ascertained that two excellent old observers, Will and Busch, had observed and figured this Siphonophoran stock. Will * discovered it at Trieste, and, like Busch † and later observers, regarded it as a *Diphyes*. He named it *Diphyes Kochii*; and under this name it was also more accurately described by Busch, with the express remark that he had been no more successful than its discoverer in the

* 'Horæ Tergestinæ,' 1844, p. 77, Taf. ii. fig. 22.

† 'Beobachtungen über Anatomie und Entwickelungsgeschichte einiger wirbellosen Seethiere,' 1851, p. 46.

detection of the second nectocalyx. As Busch describes a form evidently identical with *Diphyes Kochii* as *Muggiæa*, in consequence of supposed differences, I combine the names selected by the first observers, and designate the Siphonophoran as *Muggiæa Kochii*.

As regards its structure, which I afterwards had the opportunity of examining more accurately in Naples, the elevated flask-shaped nectocalyx exactly resembles the nectocalyx of a Diphyid (fig. 2). It is furnished with five wing-like edges, two of which are more considerably developed towards the margin of the bell and bound a funnel-shaped space, within which the stem with its appendages can be retracted. The nectosac, consisting of transversely striated spindle-shaped muscle-cells, lines the subumbrella, and terminates at the margin of the bell in a very contractile velum. On the dilated side of the nectocalyx, above the funnel-shaped gelatinous mantle [*hydrœcium*], we easily observed the so-called fluid receptacle [*somatocyst*, Huxl.], with its oil-drop, an organ which has received the most various interpretations, but, in my opinion, without the right one having been hit upon. I regard it as a hydrostatic apparatus, destined, by means of the specifically lighter oil-drop, to present in some degree a counterpoise to the heavy stem with its appendages, and to keep the nectocalyx in an approximately vertical position. From the base of this fluid- or oil-receptacle originate four vessels (overlooked by Will and Busch), which are situated beneath the musculature of the subumbrella, and open into an annular vessel close to the margin of the nectocalyx. Two of these vessels run upwards on the side-walls, then bend round in an elegant curve, and descend towards the margin; a third attains the summit of the subumbrella, and opens into the annular canal opposite to its place of origin; while the corresponding fourth vessel forms only a very short branch of union between the latter and the issue of the above-mentioned [annular] vessel. Both the vessels and the fluid-receptacle open into the contractile stem of the whole colony [*hydrosoma*] with its polymorphic groups of appendages. In general this is not very long; I have not observed on it more than twelve groups of individuals. The latter regularly diminish in size from the base of the stem to its distal extremity. Originally they consist of four buds lined with endoderm, the largest of which develops into a stomachal sac, while two smaller ones placed above it represent the rudiments of the bract and of the genital nectocalyx; the fourth, which is situated at the base of the stomachal sac, and is early much divided at the surface, becomes differentiated into the tentacle with the urticating

batteries. Without going into detail upon the development of these buds, I will only mention that the rudiment of the bract becomes flattened, and, curving like a sickle, begins to grow round the stem. Its endodermal cavity forms the liquid-receptacle, and the lateral parts, which grow out into wings, embrace the genital nectocalyx. In the lowest groups of individuals therefore we remark first of all the mobile stomachal sac with the ectodermal cell-pad at its base, and its yellowish-red mouth often dilated in the shape of a funnel; further, the tentacle, with its amœboidally movable ectodermal cell-processes, and the kidney-shaped urticating batteries, of a bright yellow colour, attached to long accessory threads; and finally the genital bell, with its central manubrium, forming the sexual products and the four vessels opening into an annular canal. The umbrella of the genital bell grows rapidly to a considerable size, and, assisted by a velum, begins to perform pumping movements, until finally the group separates from the stem at the point of insertion of the bract, in order to lead an independent existence for a considerable time.

These sexually maturing monogastric colonies (fig. 3) also have not escaped the attention of the observers Will and Busch, who have been already repeatedly mentioned, although certainly they did not recognize their relations with *Muggiæa*. Will * describes a Siphonophore under the name of *Ersæa pyramidalis* which is evidently identical with the *Eudoxia Eschscholtzii* so accurately studied by Busch †. *But* Eudoxia Eschscholtzii *represents the sexual generation of* Muggiæa. From the most highly developed individual groups of *Muggiæa* it differs externally only in the form of the bract, which has become considerably thickened, and, as the last indicatio of its wing-like dilatation, exhibits two angles, which extend from the apex towards the genital calyx. The latter has attained its full size, shows in transverse section four wing-like edges of unequal size, and always allows the four vessels with their annular canal, which were overlooked by Busch, to be recognized. That the *Eudoxiæ* are of separate sexes and produce semen and ovum in the manubrium, representing the stomachal peduncle of a Medusa, we first learned from Busch. He further called attention to the fact that, besides this nectocalyx, a second is produced, the significance of which, however, was not clear to him. Leuckart ‡ and Gegenbaur § first

* Horæ Tergest. p. 8, Taf. ii. fig. 17.

† *Loc. cit.* p. 33, Tafs. iv. and v.

‡ *Loc. cit.* p. 47.

§ "Beiträge zur näheren Kenntniss der Schwimmpolypen," 1854, Zeitschr. f. wiss. Zool. Bd. v. p. 290.

demonstrated in different *Eudoxiæ* that this second nectocalyx represents an accessory structure, destined in course of time to replace the first large one. I have detected the first rudiment of this second calyx in the form of a small bud (fig. 2, *x*) even in the groups still adhering to the stem of the *Muggiæa*. It seemed to me of interest to obtain an answer to the question whether a regular succession of new genital nectocalyces takes place, and also whether during this change the sex of the *Eudoxiæ* is altered. Without describing the precautions by means of which I succeeded by suitable aeration and nourishment in keeping the delicate colonies alive for some days, I may state that, besides the above second accessory bud, the foundation of a third, and, as I succeeded in ascertaining in one case, also that of a fourth bud became developed. As soon as the oldest calyx has emptied out its genital products, which usually takes place while it is still connected with the *Eudoxia*, it is displaced and pushed off by the rapidly growing reserve calyx, which then in its turn undergoes the same fate. But the reserve calyces always produce the same sexual products as the first calyx; no change of sex therefore takes place. As I have been able to confirm Leuckart's statements with regard to the change of the replacement-nectocalyces in *Eudoxia campanula*, and as further similar replacement-buds have been observed in all carefully investigated *Diplophysæ* and *Eudoxiæ*, we may assert generally *that the* Eudoxiæ, *without alteration of sex, successively produce a brood of medusiform sexual animals by a process analogous to strobilization*.

If we examine the genital manubrium when filled with mature ova, we observe in them a peculiar phenomenon. They lie between the ectoderm and endoderm, of which the latter almost entirely clothes them, leaving free only a small part of the surface which is in contact with the ectoderm. At this spot we always find the large peripherally placed nucleus, with its nucleolus. Between the ectoderm and the part of the periphery of the ovum which is not covered by the endoderm, some fluid collects, in which from two to three direction-vesicles are to be detected. Müller, who first called attention to this peculiarity, regarded this arrangement as a micropylar apparatus. I cannot, however, agree with him in this view, as I could neither find an aperture in the ectodermal lamella, which is sometimes dilated and thin, nor meet with fecundated ova in the genital manubrium. What Müller regards as spermatozoa that have penetrated are evidently only the direction-vesicles. The nucleus, with the surrounding plasma, is usually overflowed by the neighbouring ectoplasm, so that

it is placed at the bottom of a pit-like depression. But if we observe the perfectly mature ova, we find that the nucleus gradually arches up and the depression disappears, until finally the nucleus, enveloped by the adjacent plasma, projects above the periphery of the ovum as a lenticular elevation. The delicate ectodermal envelope is at the same time also a little pushed forward and stretched. In a short time the convexity disappears rapidly, and the nucleus draws back again so far that a pit-like depression is again produced. In this way, then, pumping movements are executed at one part of the surface of the ovum pretty regularly, about twice in a minute, their purpose evidently being to burst the thin ectodermal envelope and to render possible the exit and fertilization of the ovum. As a matter of fact, indeed, we find that the ova are evacuated from the manubrium singly, and not simultaneously.

To judge from our previous knowledge of the development of the Siphonophora, we should expect that from the fertilized egg of *Eudoxia Eschscholtzii* the *Muggiæa* would originate. I was therefore not a little surprised when, in my pelagic captures, I met with an elegant Siphonophore which at the first glance showed itself to be a true *Monophyes*, and yet presented stomachal sacs and urticating batteries which, even by the most careful examination, were not to be distinguished from those of *Eudoxia Eschscholtzii*. As regards the organization of this smallest and most simply constructed colony among all the Siphonophora, which has been seen by no previous observer, it consists essentially of a medusiform nectocalyx, a stomachal polyp, and a tentacle (fig. 1). The calyx is cap-shaped and of laterally symmetrical form. The dome of the umbrella appears drawn out into a lappet and rounded off. Close to the place of insertion of the other appendages two gelatinous pads arise as the first indication of an incomplete sheath. Four vessels, originating from the base of the fluid-receptacle, which traverses the umbrella obliquely and is furnished with an oil-drop, supply the subumbrella, finally opening into an annular canal placed upon the velum. I have already indicated that the stomachal sac and the tentacle exactly agree with those of *Eudoxia Eschscholtzii*. Only the youngest examples, however, are so simply constructed as the *Monophyes* just described; a further complication may be observed in somewhat older specimens. Thus the stomachal sac and the tentacle are somewhat removed from the base of the fluid-receptacle, and communicate with the latter by means of a contractile portion, the first indication of the stem. On the other hand new rudiments of buds make

their appearance on this little stem quite close to the fluid-receptacle, and, indeed, first of all a bud of considerable size above (towards the apex of the umbrella), and afterwards, opposite to this, a group of four buds (fig. 5). While the first developed bud, as soon appears to be the case, represents the rudiment of a nectocalyx, we are struck, in the group of four buds, with a development identical with that of those groups of buds which we have already had occasion to mention on the basal part of the stem of *Muggiæa*. In point of fact we cannot avoid the notion that the four buds represent the constituents of a *Eudoxia Eschscholtzii*, the stomachal sac, the tentacle, the bract, and the genital calyx.

But how are we to explain the enigmatical phenomenon that, by two so perfectly different forms as are represented by the *Muggiæa* and *Monophyes primordialis*, there are formed bud-rudiments which perfectly harmonize in their further development, and in both cases grow up into *Eudoxia Eschscholtzii*? The solution of all the problems which thus press themselves upon us is no less susprising. From the rudiment of a nectocalyx placed at the origin of the stem of *Monophyes primordialis* is produced the five-angled nectocalyx of the *Muggiæa*. Muggiæa Kochii *consequently does not represent a distinct species, but it is produced by gemmation from* Monophyes primordialis, *and then, carrying with it the parent stem and the future* Eudoxia-*groups, separates from the parent animal and leads a free existence.* In fig. 4 I represent a stage (captured in freedom) which clearly demonstrates the connexion between *Muggiæa* and *Monophyes*. The nectocalyx of the former has already acquired the pentagonal form, and shows distinctly the characteristic course of the vessels. The aperture of the calyx is turned away from that of the *Monophyes*-calyx, so that the two perform brisk pumping movements in opposite directions. In almost all the subsequently observed cases (and by rearing the *Monophyes* I have six times succeeded in getting the calyx of the *Muggiæa* to grow to half the size of the *Monophyes*-calyx) the calyces were arranged in the same direction. The stem is already of considerable length, and, besides the terminal stomachal sac with the tentacle, shows the rudiment of another *Eudoxia*-group. But if we place the organism in a watch-glass with abundance of water and observe the two calyces engaged in performing their very lively pumping movements, we sometimes succeed in directly convincing ourselves of their separation, inasmuch as generally after a violent pumping movement on the part of one of the calyces the delicate uniting part of the stem tears away, and the two then continue to move independently.

This also explains why in fishing we often meet with the calyces of *Monophyes* destitute of all appendages, besides the isolated sexual calyces of the *Eudoxiæ*. After its separation the calyx of the *Muggiæa* grows rapidly, and attains about three times the size of the *Monophyes*-calyx. But it is not only upon the almost fully developed calyx of the *Muggiæa* just described that the connexion of the two generations may be demonstrated, but even in the insignificant globular bud on close examination the course of the vessels characteristic of the developed calyx already makes its appearance distinctly. A glance at fig. 5 shows how the tissues of the stem take part in the construction of the bud, how the ectoderm passes continuously into the external wall of the bud (the umbrella was even previously formed by an ectodermal invagination), while the endoderm produces, by a dilatation, the first traces of the fluid-receptacle and the vascular lamella, in the latter of which the vessels take the course typical of the developed *Muggiæa*.

The fact that by the side of a small cap-shaped nectocalyx a second one so totally different in form and size is budded forth, destined to separate from and perform the same function as the primary calyx, is unique among the Cœlenterata. We find indeed on the stem of the Siphonophora the most various polymorphic appendages; but the different form is always determined by a different function; the medusiform locomotive is of different construction from the medusiform genital nectocalyx budded from the same stock. But how are we to explain the fact that in this case two calyces intrusted with the same function, namely the locomotion of the stock, acquire such a different habit? I know of no other answer to give to this question than that the small cap-shaped *Monophyes*-calyx suffices for the transportation of the single stomachal sac with the tentacle, but that with the elongation of the stem and the increase of the individual groups it becomes necessary, by a larger and more slender calyx, which can cut through the water easily, to weaken the resistance which is opposed to rapid locomotion by the long drawn-out trailing stem with its appendages. That the Diphyid-like calyx of the *Muggiæa* fulfils such requirements will be the experience of any one who attempts to take out the little stock as it shoots through the water with the rapidity of an arrow.

But although I believe that I have proved as an established fact that the cyclical course of development of these lowest Siphonophora consists of three generations, scientific method requires the proof that *Monophyes primordialis* really originates from the ova of the *Eudoxia* budded off from the

Muggiæa. Although the investigation is attended with several difficulties, arising from the minuteness and transparency of the tiny ova, and, further, from the circumstance that we can very seldom find at the same time male *Eudoxiæ* with perfectly mature pin-shaped spermatozoa and female nectocalyces which show themselves to be filled with fertilizable ova by the characteristic pumping movements of the plasma surrounding the nucleus, I have nevertheless, after several vain attempts, finally succeeded in obtaining an artificial fecundation, and furnishing the proof that from the ova of the *Eudoxia* a ciliated embryo is produced, which grows into the *Monophyes.* Seven mature ova which were contained in the manubrium of a genital calyx, and one of which was just beginning to issue from the ruptured ectodermal envelope, I placed on the 23rd September in a vessel which swarmed with spermatozoa taken from a male manubrium. As from the scantiness of the material my special object was to rear the later developmental stages, I forebore the observation of the first phenomena of segmentation. In the warm season they must take place rapidly; for as early as the next day I found to my delight seven free-swimming embryos. The youngest represented a spherical planula, with thin ciliated ectodermal cells and large polyhedrally flattened endodermal cells occupying the whole interior space. It quickly begins to assume an oval form, and at one pole differentiates yellowish-red pigment. This represents the future buccal pole, or, to speak more exactly, the spot at which the buccal aperture of the stomachal polype breaks through. During the rotating locomotion it is directed backward. At one side of the pigmentless pole, which is in front as the animal advances, an ectodermal invagination is produced, the rudiment of the subumbrella of the nectocalyx. Below this the body-wall swells up in the form of a bud, from which, by various repeated sinuations, the tentacle takes its origin. In the meantime the endoderm divides, as already recognized by Häckel and Metschnikoff, into a central cell-mass with distinctly perceptible nuclei, and a small cellular layer applied to the ectoderm. The latter represents the definitive endoderm, while the former is gradually absorbed. The rudiment of the nectocalyx enlarges considerably; the vascular lamella, with its lateral diverticulum, representing the future fluid-receptacle, makes its appearance distinctly; and the embryo attains the form shown in fig. 6. On the third day (fig. 7) the identity with *Monophyes* is unmistakable. The nectocalyx is cap-shaped, shows distinctly the cavities of the four radial vessels, with the annular canal, in its vascular lamella,

and already begins to perform pumping movements, although it is still covered with delicate vibratile cilia. A large swelling, chiefly composed of the juicy endodermic cells, is appended to it laterally, which passes over continuously into the still-closed stomachal sac. The latter is of an intensely red colour, and displays a central cavity free from juicy cells. At its base protrude the numerous fungus-like buds of the rudimentary tentacle. The juicy cells are now absorbed, the tentacle with its urticating batteries elongates, and finally the mouth of the stomachal sac breaks through; and at the close of the third day the larva acquires a form which exactly agrees with that of the youngest stages of *Monophyes* captured in the open.

The proof being thus furnished that the fecundated ovum of *Eudoxia Eschscholtzii* develops into *Monophyes primordialis*, we have to note the following stages in the course of development of the latter:—

1. The planula.
2. The embryo with the bud-rudiments of the nectocalyx and tentacle.
3. *Monophyes primordialis.*
4. *Muggiæa Kochii.*
5. *Eudoxia Eschscholtzii.*

II. *The Relationships of the* Siphonophora.

By the demonstration that three generations intervene in the course of development of the Monophyidæ, several questions are raised, some of which may serve as a directing clue to a further investigation, while others can even now be answered. In the first place, we have to find out whether (as seems to me very probable) the other species of *Monophyes* also present a third generation. In his 'Oceanic Hydrozoa,' Huxley figures several species of *Diphyes* (pl. i. figs. 3, 4, *D. mitra* and *chamissonis*), in which a second nectocalyx was not observed. These possibly represent Monophyids of the structure of *Muggiæa*. But it is not only for the Monophyidæ, but also for the whole of the Calycophoridæ that, for reasons which I shall indicate hereafter, proof of the occasional occurrence of a third generation may be obtained. A further question, which we can even now answer in an affirmative sense, is whether *Monophyes primordialis*, with its complicated alternation of heteromorphous generations, really represents the simplest Siphonophore, or whether it is not rather to be regarded as a retrograde form. In deciding against the latter conception, I depend not only upon its

simple organization, which is reflected in the simple biological conditions, but also upon its embryonic development. If it were a retrograde Siphonophore, we might expect that, as in the case of the larvæ of the Physophoridæ, larval organs would make their appearance, to be afterwards thrown off or replaced by definitive structures. Just on the contrary, the embryonic development of *Monophyes primordialis* presents a simple course, such as the other Siphonophora no longer display. A few days suffice for the conversion of the fecundated ovum directly into the fully developed animal. Finally, we have in favour of its primitive organization the circumstance that all the Calycophoridæ, in their development, pass through a stage which recapitulates, even in its details, the structure of *Monophyes primordialis*. Monophyes primordialis *is the stem form of the Siphonophora.* So far as we at present know the embryonic development of the Calycophoridæ, it follows a course almost identical with that of *Monophyes primordialis*. Throughout, the bud for a nectocalyx is first of all established on the germ, and then one for the tentacle. A larva is formed which sometimes is delusively like the *Monophyes*. Even external characters, such as the cap-like form, are so exactly reproduced, that one might actually take the figure that Metschnikoff gives of the larva of *Epibulia* (*Galeolaria*) *aurantiaca* (Zeitschr. f. wiss. Zool. Bd. xxiv. Taf. vii. fig. 14) for a representation of our *Monophyes*.

If we now examine more carefully the stage of *Epibulia* just mentioned, we are struck in it by a further complication, which engages our interest. Thus, just as the calyx of the *Muggiæa* is established at the base of the stem of *Monophyes*, there is exactly at the same spot in the larva of *Epibulia* the bud for a second nectocalyx. But is this destined to separate from the first calyx on arriving at maturity (which, judging from the opposite position of the apertures of the nectocalyces, appears not improbable)? or does it represent the foundation of the second Diphyid calyx? In one word, do the Diphyidæ also possess three generations, or do they represent more highly developed Monophyidæ, in which two free generations are contracted into one? Further investigation must furnish information upon this point; nevertheless it is to be regarded as an advantage if we are now able to indicate the time and place at which a third generation might occur.

From the preceding statements it must be sufficiently clear that the Monophyidæ show the nearest relationship to the Calycophoridæ. We may indeed regard them as the lowest of the Calycophoridæ, and should best divide this order into three families:—the Monophyidæ, with a single nectocalyx;

the Diphyidæ with two, and the Polyphyidæ with more than two nectocalyces. The family for which I propose the denomination Polyphyidæ, however, shows several peculiarities, as the most noticeable of which it is to be indicated that the individuals are certainly distributed in clusters upon the stem, but that they do not become free in the form of *Eudoxiæ*. Male and female nectocalyces possess a remarkably small umbrella, and bring the sexual products to full maturity in the large manubrium, without separating from the stem as Medusæ. While in the Monophyidæ and Diphyidæ the cyclical development is distributed over two or three generations, these are here compressed into one.

But how is it to be explained that a direct development prevails among the Polyphyidæ and Physophoridæ, to give place again to an alternation of generations in the most highly organized Siphonophora, namely the Velellidæ? In order to answer this question we must go a little further afield. As I have already indicated, the Calycophoridæ possess a hydrostatic apparatus in the form of the so-called fluid-receptacle with its oil-drop. Now in all other Siphonophora, in place of the specifically light oil, a compressible medium, a gaseous mixture, is secreted at the upper extremity of the stem. In them a new organ, the air-sac [*pneumatophore*], makes its appearance; and this, which is originally of small size, gradually acquires more considerable dimensions, until, in the *Rhizophysæ*, *Physaliæ*, and *Velellæ*, it fundamentally influences not only the physiognomy, but even the whole organization. As regards the development of the air-sac, I can confirm Metschnikoff's statements from his investigations on the embryos of *Halistemma pictum* (=*H. tergestinum*, Claus). At the pole of the planula, which advances foremost in locomotion, we observe a solid thickening of the ectoderm, which is finally constricted off from its origin, and, surrounded by the small-celled endoderm, passes somewhat inwards. By the separation of the constricted ectodermal cells a cavity is produced, which is filled with granular fluid and rapidly dilates. The ectodermal cells, with the exception of the portion turned towards the hinder pole of the planula, secrete a delicate chitinous lamella towards the inner cavity of the vesicle, and at the same time begin to secrete a gaseous mixture, which accumulates above the fluid. The perfectly closed air-sac early acquires a flask-like shape, and in the true Physophoridæ never communicates with the outer world. In its relatively inconsiderable development it plays only a subordinate part, so far as locomotion, *i. e.* a rising and sinking, is concerned. On the other hand, this is very effectively per-

formed, as also in the Polyphyidæ, by a great number of nectocalyces, or in the only Physophorid in which the latter are wanting, namely *Athorybia*, by medusa-like natatory movements of bracts.

Are we to regard it as surprising that here, where provision is made for the distribution of the species by means of numerous energetically acting nectocalyces, the sexual animals themselves remain immovably attached to the stem? That in the case of the Monophyidæ and Diphyidæ, with their comparatively insignificant locomotion by means of one or two nectocalyces, the acquisition of mobility by the sexual animals furnishes an efficacious instrument for the distribution of the species can be seen at once. In the Polyphyidæ the male and female individuals still exhibit a medusiform development, but the umbrella appears reduced; while in the Physophoridæ, which are still furnished with numerous nectocalyces, it represents merely a mantle-like envelope of the single ovum.

If, then, our notion is correct, that the separation of the sexual individuals occurs as a compensation for an insufficient power of locomotion and the resulting imperfect distribution of the species, we have, in conclusion, still to inquire how the other Siphonophora, which usually quite give up any active locomotion, effect their diffusion. The Rhizophysidæ and *Physaliæ* have been frequently united with the Physophoridæ. Nevertheless they differ so much from the latter that I prefer placing them as a distinct order, "Pneumatophoridæ," side by side with the Calycophoridæ and Physophoridæ. Their air-sac especially acquires an imposing magnitude, and communicates with the exterior by an opening. Locomotive organs in the form of nectocalyces, or movable bracts, are wanting; and the characteristic "hepatic bands" of the polyps are broken up into numerous isolated villi. While *Rhizophysa* is enabled to ascend and descend by compression of the air-sac, the adult *Physalia*, with its enormous bladder occupying nearly the whole stem, is driven about at the surface of the sea as the sport of the winds and waves.

As to their sexual relations, there still prevails a certain obscurity; and although I may be unable to dispel this completely, I believe I have advanced a step nearer to its solution. Huxley, as is well known, put forward the supposition that in *Physalia* the medusiform buds, seated beside the numerous male medusoid gemmæ, might become developed into female sexual animals and separate from the colony. I doubted long as to the correctness of this hypothesis of Huxley's; but, after the examination of perfectly mature sexual

clusters, for which I am indebted to my friend Von Petersen, I must now thoroughly agree with him. These sexual clusters are from a large *Physalia* which appeared in the Bay of Naples after the spring storms of 1879. At the first glance we detect in them a considerable number of medusæ, which attract attention by their size. By means of long peduncles traversed by a canal they are attached among the gemmæ filled with nearly mature spermatozoa and the sexual tentacles characteristic of *Physalia*. On closer examination a considerable aperture, fringed with a velum, may be easily recognized in the gelatinous umbrella, into the cavity of which it leads. The cavity is lined with ectodermal cells, which in young examples are arranged in projecting pads, in older ones are evenly diffused, and at their base differentiate numerous smooth muscular fibres running circularly. The vascular lamella surrounds the epithelial musculature of the subumbrella, and shows in transverse section the lumina of four vessels, which open within the velum into an annular canal. An ectodermal fibrous cord, which runs at the base of the velum, I am inclined to interpret as a nervous ring. On the other hand, we cannot perceive either tentacular pads, marginal bodies, or sexual organs. A stomachal peduncle, in the wall of which the sexual organs will probably originate, is indicated by a small elevation at the bottom of the cavity of the umbrella.

Now, if we take into consideration the considerable size of these medusæ (they measure 2 millim. in breadth, and 5 to 6 millim. in length with the peduncle), and their organization, which is indicative of a free independent life, there can hardly be any doubt that, after the development of a mouth-aperture and of the tentacular pads, they separate and grow up into female anthomedusæ. Thus, again, in the *Physaliæ*, which are destined to a passive mode of locomotion, the distribution of the species is secured by the acquisition of mobility by the female sexual animals. That the medusæ are really separated appears from the following observation:— In examining the sexual clusters we find now and then gelatinous stalks 3 millim. long, traversed by a vessel. They perfectly resemble the basal pedunculiform section of the medusa-buds, and are easily distinguished from the sexual tentacles. As a matter of fact, a careful examination shows that the medusæ do not separate in their whole length, but that their inferior pedunculiform half remains adherent to the genital cluster. If we consider that the *Physaliæ* always live together in crowds, and that from the enormous production of spermatozoa the contact of these with the ova produced by the

medusæ is rendered easy, it need not surprise us if only the female individuals lead a free existence.

But what I have here communicated with regard to the sexual relations of *Physaliæ*, may with the greatest probability also be applied to those of *Rhizophysa filiformis*. Hitherto certain small clusters of mulberry-like aspect, originating isolatedly upon the stem, were described as the sexual organs of the latter, although no sexual products had been detected in them. I was therefore greatly interested when I was able, in a specimen of *Rhizophysa* which made its appearance in October, to demonstrate that these mulberry-like appendages become developed into sexual clusters, which might almost be confounded with those of a young *Physalia*. Each of the knob-like pads in the cluster begins to draw out into an elongate oval form, appears diminished like a peduncle at its base, and shows in about its middle the rudiment of a medusa-bud. As is shown by still older sexual clusters, there are produced at the periphery of the bud, which still more distinctly shows the form of a medusa, about six or eight excrescences formed of ectoderm and endoderm, while the distal extremity of the whole lateral branch is produced into a sexual tentacle. The oldest genital clusters (those seated at the lower end of the stem) consequently consist of a peduncle abundantly furnished with muscular fibres and very contractile, the cavity of which communicates with that of the stem, and on the other side extends into about twelve lateral branches. Each of these lateral branches, with its appendages, so completely resembles the corresponding parts of *Physalia*, that I do not hesitate to regard the medusa-bud as the producer of the ovum, and the knob-like buds as young seminal capsules. The observation of still further advanced genital organs will show whether, as seems to me very probable, the female individuals also become free in the form of medusæ in *Rhyzophysa*.

At any rate, I believe I have proved that *Rhizophysa* and *Physalia* show a close relationship, which justifies us in raising them into the order Pneumatophoridæ. But what appears to be of special interest in connexion with the question of the origin of alternation of generations among the Siphonophora, is the circumstance that with the cessation of active locomotion (for the ascent and descent of the *Rhizophysa* can hardly come under consideration for the distribution of the species in a horizontal direction) the necessity again occurs of rendering at least the female sexual organs motile in the form of anthomedusæ. If, finally, we glance at the highest Siphonophora, namely the Velellidæ, they appear so perfectly adapted to a

passive locomotion at the surface of the sea, that they cannot compress their chambered air-sac. It is conceivable that, the exertion of any active locomotion being impossible, both male and female sexual animals are set free in the form of small medusæ, namely *Chrysomitræ*.

To summarize briefly, in conclusion, our judgment as to the cyclical process of development of the Siphonophora, I do not hesitate to assert that it shows a close relation to the locomotion. Where numerous energetically acting nectocalyces occur, as among the Polyphyidæ (*Hippopodius*) and Physophoridæ, the sexual animals remain sessile and often degenerate into medusoid gemmæ. Where only one (Monophyidæ) or two nectocalyces (Diphyidæ) produce a comparatively feeble locomotion, the diffusion of the species is provided for by the remarkable process of *Eudoxia*-formation. Nay, it may happen, as I have shown in the case of *Monophyes primordialis*, that the first nectocalyx is replaced by a second heteromorphous one, which is better fitted to carry along the long trailing stem with the *Eudoxia*-clusters. From the primitive organization of this *Monophyes* the life-history of the species therefore appears to be spread over three generations, proceeding one from the other. Lastly, if, as in the most highly organized Siphonophora the Pneumatophoridæ and Discoideæ, the locomotive organs are wanting and locomotion takes place only passively, the diffusion of the species is rendered possible by the sexual animals being rendered motile. There is an alternation of generations that intervenes, as an element of polymorphism, in the course of development of the Siphonophora, and indeed of their highest representatives, in this fashion, that on a polymorphic nurse generation anthomedusæ are produced by gemmation, either females alone (Pneumatophoridæ), or males and females (Discoideæ), which only attain sexual maturity after their separation.

EXPLANATION OF PLATE V.

General Indications:—*g.ch.*, genital nectocalyx; *v*, velum; *s*, fluid-receptacle; *m*, stomachal sac; *f*, tentacle; *st*, stem; *d*, bract; *ek*, ectoderm; *en*, endoderm.

Cyclical development of Monophyes primordialis.

Fig. 1. First generation: *Monophyes primordialis*, Chun, × 45. *x*, bud of the *Muggiæa*-calyx; *fl*, wing-like gelatinous ridges.

Fig. 2. Second generation: *Muggiæa Kochii*, Will & Busch, × 45. K, edges of the calyx. On the last group of individuals the rudiment of the reserve genital calyx is already visible (*x*).

Fig. 3. Third generation: *Eudoxia Eschscholtzii*, Busch, ♀, × 45. The large genital nectocalyx (*g.ch.* 1) had evacuated the ova from

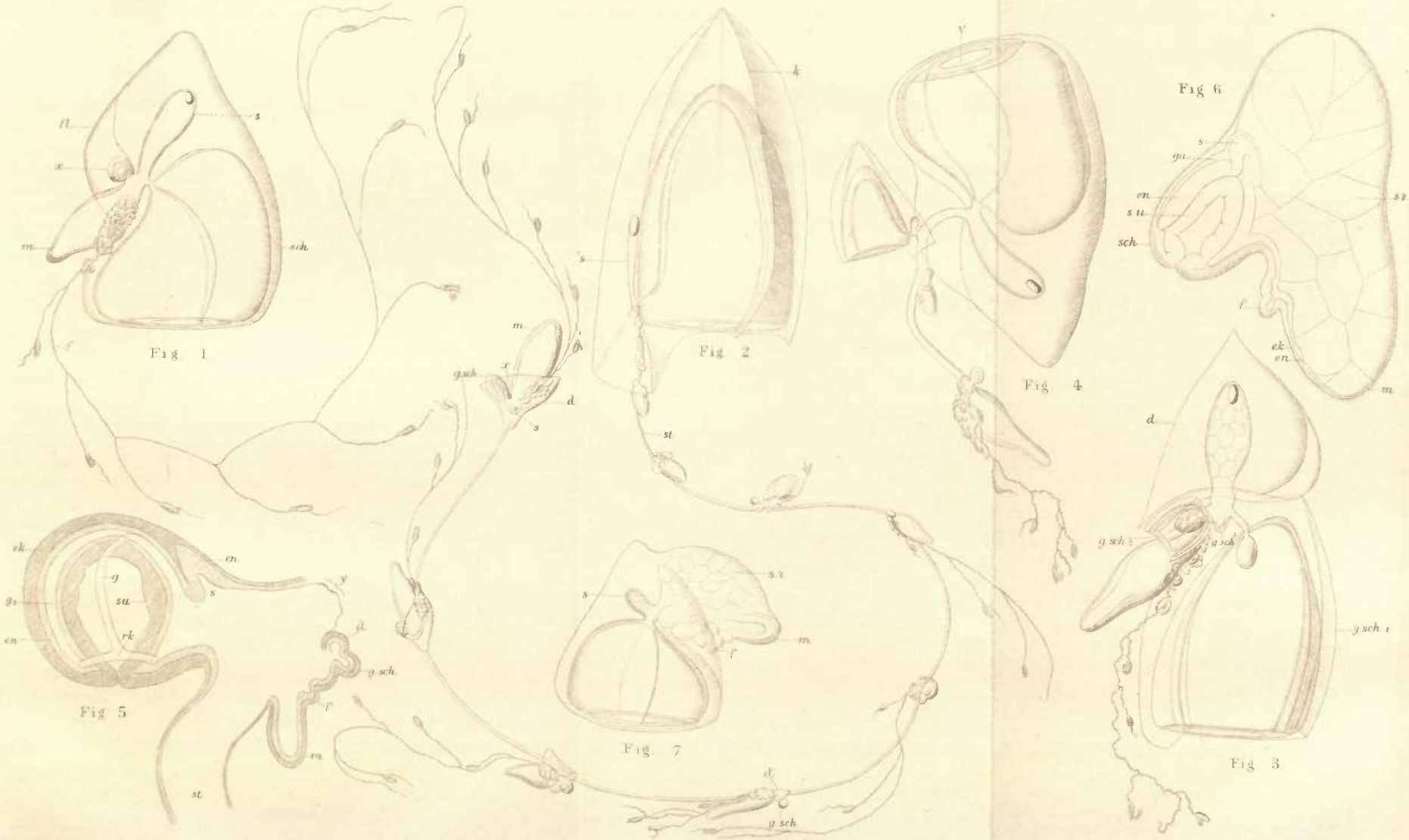
Fig 1
Fig 2
Fig 4
Fig 6
Fig 5
Fig 7
Fig 3
Mintern Bros. lith.

the genital manubrium on the previous day. The second genital nectocalyx (*g.sch. 2*) has become developed within eighteen hours from a simple bud into a nectocalyx already containing the egg-germs; and near it appears the bud-rudiment of the third genital nectocalyx (*g.sch. 3*).

Fig. 4. *Monophyes primordialis* in connexion with the *Muggiæa*-calyx, × 45.

Fig. 5. The young *Muggiæa*-bud, with the first foundation of a cluster of individuals and the uppermost part of the stem, × 210. *g*, lateral vessel; g_2, median vessel; *s.u*, subumbrella; *r.k*, annular canal; *y*, ruptured place of attachment to *Monophyes primordialis*.

Fig. 6. Embryo bud from ova of *Eudoxia Eschscholtzii* on the second day, with the rudiments of the nectocalyx, of the nettling-thread, and of the stomachal sac, × 135. *ga*, jelly; *s.u*, subumbrella; *s.z*, endodermic fluid-cell; *en*, definitive endoderm.

Fig. 7. Larva of the third day, which has already attained the form of *Monophyes primordialis*, × 67. *s.z*, adherent group of fluid-cells.

XXI.—*On Rhynchota from Mergui.*

By W. L. Distant.

The small collection of Rhynchota to which this short paper refers was recently made by Dr. Anderson in Mergui, and was placed in my hands for identification by Mr. Wood-Mason. Of course it is quite insufficient to give any estimate of the affinities which this most interesting fauna will ultimately exhibit when adequately worked, but is interesting as affording the first knowledge of the Rhynchota of this little-worked and entomologically little-known zoological district.

Hemiptera-Heteroptera.

Fam. Pentatomidæ.

Catacanthus incarnatus, Drury.

Cimex incarnatus, Drury, Ill. ii. p. 67, pl. xxxvi. f. 5 (1773).

Fam. Coreidæ.

Anoplocnemis grossipes, Fabr.

Lygæus grossipes, Fabr. Syst. Rhyng. p. 205. n. 11 (1803).