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The Morphology and Relations of the Siphonophora.

By

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'Anyone who has studied the history of science knows that almost every great step therein has been made by the 'anticipation of Nature', that is, by the invention of hypotheses, which, though verifiable, often had very little foundation to start with; and, not infrequently, in spite of a long career of usefulness, turned out to be wholly erroneous in the long run.'

T. H. HUXLEY: 'The Progress of Science' (1887).

With 57 Text-figures.

| CONTENTS. | PAGE |
|---|------|
| INTRODUCTORY | 103 |
| SUMMARY OF CHAPTERS | 105 |
| GLOSSARY OF TERMS | 107 |
| 1. DEVELOPMENT OF THE PNEUMATOPHORE | 109 |
| 2. CALYCOPHORE AND PHYSOPHORE | 117 |
| 3. DISCONANTH AND SIPHONANTH | 118 |
| 4. THE HYDROID RELATIONS OF DISCONANTHAE | 123 |
| 5. CONARIA AND THE CORYMORPHINES | 127 |
| 6. THE SIPHONANTH PROBLEM | 133 |
| 7. GASTRULATION AND THE BUDDING LINE | 135 |
| 8. THE NATURE AND ORIGIN OF BRACTS (HYDROPHYLLIA) | 139 |
| 9. NECTOSOME AND SIPHOSOME | 146 |
| 10. CORMIDIAL BUDDING IN MACROSTELIA | 150 |
| 11. GROWTH AND SYMMETRY IN BRACHYSTELIA | 155 |
| 12. GENERAL CONCLUSIONS | 175 |
| 13. SYSTEMATIC | 189 |
| PROPOSED CLASSIFICATION OF SIPHONOPHORA | 190 |
| LITERATURE CONSULTED | 191 |

INTRODUCTORY.

WISHING recently to put together the evidence concerning the origin of the Pelagic Fauna, I found, when I came to the Siphonophora, that their morphology was so dominated by

dubious theories under the aegis of great names that a review of the literature would be necessary to disentangle fact from fiction. The present paper is an outcome of that review, and contains some remarkable examples of the persistence of doctrines long after their foundations had disappeared.

Following their classical investigations of Siphonophore development, Haeckel (1869) and Metschnikoff (1874) both came to regard Siphonophores as transformed Medusae, the great larval bract of *Physophora* being interpreted as a split and reduced umbrella and the polyp as its manubrium—a view which even the judicious Balfour (1885) approved. To this Metschnikoff, protagonist of the ‘poly-organ’ theory, added the idea that the float itself was a second umbrella, but retroverted, like the domestic article turned inside out, as a gas-holder. Both were impressed by the budding powers of the manubrium in various species of *Sarsia*, and Haeckel built upon them his elaborate ‘medusome’ theory, according to which all the zooids of a Siphonanth colony were interpreted as dislocated parts of so many dismembered medusoid buds of a proliferating Anthomedusan. But he treated the Disconanths differently. A *Velella* or a *Porpita* was not a colony of medusomes, but a single Trachomedusan, of which the manubrium alone has been multiplied on the subumbrial surface. To these medusa-based speculations of the ‘heroic age’ have since been added the ‘Bipolaria’ hypothesis of Woltereck (1905) and the ‘Heteromedusa’ theory of Moser (1925). All imply a pelagic ancestry of the group, and the last is as recent as the latest textbook.

On the other hand adherents to the earlier view of Leuckart and Vogt (1848–54), that Siphonophores are simply Hydro-medusan colonies adapted by further polymorphism to a pelagic life, have not been wanting (e.g. Claus, Chun, Schneider), though their advocacy has scarcely advanced their cause. Rejecting Metschnikoff’s interpretation of the float as an inverted umbrella, Leuckart himself claimed (1875) that the initial invagination which gives rise to it may be identified with the entocodon or *Glockenkern* of a medusa bud; Claus (1878) followed this up by homologizing the pericystic spaces between the radial septa of *Physonects* with the radial canals of a medusa; and Chun

(1897 *a*) completed the argument by identifying this medusa with the primary nectocalyx of the Calycophore cycle. This view of the pneumatophore as a modified nectocalyx is the view now generally held, except for a minor qualification by Woltereck and Moser, that it should be homologized with the second or 'dorsal' bell of Calycophora, and not with the first or larval bell, which is caducous. It will be noted that this theory, while preserving the homology of the larva with a Hydromedusan Planula, sets up the Calycophore as the primitive type of Siphonophore, and thus indirectly leads to much the same result as the previous 'medusoid' theories, viz. the derivation of Siphonophora from an actively swimming original stock, one, however, which, in its organization as a whole, appears to be most remote from the Hydromedusan type.

It will be convenient to deal with this special proposition at the outset, for it lies at the base of Siphonophore morphology, and its widespread acceptance makes it the more serious. In the last half-century Haeckel has been its only outstanding opponent, for, although holding the Siphonophore larva to be a transformed medusa, he refused to see anything more in the float than an invaginated aboral gland. In this, as we shall see, he was probably right.

SUMMARY OF CHAPTERS.

1. DEVELOPMENT OF THE PNEUMATOPHORE.—The float is developed from a simple apical invagination without an entocodon and shows no traces of origin from a medusa or nectocalyx. Its 'radial septa', when present, result from a secondary protrusion of giant cells from the gas gland as 'hypocystic villi', which may, or may not, fuse with the outer endoderm of the pericytic coelenteron. (P. 109.)

2. CALYCOPHORE AND PHYSOPHORE.—In Calycophora the aboral extremity of the larva atrophies, so that the pneumatophore has no homologue in this group, medusoid or otherwise. The primary nectocalyx is a ventral bud which secondarily assumes a subapical position. There is no 'aboral manubrium'. (P. 117.)

3. DISCONANTH AND SIPHONANTH.—Haeckel's distinction is valid, and independent of his phylogenetic theories. The former type is radially symmetrical, with an aboral whorl of simple tentacles, and developed from an Actinula larva (*Conaria*): the latter, bilaterally symmetrical, with a separate basal tentacle to each polyp, and developed from a solid Planula larva by unilateral (ventral) budding. (P. 118.)

4. THE HYDROID RELATIONS OF DISCONANTHÆ.—These show close relationship with Tubularians, especially *Corymorphpha*, in the dominance of a large axial polyp with plexiform aboral coelenteron, aboral wreath of tentacles, free Anthomedusan gonophores, and an Actinula larva. (P. 123.)

5. CONARIA AND THE CORYMORPHINES.—Woltereck's larva of *Velella* (*Conaria*) has a complete gastric diaphragm, homologous with that of Corymorphine Hydroids, but modified as a larval organ of flotation secreting oil-drops. Its aboral chamber gives origin to the primary radial canals and plexus around the float, as that of Corymorphines does to the branching canals of the stalk. (P. 127.)

6. THE SIPHONANTH PROBLEM.—The differences from Disconanths are reviewed. Although the actual larvae of Siphonanths are Planulae, they develop from large yolk eggs, usually one in each gonophore like Actinulae, and begin to bud with extraordinary precocity, so that original Actinuloid characters may have been suppressed or retarded. (P. 133.)

7. GASTRULATION AND THE BUDDING LINE.—The precocity of Siphonanth budding associates it with the meridian of first gastrulation, which proceeds slowly up each side from venter to dorsum. This initial budding line is made permanent by development of a thick muscular layer everywhere else, which is prohibitive of radial budding. (P. 135.)

8. THE NATURE AND ORIGIN OF BRACTS.—These early appendages are regarded as larval tentacles primarily adapted for locomotion—a view supported by particular life-histories and by reference to *Pelago hydra* and the multi-tentaculate Actinula of *Myriothela*. (P. 139.)

9. NECTOSOME AND SIPHOSOME.—The distinction of these regions, with a budding zone between them, corresponds with that of hydrocaulus and hydranths in a Hydroid (cf. *Pelago hydra*). The cormidia correspond to the trimorphic branches of *Dicoryne*, with terminal polyp, blastostyle, and gonophores. The chief difference between them is in their arrangement: perpetual forking in Hydroids, a linear succession in Macrostelia, and the formation of homogeneous whorls in Brachystelia. (P. 146.)

10. CORMIDIAL BUDDING IN MACROSTELIA.—The buds of each polymorphic cormidium arise as a group (in Calycophora from a single pro-bud), and are carried backwards as fast as they are produced by a pronounced longitudinal growth of the oozooid in the zone of proliferation. This 'metameric' attenuation is no primitive feature, but a simple adaptation for better fishing: it extends the slender fishing tentacles (one to each cormidium) through a greater range of water. (P. 150.)

11. GROWTH AND SYMMETRY IN BRACHYSTELIA.—The oozooid remains short, and in contrast with the Macrostelia, exhibits, especially in the siphosome, an excess of horizontal over longitudinal growth. This carries the buds of each cormidium from the ventral line successively towards the dorsum, with the resultant formation of homogeneous parallel or concentric whorls. This growth may proceed (i) with complete bilateral symmetry, as

in *Anthophysa* and in the nectosome of Rhodaliidae, or (ii) asymmetrically from one side only, as in the siphosome of *Physophora*, a condition which leads to (iii) the continuous cormidial spires of *Discolabe* and the Rhodaliids. Though imperfectly known, there is reason to expect that *Epibulia* may be found to be perfectly biradial, like the Corymorphine Branchiocerianthus. The bracts of *Nectalia* are not cormidial but coronal, and relate this genus to *Anthophysa* rather than to the Agalmids. (P. 155.)

12. GENERAL CONCLUSIONS.—The gap between Disconanths and Siphonanths is materially reduced, but not bridged, by these results. On present knowledge it would appear that Disconanths are especially related to Tubularians, and Siphonanths to Corynoids; but the structure of *Pelago hydra* and *Myriothela* suggest the possibility of a common origin from some intermediate type of Gymnoblast which gave rise to both stocks. A settlement of this issue can hardly be expected without additional knowledge on various points, especially the development of *Myriothela* and *Corymorpha*. (P. 175.)

13. SYSTEMATIC.—The results of the present study are expressed in a revised classification based on Eschscholtz's tripartite division into Chondrophorae, Physophorae, and Calycophorae, and in that order, which reverses Chun's system; but it is combined with a retention of Haeckel's major groups to mark the gap between Chondrophorae and the remainder. Pending the establishment of definite lineages, Haeckel's terms Brachystelia and Macrostelia are also used in each sub-order of Physophorida as descriptive terms, the long-bodied forms having plainly arisen at least twice independently from the more archaic Brachystelia. The term 'Amphinecta' is proposed as a substitute for Haeckel's 'Physonectae'. (P. 189.)

GLOSSARY OF TERMS.

(For systematic names see Revised System, § 13, p. 189.)

ACTINULA.—Hydrozoan larva with precocious coelenteron, mouth and tentacles.

BASIGASTER.—Basal region of a Siphonanth polyp, packed with young cnidoblasts, and giving off the tentacle.

BLASTOSTYLE.—See GONOPHORE. Often wrongly used in Chondrophora.

BLASTOZOOID.—A zooid budded from the primary individual or oozoid.

BRACHYSTELIA.—Descriptive term for short-stemmed Physophores.

BRACT or **Hydrophyllum.**—An appendage of Siphonanths with a narrow blind, axial canal and much mesogloea, variously modified.

CENTRADENIA.—The 'central gland' or organ of Chondrophora, derived from the ectoderm, lodged in the mesogastric septum, packed with young cnidoblasts and eventually traversed by endodermal canals.

CORMIDIUM.—A polymorphic cluster of blastozoids in Siphonantha, including a gonodendron or gonophore and a siphon, with or without one or more bracts and palpons.

CORONA.—A ring of uniform appendages or zooids around the nectosome.

DIAPHRAGM.—The iris-like annular septum which divides the gastric cavity of Corymorphine polyps.

ENDOCHORD.—Name here given to the solid endodermal axis, surrounded by a longitudinal plexus of canals, in the Tubularian stalk.

ENTOCODON or **Glockenkern.**—The terminal proliferation of ectoderm in a medusoid bud which eventually hollows out to form the bell-cavity.

EUDOXIA.—The free-swimming cormidium of certain Calycophores, which consists of a bract with phyllocyst, a gonophore, and a tentaculate polyp, with or without a special nectocalyx.

GONOPHORES.—The production of these in Hydrozoan colonies is associated with various stages of gastro-genital differentiation, and differences of nomenclature are linked with each stage. Those which most concern us are the following:

- (a) Oozooid (?) and all blastozoids fully polypoid, and fertile in the sense that each gives rise directly to sexual medusoid gonophores. Most arborescent Gymnoblasts.
- (b) Oozooid itself sterile, but giving rise by budding to complete and fertile **SECONDARY POLYPS**, which directly produce medusoid gonophores. Chondrophora.
- (c) Oozooid sterile; blastozoids differentiated into sterile Gastrozoids (fully formed Polyps) and fertile mouthless Gonozoids (**BLASTOSTYLES**) which alone produce gonophores. *Dicoryne*. *Myriothela*. *Pelago hydرا*?
- (d) As (c), but the sterile Gastrozoids are further differentiated into 'Siphons' with mouth and 'Palpons' mouthless; and the Gonozoids (**GONOPALPONS**), by branching, give rise to dense clusters of gonophores, together known as **GONODENDRA**. These again may be divided into male branches, forming Androphores, and female branches, producing Gynophores. *Physophorida*.

In Calycophorida gonophores are produced in limited numbers and separate blastostyles (gonopalpons) have apparently disappeared.

HYPOCYSTIC.—i.e. below the pneumatocyst.

MACROSTELIA.—Descriptive term for long-stemmed Physophores.

NECTOCALYX or **Nectophore.**—An asexual medusoid gonophore specialized for locomotion of the colony.

NECTOSOME.—Aboral region of oozooid bearing the float and/or the locomotive bracts or nectocalyces. Opposed to Siphosome.

Oozooid.—The primary individual or zoid produced from an egg, and itself producing additional zooids (blastozoids) by budding.

PALPON.—A Siphonanth polyp arrested in development at the mouthless stage and specialized. Its tentacle ('palpae') may persist (e.g. *Physophora*) or be suppressed (*Epibulia*). One form (gono-palpon) is the Siphonanth blastostyle.

PERICYSTIC.—i.e. around the pneumatocyst.

PHYLLOCYST.—The dilated axial canal of a cormidial bract, usually laden with oil-drops and serving as a float (Calycophora).

PLANULA.—The early larva of primitive Hydroids and of Siphonanths, lacking mouth and appendages, and solidly filled with yolk-endoderm.

PNEUMATOCYST.—The chitinous ‘float’ of Siphonophora, secreted by an invaginated sac of the apical body-wall.

PNEUMATOPHORE.—The whole aboral extremity moulded around the enclosed float. It consists of three parts: the outer body-wall (pneumatocodon), the invaginated body-wall (pneumatosaccus), and the pericytic coelenteron between them.

PROTOSIPHON.—The gastric region (hydranth) of the primary polyp or oozoid.

SIPHON.—The gastric region (hydranth) of a polyp reproduced in blastogenesis; hence almost synonymous with polyp.

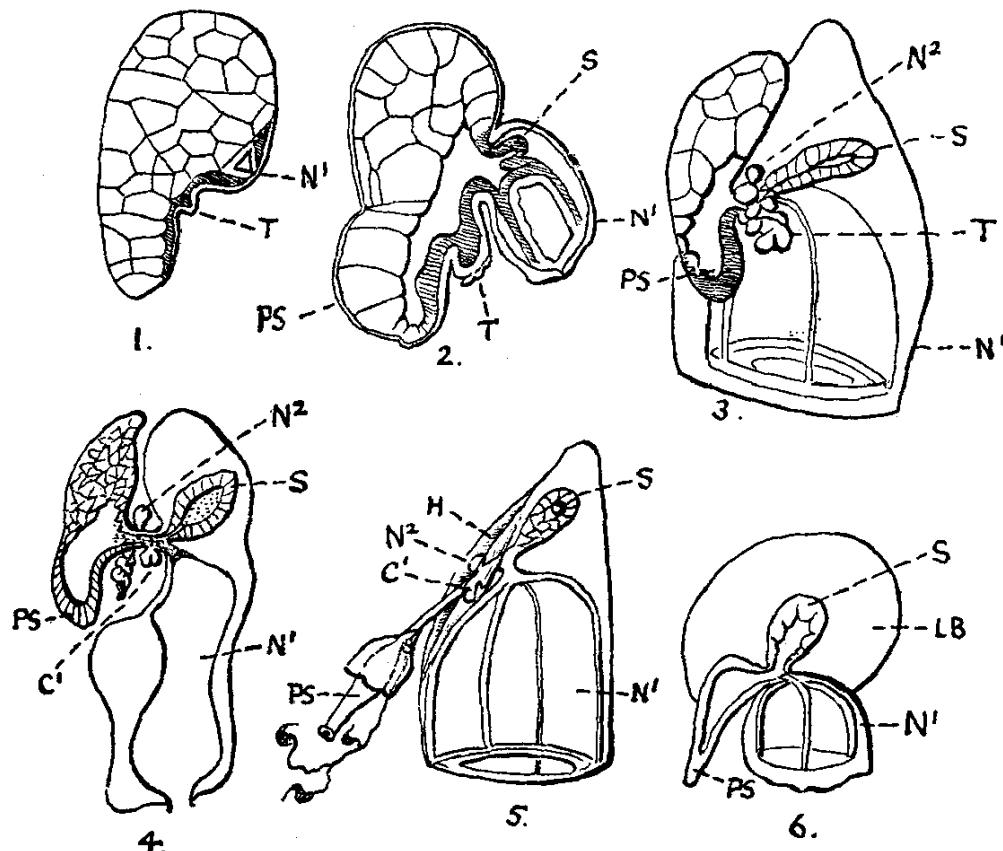
SIPHOSOME.—The gastro-genital hind-body, composed of the hydranth of the oozoid (primary polyp) together with its budding zone and the blastozooids produced from it, which constitute the cormidia. Opposed to Nectosome.

SOMATOCYST.—The endodermal outgrowth with surrounding mesogloea at the base of a developing nectocalyx in Calycophora. It becomes usually filled with sappy cells secreting oil-drops, and corresponds to the phyllocyst of a cormidial bract. Its inclusion in the nectocalyx implies the incorporation of a bract, Schneider’s ‘bract-bell’.

STEM.—The axial foundation of a Siphonophore colony, i.e. the mid-body of the oozoid from which the buds arise. By intermittent elongation it produces the metamerized colonies of Macrostelia; by intermittent growth in width it carries the cormidial buds dorsally, thus producing the homogeneous whorls of Brachystelia.

1. DEVELOPMENT OF THE PNEUMATOPHORE (with Text-figs. 1-11).

Omitting earlier history, of which excellent summaries have been given by Schneider (1896) and Chun (1897 *a*), I take Chun’s illuminating article ‘Ueber den Bau und die morph. Auffassung der Siphonophoren’ (1897 *a*) as giving mature expression to the case for regarding the pneumatophore as the homologue of a nectocalyx. It rests on three propositions: (*a*) that its position is comparable with that of the primary nectocalyx of the Calycophore, (*b*) that the ‘thickened ectodermal invagination’ from which it arises represents the Glockenkern of a nectocalyx, and (*c*) that it is surrounded (with certain



TEXT-FIGS. 1-6.

Development of Calycocephorida, showing atrophy of aboral region of oozooid and composite nature of primary nectocalyx. *C*, cor midium; *H*, hydroecium; *LB*, larval bract; *N*, nectocalyx; *PS*, protosiphon; *S*, somatocyst (= endoderm of larval bract); *T*, tentacle.

Figs. 1, 2, 3.—*Galeolaria quadrivalvis* (Metschnikoff, 1874). Figs. 4, 5.—The same, after Lochmann, 1914. Fig. 4 in sagittal section.

Fig. 6.—Metschnikoff's larva of 'Praya inermis?' (probably *Sphaeronectes truncata*), showing incomplete fusion of larval bract (*LB*) with nectocalyx (*N*). Cf. fig. 12.

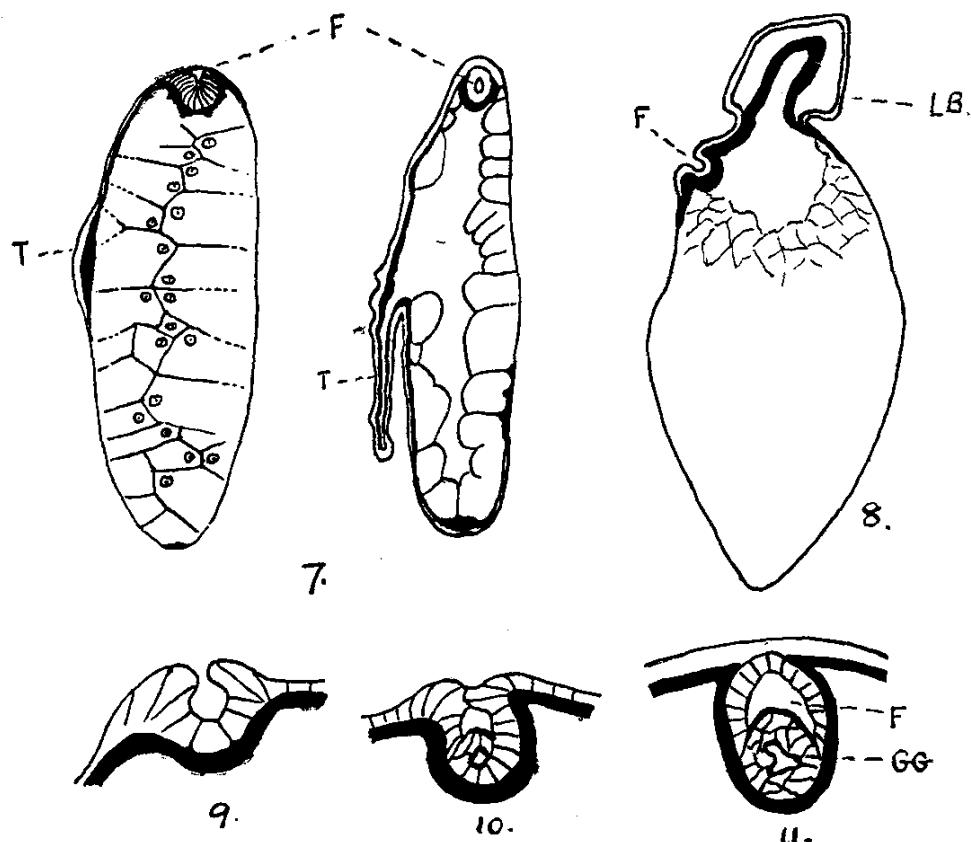
exceptions) by a series of radial cavities of the coelenteron which are homologous with the radial canals of the nectocalyx.

(a) The first of these propositions is largely a matter of judgment, for in some of the more yolk Agalmid larvae, which retain the spherical form of the embryo, exact determination of the apical pole is wellnigh impossible; but if the comparison is limited to the more elongated types of larvae (e.g. *Stephanomia picta*, *Physophora*, *Galeolaria*, *Muggiaeae*) (Text-figs. 1-11), then there can be no doubt that, while in Physophores the rudiment of the pneumatophore is truly apical, that of the primary nectocalyx of Calycophores is definitely ventral. This discrepancy of position is confirmed on the one hand by the strictly median and aboral position of the pneumatophore invagination in the larva of *Velella* (Text-figs. 15-24), and on the other by the fact that in larval Calycophores the aboral region of the larval body remains stuffed with yolk during the critical stages of development, and is finally absorbed without having contributed anything to the formation of the nectocalyx.

The atrophy of the aboral half of the larval body in Calycophores was described seventy years ago with full illustrations by Metschnikoff (1874, Pls. vi, vii), after rearing the eggs of *Galeolaria quadrivalvis* (his 'Epibulia aurantiaca'), and isolated stages of other species have been described which show it to be a general feature. The sequence was confirmed in all respects thirty years ago by Lochmann (1914), who reared the same species to an even later stage. The failure of all the experts to realize its significance is truly astonishing. As only the early stages of Metschnikoff's series have been figured in the textbooks I here give copies of later figures from the two papers mentioned (Text-figs. 3 and 4).

Moser's proposal (1924, 1925) to homologize the pneumatophore with the definitive or so-called 'dorsal' nectocalyx, instead of the larval bell, is equally invalid, for this second bell develops as a bud from the stalk of the first, and is therefore also of ventral origin.

(b) The second proposition was based on Metschnikoff's early accounts already cited (1874), and the relevant figures of



TEXT-FIGS. 7-11.

Physophorida, showing development of float in Agalmids. Endoderm black in 8-11. *F*, float; *GG*, gas-gland; *LB*, larval bract; *T*, tentacle.

Fig. 7.—*Stephanomia picta*, two stages (Chun, 1897).

Fig. 8.—*Halistemma rubrum* (Woltereck, 1905).

Figs. 9, 10, 11.—Successive stages in *Agalma elegans* (Woltereck, 1905).

Galeolaria (his ‘*Epibulia*’) and *Stephanomia* (*Halistemma*) are in the textbooks. But these were impressions from surface views or optical sections, and in 1897 Chun figured the earliest stage of the pneumatophore in the same *Physophore* (‘*Halistemma pictum*’) as a shallow open invagination which subsequently closed (1897, fig. 15: my Text-figs. 7–11), and in 1905 Woltereck, from sections demonstrated to the German Zoological Society, figured the rudiments of the float as open invaginations, both in the *Actinula* larva (‘*Conaria*’) of *Velella* (1904) and in the *Planulae* of *Agalma elegans* and *Halistemma rubrum* (1905 b). There is, therefore, nothing in the early rudiment of the float to point specifically to a medusoid origin, even though Chun and Woltereck still clung to that idea. All sorts of organs have developed from ectodermal pits, and the demonstration in this case of the absence of any entocodon-like proliferation removes the only feature that might be regarded as demonstrative.

In her ‘Gauss’ Report, as well as in her article in Kükenthal’s great ‘Handbuch’, Dr. Fanny Moser states that a ‘Glockenkern’ is absent in the development of most Calycophore bells, whether gonophores or nectocalyces, while all bells of *Physophores* (including the pneumatophore!) pass through a *Glockenkern* stage. I have been unable to find upon what evidence she based her statement about Calycophora which, if correct, would be of much interest in connexion with the problem of ovogenesis in that group; but in any case the absence of an entocodon would not affect my point that a simple open invagination of ectoderm is no proof of a medusoid origin. It is also far from supporting the extraordinary view she maintains that the absence of a *Glockenkern* in Calycophores is a more primitive feature than its presence in *Physophores*!

(c) A similar lack of cogency applies to the arguments based on the so-called ‘radial pouches’ of the pericycistic region of the coelenteron (Claus, 1878; Chun, 1887, 1897 a). These spaces vary greatly in number according to size and age, and are very rarely limited to the number (4) of the radial canals. They do not diverge from a common stalk-canal, as do the radial canals of a medusa bud (for there is no ‘stalk’ to contain one!), but

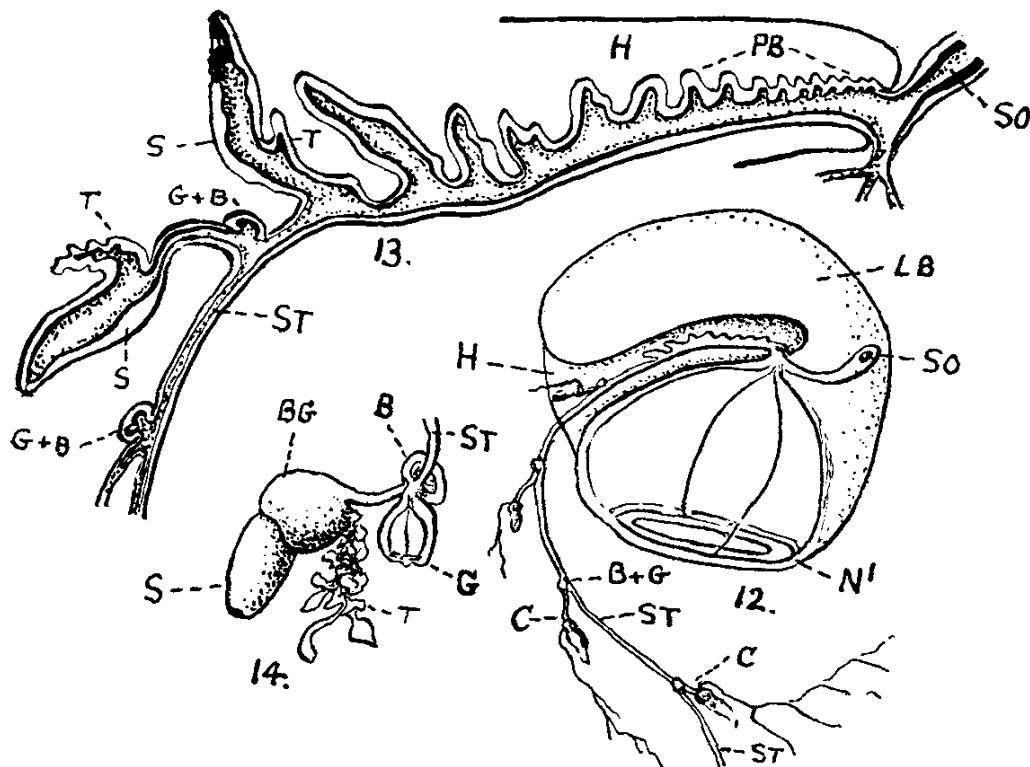
proceed directly and independently from the axial gastral cavity. They are in fact not 'pouches' from this cavity, put parts of it. Referring to Chun's figure of the relations in *Physophora* (1897 *a*, fig. 16), it will be seen that it is not the 'pouches' that need consideration, but the radiating septa which divide and create them. Far more appropriate than the comparison with Medusan canals was that with Actinian mesenteries which was drawn by their discoverer, Milne-Edwards, when describing them 100 years ago: 'The air-vesicle [of *Forskalia*] is . . . retained in a central position by membranous partitions disposed in a radiating manner, and stretched between its parietes and those of the great pyriform cavity (of the upper end of the stem) nearly in the same way as the mesenteries by which the alimentary canal is surrounded in the Alcyonarian polyps' (quoted by Huxley, 1859, p. 6). But the septa of the pneumatophore cannot be regarded as primarily for the support of the air-sac, since they are absent in Cystonectae, where the pneumatophore and air-sac are most voluminous; they do not grow inwards from the outer wall, like those of Actinians, but outwards from the wall of the air-vesicle, and each encloses one of the remarkable rows of ectodermal giant-cells, which project outwards as rootlets from the gas-gland of the air-sac.

In Cystonectae neither pouches nor septa are present, but conspicuous tufts of these giant-cells protrude freely as 'hypocystic villi' from the air-sac into the undivided pericystic space, each clothed with the ciliated endodermal epithelium which they have pushed before them (Chun on *Rhizophysa*, *i.e.*, fig. 17; Huxley, *i.e.*, figs. 14 and 15; Haeckel, 1888, Pl. xxiv). In *Anthophysa* (Text-fig. 45)—usually classified under Phyonectae, but in many ways a connecting link with Cystonects—which Chun described as possessing free upstanding villi (*i.e.*, fig. 20), it has since been shown by Bedot (1904) and Bigelow (1911, Pl. xxi) that, while most of the villi are free, those on the dorsal side extend across the pericystic space, where their endodermal coat fuses with the outer endoderm, thus forming true septa. Finally, in *Physophora* and the Agalmids all the septa are complete, and all contain their axial core of giant-cells. Even in Rhodaliids (Haeckel's 'Auronectae'), in which the

secretory funnel ('aurophore') of the air-sac has undergone its strange displacement, the septa, though irregular, have accompanied the funnel, and conspicuous giant-cells have been recognized in them (Lens and Van Riemsdijk, 1908, in *Archangelopsis*; Bigelow, 1911, in *Dromalia*).

Thus in no Siphonanth is there any real resemblance between the radial pouches and medusoid canals. In the one group (Cystonectae) in which the air-sac retains a functional apical pore (i.e. the bell-mouth of its supposed medusoid predecessor), and should *ex hypothesi* be most medusiform, radial pouches are completely lacking. They are also absent in *Apolemia*, which has been widely claimed as the most primitive Physophore (Chun, 1887). On the other hand there are excellent grounds for holding that the radial septa, when present, have been specially produced within the group by the outgrowth of hypocystic villi from the gas-gland, followed by fusion with the outer endoderm across the pericystic space. Successive stages of this development are exhibited by the sequence Cystonects—Anthophysids—Physonects—the very reverse of the systematic sequence that has been built up on the medusoid hypothesis.

Summing up, I submit that the air-sac of Physophorida is not a transformed nectocalyx, but an independent differentiation of the aboral end of the larval body. It has no counterpart in the Calycophorida in which the aboral region shrivels up without producing anything but yolk. Accurate methods of investigation have shown that the supposed development of the air-sac through an entocodon-stage or *Glockenkern* does not take place. Not a scrap of evidence remains to suggest that the pneumatophore is a medusoid bud: it never starts as a bud, but as a simple involution of the aboral extremity, and the pericystic radial septa which subsequently surround it in one group, are secondary additions to it, entailed by the development of specialized processes from the gas-gland. If Chun and Bigelow are right, as they appear to be, in identifying Haeckel's '*Cystalia*' (l.c., Pl. xxii, 5) with a young stage of *Epibulia* (fig. 6), the hypocystic villi in Cystonects do not project until long after the pneumatophore is well established.



TEXT-FIGS. 12-14.

Calycophorida. Development of cormidia in *Sphaeronectes*.
BG, basigaster; *H*, hydroecium, between larval bract (*LB*) and
nectocalyx (*N*); *PB*, probuds of cormidia; *SO*, somatocyst; *ST*,
stem.

Fig. 12.—Mature colony, stem curtailed. (Chun, 1897 *a*). Cf. Text-
fig. 6.

Fig. 13.—Basal portion of stem, enlarged. (Chun, l.c.)

Fig. 14.—Terminal cormidium, with bract (*B*), gonophore (*G*), siphon
(*S*), and tentacle (*T*). (Schneider, 1896.)

2. CALYCOPHORE AND PHYSOPHORE (with Text-figs. 12-14).

The doctrine of the medusoid nature of the pneumatophore resulted in a general acceptance of the idea that Calycophores were the primitive, and Physophores the derivative stock of Siphonophora, so that the little *Sphaeronectes* (Text-figs. 12-14), as the simplest Calycophore, has been frequently cited as the nearest approach to an archetype of the whole order. Its structure has been summed up as a gelatinous nectocalyx with an exumbral manubrium, which eventually elongates to form the stolo prolifer.

This seemed to confirm a quasi-medusoid theory of the larval forms, since, with the pneumatophore of the one group homologous with, and derived from the primary nectocalyx of the other, a common larval type could be set up, consisting of a medusa at one end, a polyp at the other, and ultimately a stolo prolifer between the two, exactly as in *Sphaeronectes*.

These ideas, doubtless inspired by Woltereck's speculations (1905; cf. p. 129), dominate Dr. Fanny Moser's treatment of the group in the latest of German textbooks, in an article which so far ignores the bounds of fact and fancy as even to define the Siphonophora as 'Proliferating, bilaterally symmetrical Medusae (Heteromedusae) with exumbral (aboral) manubrium'. (Küenthal's 'Handbuch der Zoologie', the character of which its founder had declared 'auf dem realen Boden der Tatsachen stehen soll!')

As a steady, if not very effective, supporter of the Hydro-medusan theory, Chun (l.c., p. 108) recognised the 'difficulty' of the abnormal position of the manubrium. It never occurred to him that the anomaly might be due simply to the mistake of homologizing an aboral pneumatophore with a ventral nectocalyx. If this homology be set aside, and due recognition given to the atrophy of the aboral region of the Calycophore larva, the 'exumbral manubrium' of *Sphaeronectes* and the larval forms disappears at once. The 'manubrium' of both is the original larval body, secondarily shortened in the Calycophore, in which, in spite of the great disparity in size, it is the little larval body or polyp which bears the gigantic nectocalyx as a

ventral bud—not the nectocalyx which produces an exumbrial manubrium (cf. Text-figs. 2 and 3).

It may be as well here to quote from Metschnikoff's original account: 'In the course of the 7th and 8th days the nectocalyx enlarges to such an extent that all other parts of the larval body appear as mere appendages of it.' 'In further development' the shrinking aboral region 'in which the yolk cells remain longest verändert sich in den obersten Theilen des Magens' (1874, p. 43).

It follows that it is the Physophore which most fully retains the primitive condition, and the Calycophore which has undergone the most radical change. It is even possible that the atrophy of the aboral extremity of the Calycophore larval body may imply the previous possession of an aboral float, which has been discarded in favour of a precocious nectocalyx.

In any case the facts now appear to lend support to Korschelt and Heider's view of the general direction of Siphonophore evolution, i.e. from passive flotation to active swimming, rather than the reverse, as was implied in all the medusoid hypotheses we have seen reason to reject. This view is in harmony with the evidence of pneumatophore development, which reveals an evolutional line from Cystonects with a large float and no nectocalyces to Physonects with nectocalyces and a small float, culminating, as we now suggest, in the Calycophore type with nectocalyces and no float at all.

3. DISCONANTH AND SIPHONANTH (with Text-figs. 15–16).

Haeckel's distinction between these main sections of the Siphonophora was so mixed up with phylogenetic speculations that the solid grounds for their separation have been largely overlooked. His definitions, couched in terms of his medusoid hypotheses, involved a Trachymedusan ancestry for the Disconanthae and an Anthomedusan for the Siphonanthae. This diphyletic theory has been generally rejected, with the result that the Disconanths have once more been lumped with the Siphonanths, and their distinctive features unduly minimized or ignored.

These features in brief are, for the Disconanthae, their essentially radial symmetry, with peristomial rings of secondary

polyps acting as blastostyles, their slight degree of polymorphism, lacking nectocalyces, bracts and palpons, their aboral corona of simple tentacles, peripheral canal plexus, and their possession of a highly peculiar central reservoir of nematocysts, penetrated and nourished by an elaborate network of endodermal canals, Haeckel's 'centradenia'.

On the other hand they are linked with the Physophores by their possession of a chitinous float, although this is destitute of a gas-gland and has other peculiarities. Their gonophores have the same Anthomedusan structure, but are ultimately liberated and not permanently sessile or reduced to sporosacs as in most Siphonanths.

Apart from their centradenia, which is unique in Coelenterates, this combination of characters marks the Disconanths as much nearer the Hydromedusan type than the highly polymorphic bilateral Siphonanthae, so that in a natural system they should be placed either at the base of the Siphonophora or as an independent branch. Haeckel not unwisely, but on highly speculative grounds, chose the latter course. Whether they can eventually be regarded as primitive Physophorida depends mainly on the homology of the float and on the position assigned to the Calycophora.

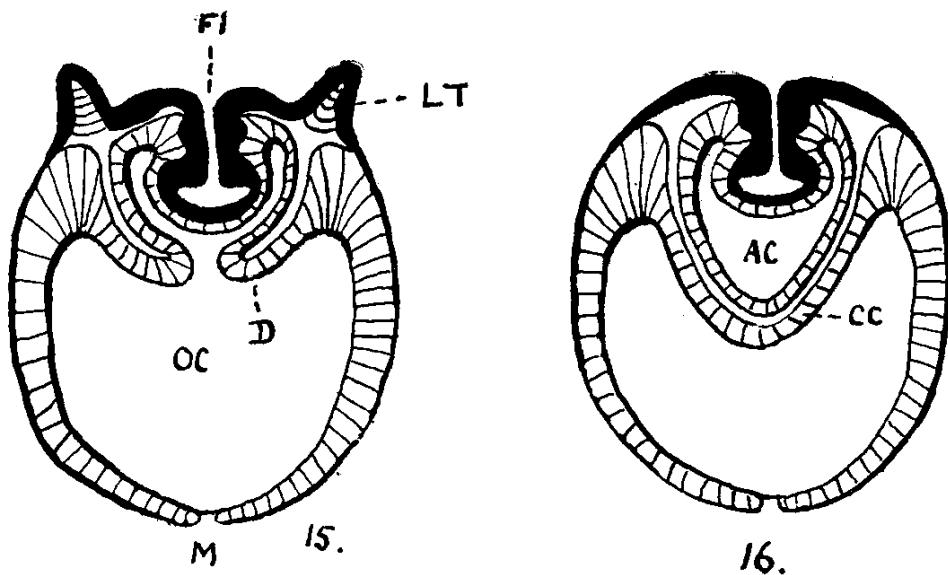
In his opposition to Haeckel's views, Chun (1897 *a*) took the homology of the float for granted, but, using Chamisso's earlier name, placed the Chondrophora (Disconanthae) at the apex of his system as aberrant Physophores, with the Calycophora at its base. This system is still in general use. He justified this procedure by pointing to Bedot's unfortunate account of a supposed early larva of *Velella* with a single tentacle (1885), which he claimed as evidence of a primary bilateral symmetry of the group, and suggested that the float of Chondrophora might possess a gas-gland in larval deep-sea stages still unknown. The uni-tentaculate larva was subsequently recognized as no larva at all, but a detached 'blastostyle' which had swallowed an air-bubble and carried a gonophore bud as its 'tentacle' (Woltereck, 1904, p. 359). He was equally unfortunate in his suggestion of a larval gas-gland.

Young stages of *Velella* have long been known under the

name *Rataria*, and one of these with eight tentacles and rudimentary sail was carefully described by Chun (l.c., fig. 23). But true larvae were first fished by Woltereck (1904, 1905) in 1903 from the deep water off Villefranche, when the surface was swarming with young *Rataria*. They were found to be not Planulae as in *Siphonanths*, but Actinulae already provided with a rudimentary mouth, and in the youngest of all (unfortunately the only specimen) with a pair of short, solid, aboral tentacles, on either side of a narrow, open, involution of the ectoderm, the rudiment of the future float, the orifice of which was temporarily closed by a plug of chitin (Text-figs. 15–16, 21–4). In later stages the thickened lip opens out and develops a projecting circular ridge, which is carried outwards and downwards as the incipient mantle-edge or limbus by eversion and extensive growth of the lip region. Woltereck named this larva *Conaria* from the conspicuous crimson cone of aboral endoderm which projects within the gastric cavity. It is a larval organ of flotation which secretes oil-drops, and disappears by flattening out when the larva reaches the surface. The chitinous plug and fluid contents of the float are then expelled, and the float refills with air. (For further details of the ‘cone’, see below, p. 129.)

The single aboral pair of tentacles closely resemble those of larval *Narcomedusae* and suggest the possibility of temporary fixation by them in early stages; but they are soon cast off or absorbed, after which the *Conaria* goes through a phase without any tentacles (beautifully figured by Woltereck), which seems to coincide with its period of ascent from deep water, and is followed by the *Rataria* stage, when it reaches the surface and its hollow adult tentacles begin to sprout. These develop by successive diagonal quartets and pairs, at first with strict cruciform symmetry (4×2), then with a touch of bilaterality, which Woltereck justly attributed to the influence of the growing obliquity of its float and diagonal sail.

These facts, taken in conjunction with the perfect radial symmetry of young *Porpitas* (i.e. Haeckel’s *Discalia* and *Disconalia*), leave no doubt as to the essentially radiate organization of the entire sub-order Chondrophora, while the difference in larval type increases the gap between them and the



TEXT-FIGS. 15 AND 16.

Disconantha. Conaria larvae of *Velella* (Diagrams after Wolter-
eck, modified). *AC*, aboral chamber; *CC*, crimson cone; *D*, dia-
phragm; *FI*, float invagination; *LT*, larval tentacle; *M*, mouth;
OC, oral chamber.

Fig. 15.—The younger Tentaculate Stage, showing hypothetical origin of the 'crimson cone' as a gastric diaphragm.

Fig. 16.—The later Non-tentaculate Stage, after loss of tentacles and completion of cone.

bilateral Siphonanthae, the larvae of which are invariably solid, mouthless Planulae with unilateral budding.

As regards their float we have to remember that it differs from that of Siphonanths not merely in the absence of a gas-gland, but in its chambered structure and the peculiar tracheal rootlets, the function and significance of which are still matters of dispute (cf. p. 178, below). Chun's suggestion that a gas-gland might be present in early deepwater stages is now vetoed by Woltereck's discovery that *Conaria* reaches the surface not by the generation of gas, but of oil! For the moment, until some other aspects have been considered, I leave the question of its homology in suspense, the more so as we know at least one other group of Coelenterates, the Minyad Actinians, which have developed an aboral air-float independently. The same may well have happened in these two tribes of Siphonophora.

As the very existence of predators depends on the efficiency of their food-catching apparatus, it is worth noting that the great difference between Disconanths and Siphonanths in the form and arrangement of their tentacles appears to be associated with an essential difference in their mode of feeding. That of Siphonanths is well known: the deadly character of a *Physalia*'s trailing 'long lines' has often been experienced, and the same extensibility, stinging power, and retractility prevail with little change throughout the group. But I have come across no account of the feeding process in any Disconanth, even in the common *Velella*, and in this type particularly the tentacles by themselves seem very ill adapted for the capture of struggling prey. On the other hand, unlike the arrangement in Siphonanths, the ring of tentacles is closely associated with the peculiar mantle-edge or limbus above it, the margin of which is densely studded with mucus glands (Text-fig. 24, MG). Moreover there is a clear correlation between the power of the tentacles and the size (breadth) of the limbus, which is broad in *Velella*, where the tentacles are simple and feebly armed, and narrow in *Porpita*, where they are more or less clavate and studded with nettling knobs. Describing what he regarded as 'respiratory' movements in these forms, Chun writes (1897 a): 'If you observe a living *Velella* or *Porpita*, you will see a peculiar movement in

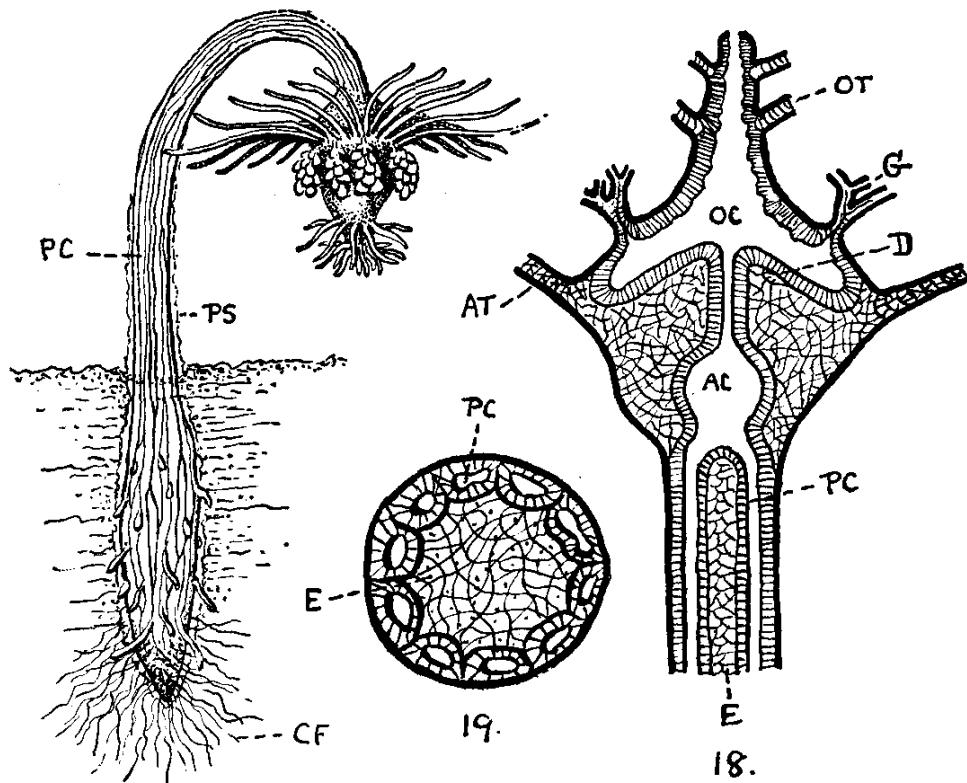
the colony. Twice in a minute all the tentacles bend downwards, while all the feeding polyps contract and the whole under-surface of the body is pressed upwards against the base of the chambered pneumatophore. Then all the appendages slowly resume their resting position.' The respiratory function of the 'tracheae' is still an open question, but, whether these movements are respiratory or not, something more than respiration seems to be involved in them. If the mantle-glands, as seems likely, are engaged in the secretion of mucilaginous threads, the reciprocal up and down movements of mantle-flap and tentacles would afford an excellent means of spreading these threads like a veil over the body as a means of entangling prey.

In any case the structure and armament of Disconanth tentacles are much simpler than in Siphonanths, and almost identical with those of ordinary Hydroid polyps.

4. THE HYDROID RELATIONS OF DISCONANTHAE (Text-figs. 17-19, 20).

Not only are the Disconanths more primitive than the Siphonanths by the preservation of their radial symmetry, the slightness of their polymorphism, and the simplicity of their tentacles, but they show distinct relations with the Tubularian group of Hydroids, especially *Corymorpha*, in their aboral wreath of tentacles, their development of an Actinuloid larva, and the labyrinthine transformation of the aboral region of the coelenteron. With *Corymorpha* their relations are particularly close owing to their production of free Anthomedusan gonophores and the dominance of a large central polyp.

All Disconanth colonies have their zooids radially arranged around a large axial polyp, the coelenteron of which is divided up aborally into a dense network of endodermal tubes (the so-called 'liver'), from the peripheral parts of which the endoderm of the tentacles and 'blastostyles' arises, and from which radial canals ramify over the walls of the float. So also the arenicolous colonies of *Corymorpha* (Text-figs. 17-19) are reduced to a solitary gigantic polyp in which the aboral coelenteron is differentiated into an axial parenchyma (endochord) surrounded by a network of longitudinal branching canals. The gonophores



17.

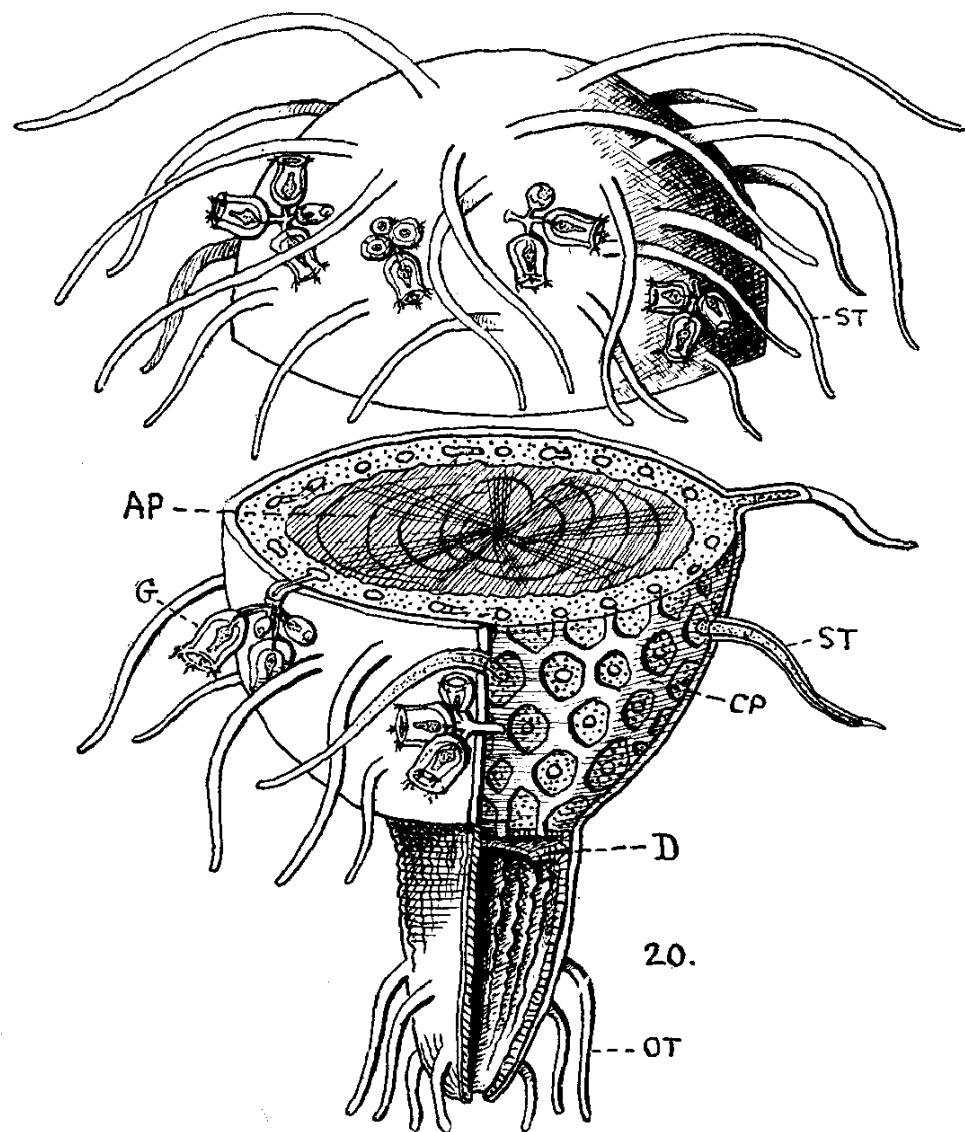
TEXT-FIGS. 17-19.

Corymorpha. *AC*, aboral chamber; *AT*, aboral tentacles; *CF*, caudal filaments; *D*, diaphragm; *E*, endochord; *G*, gonophores; *OT*, oral tentacles; *PC*, peripheral canals; *PS*, perisarcal sheath.

Fig. 17.—Generalized diagram of *Corymorpha nutans* and *pendula*, showing habitat and attitude. (Original, after Hincks and Agassiz.)

Fig. 18.—Vertical section of *Corymorpha nutans*, showing gastric diaphragm and openings of stalk-canals into aboral chamber. (Allman, 1871.)

Fig. 19.—Transverse section of stalk. (Allman, l.c.)



TEXT-FIG. 20.

Pelagohydra, showing the stem expanded as a 'float', with axial parenchyma (= endochord) and peripheral canal-plexus, and the hydranth (proboscis) with narrow gastric diaphragm covering the ring of peripheral ostia (original diagram, after Dendy, 1903).

Fig. 20.—*AP*, axial parenchyma; *CP*, canal plexus; *D*, diaphragm; *G*, gonophores; *OT*, oral tentacles; *ST*, swimming tentacles.

arise in tufts from the enteron of the hydranth, as in *Tubularia*.

The ramified endoderm of *Corymorpha* and its allies is limited to the stalk (hydrocaulus). In Dendy's *Pelagohydra* (1903) the sharp distinction between hydranth and stalk at first sight seems to have vanished (Text-fig. 20). In reality the boundary is just as in *Corymorpha*, but the stalk-region or hydrocaulus, with its axial parenchyma and peripheral labyrinth of canals, has been dilated to form a kind of float, and the hydranth with its oral tentacles is relatively reduced. The caudal float is studded all over with tufts of gonophores and long filiform tentacles, the former arising from the endoderm canals, the latter from the parenchyma in their meshes. A special wreath of tentacles on the hydranth in this case is absent.

This remarkable Hydroid is still known only from the single original specimen which was picked up on a New Zealand sand-beach. It was still alive, though moribund, and floated at the surface, mouth downwards, when transferred to sea-water. It even gave faint signs of concerted swimming movements of its tentacles. Its gonophores were fully constituted Anthomedusae with tufts of tentacles at the ends of their four radial canals. Exactly how *Pelagohydra* floats is not yet quite clear, but, from Dendy's account of its histology, it is almost certainly by means of endodermal oil-drops, as in *Conaria*. Further information on its habits and larval form is much to be desired.

In the adult *Velella* or *Porpita* the precise correspondence of the aboral coelenteron with that of *Corymorpha* or *Pelagohydra* is obscured by several secondary changes, partly due to the addition of the centradenial complex, and partly to the development in the stalk of the enormous air-float. The original ring of separate openings to the canals of the peripheral labyrinth becomes lost in the hepatic plexus which penetrates the centradenia; and the originally cylindrical stalk is flattened downwards and expanded outwards, so that the canals which run longitudinally in the stalk of *Corymorpha* now radiate horizontally outwards below the float, and create the illusion of Trachomedusan structure which deceived Haeckel. That this appearance is illusory is clearly seen when we examine

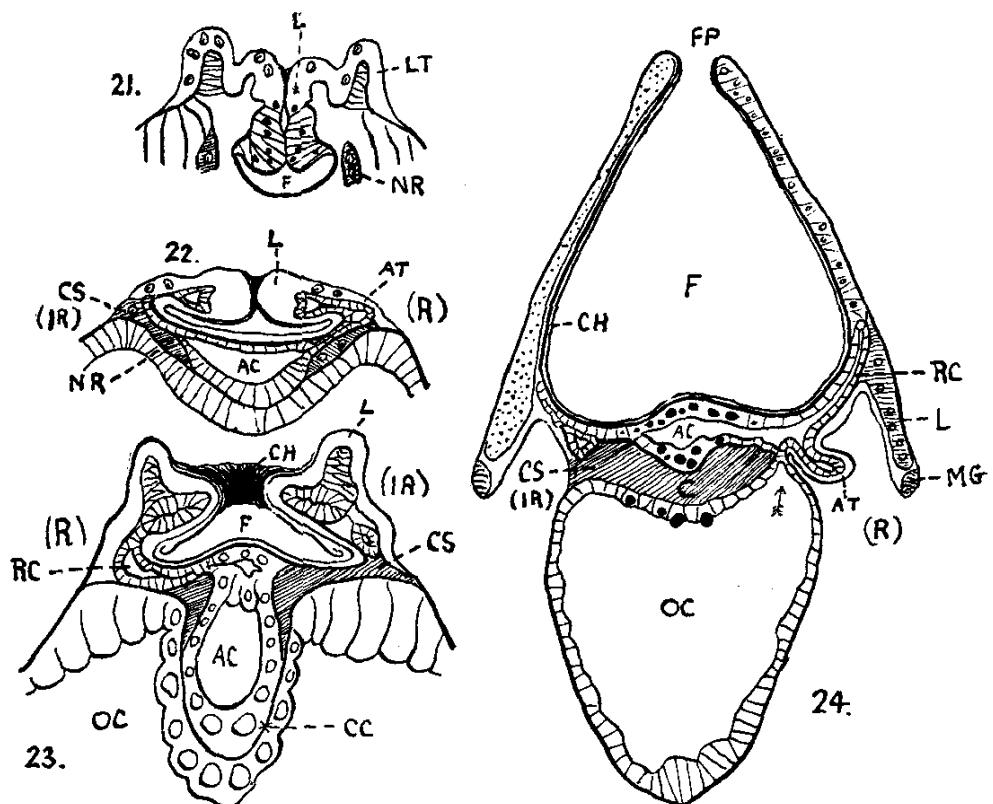
more closely the development of the system in Woltereck's epoch-making larvae.

5. CONARIA AND THE CORYMORPHINES (Text-figs. 21-4).

Like Haeckel's account of Siphonophores in general, Woltereck's terse description of *Conaria* and its development is closely interwoven with a medusoid interpretation of his own, which makes the disentanglement of fact and fancy unusually difficult in parts. His scrupulous workmanship, however, is beyond question, and the features essential to this discussion are borne out by drawings of actual sections which inspire every confidence. The more important of these are here reproduced (Text-figs. 21-4), as well as one of his diagrams very slightly modified (Text-figs. 15-16).

The general features of these early larvae of *Ve lella* were briefly summarized above (p. 120), and their remarkable internal structure was diagrammatically represented in Text-figs. 15-16. The vacuolated endoderm of the youngest larva, brought up from a depth of some 500 fathoms, was completely destroyed, but has been restored hypothetically from the following stages, actual sections being represented in Text-figs. 21-4. In the earliest stage taken after loss of the larval tentacles the coelenteron is seen to be completely divided into two chambers, a small aboral chamber immediately below the floor of the float, and a large oral chamber, the greatly distended larval stomach. Until the larva reaches the surface as a *Rat aria* this oral region floats uppermost, but I use the terms 'above' and 'below' with reference to the adult orientation, and all the figures are similarly placed.

Wedged between the two layers of endoderm is a flat ring of nematocystic ectoderm, which is seen in the sections to be continuous with the outer ectoderm interradially, i.e. in the intervals between two adjacent radial canals. At their inner ends these radial pieces are united with their neighbours to form a 'nettle-ring', which burrows between the apposed walls of the oral and aboral chambers (Text-figs. 22 and 23) until, in later stages, these walls finally separate from one another (Text-fig. 24), when the ring fills up in the middle to form a solid lenticular



TEXT-FIGS. 21-4.

Conaria and Rataria larvae of *Velella* (vertical sections from Woltereck, 1904). *AC*, aboral chamber; *AT*, adult tentacle; *C*, centradenia; *CC*, crimson cone; *CH*, chitin; *CS*, centradenial spoke; *F*, float; *FP*, float pore; *(IR)*, interradial plane; *L*, limbus; *LT*, larval tentacle; *MG*, mucus gland; *NR*, nettle ring; *OC*, oral chamber; *(R)*, radial plane; *RC*, radial canal.

Fig. 21.—Aboral region of tentaculate Conaria, showing float rudiment and 'nettle-ring' stage of centradenia. Note extreme compression and partial involution of the aboral ectoderm above that of the float.

Fig. 22.—Later stage after loss of tentacles and closure of diaphragm. A radial canal is seen on the right, and an interradial spoke of the nettle-ring on the left (*CS*).

Fig. 23.—Conaria with fully developed crimson cone. The aboral ectoderm has opened out, but the aperture of the float remains plugged by chitin. Indications of limbus and adult tentacles.

Fig. 24.—Rataria stage. The float is large, chitin-lined, and with apical pore functional. The 'cone' has flattened out; the centradenia is solid; and communications are being formed peripherally between oral and aboral chambers (one marked by arrow).

mass, Haeckel's 'centradenia'. Woltereck attaches a high theoretical importance to the annular character of the earlier stage (see his diagrams in 1904, Text-figs. 15–20), but there is no evidence of a ring-like origin. It probably arises as a series of eight independent interradial proliferations, and the ring-form is merely the first step towards consolidation. Its interradial spokes of contact with the outer ectoderm persist at least to the Rataria stage, when consolidation becomes complete (Text-fig. 24). In the adult *Velella* Bedot (1884) has shown that the organ is separated from the ectoderm by a thin tough mesogloal envelope pierced by a large number of well-defined pores, which permit the passage outwards of cnidoblasts to the appendages. These pores would seem to be the result of extensive subdivision of the original points of ectodermal continuity.

Coming back now to the aboral endoderm, we see the 'cone' in Text-fig. 23 near the height of its development, and projecting into the oral chamber like the manubrium in the bell-cavity of a medusa, though in life the other way up. It is seen to be produced by a downward growth of both endodermal walls, each laden with oil-drops. The pericystic endoderm is already differentiated into the first octoradiate system of radial canals, which are connected distally by a ring-sinus round the lip of the float, and open below into the aboral chamber. There is still no communication between the two chambers. What is the meaning of this extraordinary separation?

Woltereck regarded it as the division between two separate organisms, a primary polyp orally and a medusoid bud aborally, and speaks confidently of the two chambers as the 'polyp gut' and 'medusa gut' respectively. As the 'medusa' has been converted into a pneumatophore it is 'eingesenkt', but the nettle-ring between the two creatures is regarded as a fused vestige of the originally constricted neck of ectoderm—now doubled inwards—between the parent polyp and its medusan bud. Having already remarked on the discontinuity of the connexions between the nettle-ring and the outer ectoderm, I will add only one further comment on this 'Bipolarian' hypothesis. If the centradenial ectoderm really represents the original neck between parent and bud, it is essential that the larval

(‘polyp’) and adult (‘medusan’) tentacles should arise from opposite sides of the dividing nettle-ring. Woltereck completely failed to establish this crucial point. He noted that the interradial connexions with the skin (‘Berührungsstellen’) were situated where the thick aboral ectoderm tapers off into the thin pavement epithelium covering the ‘polyp’, and had no difficulty in showing that the adult tentacles arise in the Rataria on the aboral side of this line (Text-figs. 21–4). But of the single tentaculate larva he drew only a perradial section through the tentacles—a radius in which no peripheral spoke of the ring occurs—and says merely that the tentacles lie ‘opposite the ring’, which means nothing (Text-fig. 21). Yet the section clearly shows that the larval tentacles arise from the same thick plate of aboral ectoderm as do the adult tentacles at a later stage, so that, on the evidence submitted, the larval tentacles, like the adult tentacles, belong to the medusa-bud and not to the polyp—which, as Euclid would say, is absurd. There is also no evidence for Woltereck’s view that the adult tentacles arise more aborally than the larval, for the two sets do not occur together, and the mere position of the larval tentacles ‘opposite the ring’ is no criterion.

In fact, as in other cases, the larval tentacles would seem to be simply forerunners of the adult tentacles (e.g. Tubularian Actinula), but specialized for some larval function (as in *Myriothela*, p. 146), in this case probably for temporary attachment to the manubrium of the parent gonophore. Such a function would explain the resemblance of these tentacles to those of *Cunina*-larvae, both as regards their restricted number, extreme aboral position, and structure. The peculiar eversion and expansion of the aboral disk after the tentaculate stage implies a previous crowding of these parts aborally, as if to facilitate such a function.

Alternatively let us now turn to some simple facts of Comparative Anatomy. It has long been known that in the Hydroid *Corymorpha* the coelenteron is not merely labyrinthine in the stalk, but is partially divided in the hydranth itself into oral and aboral chambers by a solid annular ingrowth (Text-figs. 17–19), so thick that only a narrow axial passage remains to

connect the two compartments. It is very similar in *Tubularia* (Kükenthal, fig. 386), except that the aboral chamber, following the degeneration of the labyrinth, is itself reduced to a mere vestige (cf. Grönberg, 1898, and below, Text-figs. 50-3). Although the early development of *Conaria* is unknown, it is manifest that a complete septation of the coelenteron which cuts the body off from all connexion with its feeding chamber cannot be primitive either in phylogeny or ontogeny. The septum must have begun as a simple annular fold of the endodermal wall, which, as a larval adaptation, grew inwards and downwards until the central aperture closed altogether, as represented by Woltereck himself in a later diagram (Text-figs. 15-16), freed from the extravagances of his medusoid theory. The condition of an open diaphragm, transitory in *Conaria*, is exactly the condition permanently retained in *Corymorphida*, *Tubularia*, and their monogastric relatives. In *Branchiocerianthus* it is a thin iris diaphragm (Text-figs. 48-9), modified peripherally by adhesions of its upper surface with the peristomial disk. Even in *Pelagohydra* the same division prevails, for Dendy described and figured an annular valve-like fold near the aboral end of the proboscis cavity, which covers the ring of ostia leading to the canals of the labyrinth (Text-fig. 20). In *Tubularia* the longitudinal canals are vestigial (see Grönberg, 1898), but in the others, with the possible exception of *Branchiocerianthus* (in which the exact relations are not yet known), all the longitudinal canals of the stalk open by a peripheral ring of ostia into the aboral chamber defined by the diaphragm.

This arrangement (except for the complete separation of the two chambers) precisely corresponds with the conditions in *Conaria* up to the Rataria stage, and confirms the homology of the aboral chambers throughout, for, as shown in Text-figs. 21-4, it is the aboral chamber which receives all the peripheral radial canals that ramify round the walls of the float, the region which obviously corresponds to the hydrocaulus of the Hydroids.

It is worth noting that in the Hydroids mentioned the function of the diaphragm appears mainly to be one of controlling the distribution of food-products from the digestive cavity to-

the stalk, whereas that of the crimson cone of *Conaria* is merely one of increasing the oil-producing surface, since the larva takes no external food before the *Rataria* stage when its tentacles grow. It is significant that in *Tubularia* also the gastric epithelium is produced into ridges (the 'pendulous processes' of Allman) which were described by Allman as of a bright vermillion colour from their production of 'clear spherical elements, probably oil-drops', and, with differences of colour, similar phenomena have been described in the adult polyps of various *Siphonophora* (e.g. *Forskalia*, *Physalia*, *Athorybia*) by Kölliker, Huxley, and Haeckel, usually as *Leberstreifen*.

It remains to add that when the larval *Velella* reaches the surface as a *Rataria*, the cone flattens out, but any reopening of the central aperture is precluded by the ever-growing centradenial ring which forces the two endodermal layers apart and interposes a solid mass between them. But it thins out laterally, and in the radial intervals between its connexions with the skin the two layers meet peripherally and fuse to form a ring of eight ostia, which put the oral chamber into communication with the eight aboral radial canals (Text-fig. 24. Incipient ostium marked by arrow). The ostia subsequently elongate into vertical canals, while the aboral chamber itself breaks up into the 'hepatic plexus' traversing the centradenial mass. These changes explain Haeckel's error in homologizing the adult canal system with that of an octoradiate Medusa. The primary radial canals do not arise, as he thought, from the eight gastric ostia, but from the aboral chamber, and his 'subumbrial vessels' are the composite channels brought about by secondary connexions of the primary canals with the oral chamber through these peripheral ostia. The primary radial canals, on the other hand, we have seen to be the strict homologues of the eight or ten longitudinal canals of the stalk of *Corymorpha*, their more regular cruciform or medusan symmetry being the natural result of their development under the uniform conditions of free flotation (cf. Bigelow, 1911, pp. 328, 339, and his fig. B for accounts of the very similar canal systems of Porpitids, and other corrections of Haeckel's descriptions).

Thus both Haeckel's and Woltereck's medusoid theories of Disconanth origin must share the fate of those other medusae which have been invoked to 'explain' the origin of the pneumatophore. The salient features on which they depend are seen to be based on structural conditions already present in various monogastric Hydroids related to *Corymorpha*, so that medusan interpolations are superfluous. *Entia non sunt multiplicanda.*

6. THE SIPHONANTH PROBLEM.

The Siphonanthae differ radically from the Disconanthae in almost every respect. They are bilaterally symmetrical; budding is restricted to a single meridian ('ventral'); polymorphism is more pronounced by the addition usually of bracts, palpons, and nectocalyces, or at least of one of these; the gonophores, though Anthomedusan, are with rare exceptions sessile and borne as members of special polymorphic clusters ('cormidia'); there is no general wreath of tentacles, and no central reservoir of cnidoblasts, but each polyp has its own prehensile tentacle and basal store of cnidoblasts ('basigaster'); the coelenteron is simple, though plexiform throughout in one family (Rhodaliidae, Haeckel's 'Auronectae'); the float is simple, but provided with a more or less complex gas-gland: it is absent only in one group (Calycophora), in which, however, nectocalyces are present; lastly the larva, prior to budding, is a solid, mouthless Planula.

These differences present formidable obstacles to the maintenance of Siphonophora as a homogeneous group, especially if Calycophora, as at present, are regarded as primitive. It is noticeable, however, that in many respects the Siphonanth condition is more advanced, less primitive, than that of Disconanths, so that it is worth an effort to see whether the gap between them can be explained as the result of increased divergence of the former from a common source.

In Tunicata which present similar problems in the origin of pelagic from sessile stocks, the original life-history is like that of a Hydromedusan, with the same three stages: a purely locomotive larva, followed by fixation of the larva, and this by an adult stage of feeding and growth, with budding last of all. But in

some forms additional yolk is deposited in the egg, fixation is postponed, and budding is accelerated until it begins in the larva. Finally fixation is abandoned altogether, the original metamorphosis is abbreviated, a nondescript oozoid, neither larva nor adult, but an asexual mixture of both, carries the buds about until they can feed themselves (*Salpa*, *Doliolum*), or a precocious group of buds supersedes it altogether (*Pyrosoma*).

There are grounds for thinking that a sequence of this kind has profoundly affected the character and organization of Siphonanth colonies. For budding begins in the earliest larval stage, the eggs of all Siphonanths are exceptionally large, and in Physophores only one egg is produced at a time—a feature which in Hydroids is associated with the formation of Actinula larvae (Lowe, 1926). It seems possible, therefore, that the original larva of Siphonanth ancestors was not a Planula but an Actinula, and that the Planuloid appearance of Siphonanth larvae is due to the precocity of budding before the typical Actinuloid characters have developed. This view has proved so illuminating that I venture to assume it, and confidently leave it to be judged by results.

It is true that in Calycophora the female gonophore is not so limited in egg-production as it is in Physophorids. From the imperfect data on their ovogenesis at present available I cannot fully explain the contrast, but it is at least possible that the 'polyovon' condition in Calycophora may be consequential on the many modifications (largely simplifications) of structure which the group has undergone during its evolution. In all other Siphonanths the gonophores are produced as buds from specialized secondary polyps (blastostyles or gonopalpons), the real source of their reproductive cells, whereas in Calycophora they arise directly from the budding stem, apparently without the formation of an entocodon (Moser, 1925 b), and their ova are endodermal in position from the outset. The single final egg of Physophorids is produced, as in *Tubularia* and *Hydra*, by the fusion or absorption of many young ova: the equally large eggs of Calycophores are predetermined without any such process. Moreover in each cormidium (which will be shown to be the equivalent of a whole Hydroid branch) there is usually only one gonophore, instead of the dense clusters in other Siphono-

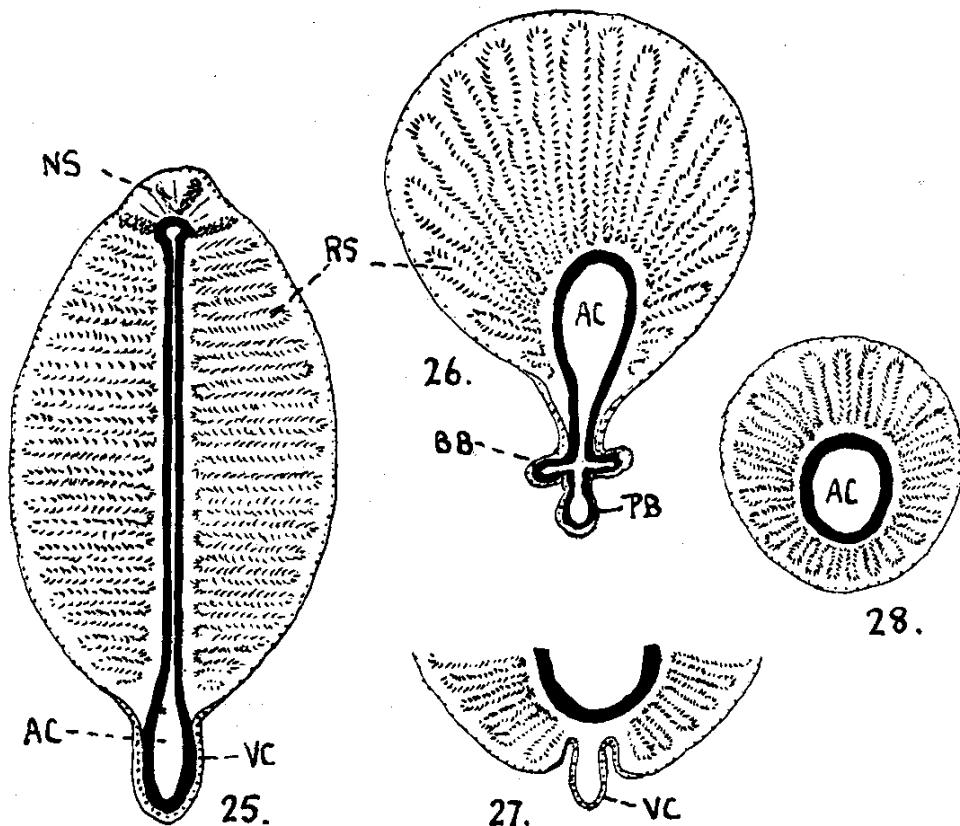
phores. As the whole cormidium is usually detached in Calyco-phora as a free-swimming reproductive unit ('Eudoxia'), this novel procedure would be futile if each polymorphic cluster were limited to the production of one egg at a time. In any case the subsequent development of the fertilized egg follows exactly the same lines as in Physophorida.

Dicoryne conybeari (Text-figs. 34-5) may be an exception to the rule that gonophores producing single eggs give rise to Actinulae, but its eggs barely exceed 0.1 mm. in diameter.

7. GASTRULATION AND THE BUDDING LINE (Text-figs. 25-8).

The eggs of Siphonanths vary in diameter from something like 0.4 mm. in Calycophores to 0.6 mm. in typical Physonects, a size at least five times greater than that of typical Planula-producing eggs of ordinary Hydroids. They are filled with a highly translucent, peculiarly buoyant sap or yolk. They are liberated as eggs, not larvae, and usually shed the membrane which surrounds them in the gonophore at the time of liberation. They are thus naked from the start, fertilization apparently, and segmentation certainly, taking place outside the gonophore. In some cases (e.g. *Halistemma rubrum*) the eggs are so large that the segmentation stages can be followed without the aid of a lens (Metschnikoff, 1874).

It follows that no distinction can be drawn between embryo and larva, except by analogy. The larger and yolkier larvae preserve the spherical form of the egg long after the first larval organs and buds have arisen (e.g. *Agalma*, *Crystallodes*, *Athorybia*), and these in all cases make their appearance long before the endoderm has completed its delamination from the yolk cells of the primary morula. The germ-layers are in fact first formed along a particular meridian, and then extend to right and left, first the ectoderm, then the endoderm more slowly until gradually the whole surface of the yolk is covered. There are variations in detail, and there is a tendency towards acceleration of the process aborally, but the region opposite the meridian of first formation is the last to be differentiated. The primary or zero meridian is naturally also the site of precocious



TEXT-FIGS. 25-8.

Stems of *Macrostele Siphonanths*. Diagrams of transverse sections.
AC, axial canal; *BB*, bract buds; *NS*, nervous system; *PB*, polyp bud;
RS, radial septa of mesogloea supporting muscle fibres;
VC, ventral crest.

Fig. 25.—*Forskalia ophiura*. (After Korotneff, 1884.)

Fig. 26.—‘*Agalmopsis*’ *sarsii*. (After Claus, 1878, modified.)

Fig. 27.—*Apolemia uvaria*, internode. (Korotneff, l.c.)

Fig. 28.—*Praya diphyes*, internode. (Korotneff, l.c.) Calyco-phorida.

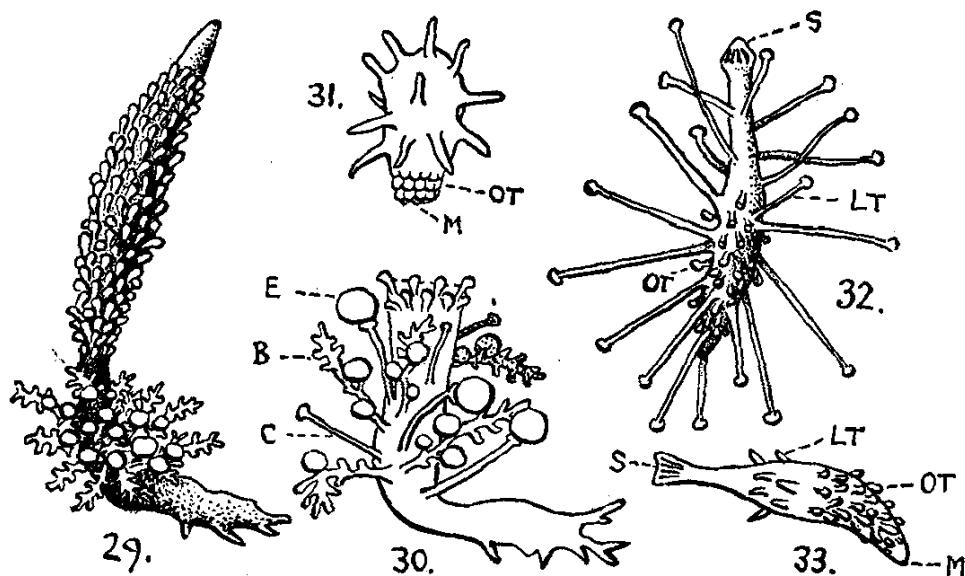
} Physophorida

budding, and was conveniently termed 'ventral' by Claus and Haeckel. The term, of course, has no necessary relation to the orientation of the animal in space (pace Schneider, who objected that a *Sphaeronectes*, when swimming, carries its budding line uppermost).

There can thus be no doubt as to the precocity of budding. Buds arise in the first patch of the embryo that has acquired its diploblastic coat, while the rest of the body is solid with yolk—long before there is any possibility of it showing typical Actinuloid features. It would thus appear that the slow bilateral course of gastrulation, combined with the precocity of budding, is the prime cause of the unilateral 'budding line' and the bilateral symmetry of Siphonanth colonies.

This initial factor is reinforced, as development proceeds, by histological differentiation of the larval body-wall, which, outside the ventral tract, becomes increasingly thickened and specialized by the development of a powerful musculature and radial sheets of mesogloea to support it. A cross-section of the stem of any long-stemmed Siphonanth reveals a narrow central lumen and, between ectoderm and endoderm, a thick ring of longitudinal muscle-fibres (ectodermal) arranged in close-set radial series on each side of corresponding centrifugal bands of mesogloea (Text-figs. 25–8). This elaborate muscular envelope tapers from the dorsum down each side to the ventral line, where it is replaced by a thin fold of the undifferentiated primary layers, the so-called 'ventral crest'. Only along this tract is budding possible, and there are limitations even here. In *Forskalia* and the Agalmids the crest is continuous, thus permitting the formation of 'dissolved cormidia' below and tiers of nectocalyces above; but in forms with 'ordinate cormidia' the crest is interrupted along the internodes of the stem, either by lack of the endodermal element (e.g. *Apolemia*) or by complete suppression of the crest (*Calycophora*) outside the segmental nodes.

Korotneff (1884) to whom, after Claus (1878), this survey is mainly due, arranged these modifications in the reverse order, which he thought represented successive grades of departure from Hydromedusan conditions, as presented by the 'solitary'



TEXT-FIGS. 29-33.

Myriothela. Life-history of British species. *B*, blastostyles, coryniform, bearing gonophores below; *C*, 'clasper' (modified tentacle ?) which withdraws a ripe egg from gonophore; *E*, egg (or embryo) held by clasper; *LT*, larval tentacles; *M*, mouth; *OT*, oral tentacle; *S*, sucker.

Fig. 29.—Colony with blastostyles. (Hinks, 1868.)

Fig. 30.—Blastostyle region enlarged. (After Allman, 1875, simplified.)

Fig. 31.—Larva on hatching, oral end below.

Fig. 32.—Larva fully formed, with larval tentacles extended and proboscis developing; sucker (*S*) above.

Fig. 33.—Larva on fixation, larval tentacles withdrawn. (Figs. 31-3, Allman, l.c.)

Gymnoblast *Myriothela*. But those conditions are much more closely approached in the body-wall of *Physophora* (Korotneff, l.c.) and doubtless of other 'Brachysteles' (though in none of these are figures of the ventral line available), as well as in the long-stemmed *Cystonects Rhizophysa* and *Bathyphysa*. In any case it seems clear that in Siphonanths generally the post-larval structure of the stem (i.e. of the body-wall of the oozooid which bears the colonies) prohibits all budding except along the ventral tract, and there only in a limited belt at the base of the protosiphon.

Other relations of the ventral tract to processes of growth will be dealt with in the sequel.

8. THE NATURE AND ORIGIN OF BRACKETS (HYDROPHYLLIA) (Text-figs. 29-33).

These structures in their manifold variety are perhaps the most characteristic of Siphonanth appendages, but their history, in the perpetual wrangle over polypoid and medusoid theories, has never been made clear. To Haeckel they were in some cases the split and isolated umbrellas of ancestral medusae, and in others simply elongated and degraded nectocalyces—the former view being based on his early observation of larval *Physophora*, the latter on his alleged detection of vestigial nectosacs at the tips of the coronal bracts of several forms, notably '*Athoria*' and '*Rhodophysa*' (1888). Unfortunately the single specimens of these forms, which had been seen by Haeckel only, have been lost, and his idealized pictures of the former (Pl. xxi, 5 and 6) can scarcely be regarded as evidence; for the tip of a larval bract is so frequently provided with a nest of large nematocysts, sometimes four in number, set up side by side in a little terminal pocket, that a lively imagination could easily convert this into a minute vesicle segmented by four little radial canals (cf. Haeckel's Pl. xxi, figs. 10 and 12, with Metschnikoff's figures of larval *Agalma*, 1874, or Schneider's special drawings of them, 1896, Pl. xlili, 1-3). Moreover it should be noted that in his original description Haeckel's words were less emphatic than his figures, for all he said was that 'four very small radial canals seem to arise from it (i.e. the bracteal canal)' (l.c.,

p. 202). If to Haeckel's keen eye they only seemed', we may certainly discount the hard strokes of his pencil, as well as his subsequent overstatement that these 'seeming' nectosacs are a 'proof that the bracts in these cases are reduced nectophores'.

Oddly enough Schneider claimed these same structures in larval bracts as proofs of their polyp nature. Like Claus he took the terminal pockets to be the mouth-openings of bracteal canals, which became shut off from them in adult *Agalmas*, but remained open through life in the 'very primitive' Calycophore *Praya*. Such openings were later denied by Moser from her own observations at Naples (1924, p. 27).

Bracts as swimming organs were tersely described by Huxley in his account of *Athorybia* (1859, p. 88, Pl. ix), but more fully by Kölliker (1853, pp. 24-5), whose account I translate: 'Swimming bells are altogether absent, and replaced by a crown of solid covering-bracts which, from their attachment by moveable stalks, serve not only for protection of the remaining parts but also for swimming. . . . Both singly and all together they make energetic movements, which appear as a rising and falling of the individual leaflets, and, when all work together, they bring about a self-opening and self-closing of the composite crown. When an *Athorybia* rests at the surface of the water, quietly lurking for prey, often all its bracts are widely unfolded and it has the form of a perfectly flat shell [admirably represented by Haeckel, Pl. xi]; but if one touches it, however gently, it instantaneously shuts up, so that the points of all the bracts meet below, the animal assumes an oval shape, and the polyps and other organs are completely enclosed (Pl. vii, 1). Still more striking are these movements when an *Athorybia* swims, always by the activity of its bracts alone, which, without any alteration in their shape, but opening and closing alternately as a whole like the umbrella of a Medusa, drive it forward in the direction of its pneumatophore, through the combined impulse of the water contained in the common cavity.'

Thus the coronal bracts subserve passive flotation or active locomotion as required, and provide a protective cover for the retracted tentacles. Of these functions that of locomotion would

seem to be the chief, since in larval Agalmids (which closely resemble the adult *Athorybia*) all the bracts are shed as soon as nectocalyces become functional. Confirmation of this view is provided by *Stephanomia (Halistema) rubrum*, the largest of Mediterranean Agalmids, in which the nectocalyces make their appearance exceptionally early, and the larval bract either fails to appear (Metschnikoff, 1874) or has a very short and precarious existence (Woltereck, 1905 b).

The early development of *Athorybia* was traced by Haeckel (1869, Pl. xiv) and is practically identical with that of *Agalma* and *Crystallodes*. The first appendage is a smooth gelatinous subapical bract, which extends backwards over the antero-ventral budding area of the Planula, as in *Physophora*. It arises extremely early, even before the float, its axial canal springing from the earliest patch of gastrid cavity. Then the typical leaf-shaped bracts arise beneath it and radiate outwards from their ventral attachments so as to enclose the whole embryo. The pneumatophore at length pushes up between them, the primary bract is thrown off, and the secondaries continue to multiply on both sides to form a bilateral corona, as in *Anthophysa* (Text-figs. 45-7).

At this stage in Agalmid larvae the first nectocalyces arise on the stalk of the pneumatophore, and the larval bracts are soon afterwards thrown off. But they persist and continue to multiply, as we have seen, in *Athorybia*, although rudimentary 'nectocalyces' may arise in front of them which never function (Chun, 1897 b), and in *Nectalia* they persist and become remarkably differentiated (see p. 172) along with functional nectocalyces and a float. As these are short-bodied forms, it would seem that the disappearance of the coronal bracts in long-bodied forms like *Agalma* is partly due to the elongation of the stem, which develops its own bracts, often in great profusion (cf. p. 153, below).

These stem-bracts in the long-bodied Physonects are present in hundreds, even thousands, and would seem to play an important part in the adaptation of Macrostele Siphonanths to a life of incessant vertical migrations. As the Copepods, Euphausids, and other prey periodically rise and sink, many Siphono-

phora must do the same or starve; so during their slow descents—it may be through several hundred fathoms—the bracts will probably all be spread out horizontally, like the coronal bracts of *Athorybia* when quietly drifting, and during the quicker ascents, whether by nectocalyces or pneumatophore, will be pressed against the stem to reduce resistance. In a few forms they are transformed into cubical or prismatic gelatinous floats, which may be found with more knowledge to be indicative of a more restricted range of depth. The complete absence of bracts as well as nectocalyces in *Cystonectae* is doubtless to be correlated with the great size and perfection of their float, in which gas-pressure can be adjusted by its aperture, and thus control both ascent and descent. *Anthophysa*, as we have seen before, is again the intermediate link, since, along with a large but closed float, it retains paddling bracts, but lacks nectocalyces.

In Calycophorida only the stem-bracts survive as free structures, one in front of each cormidium, which they serve partly as a protective cover, and partly, in the case of free Eudoxids, as floats. They are highly gelatinized, and in the latter case assume fantastic shapes, prismatic, cuboidal, polyhedral, but in their simplest form they resemble the primary larval bracts of Physonects, pointed distally, convex externally, and concave towards the cormidium, which they more or less embrace. In Eudoxids their axial canal is usually much dilated as the so-called 'phyllocyst', the walls of which are highly vacuolated, and usually secrete a terminal oil-drop as a float. Only in Polyphyidae are bracts entirely lacking, the cormidia being sessile and the whole stem retractile within the cavity of the strangely built spire of nectocalyces. (*Hippopodius*, p. 157).

But, although bracts are not present in the nectosome of Calycophores as independent organs, it was pointed out by Schneider (1896) that the more gelatinous of their nectocalyces, especially the primary bells, by the possession of a *Sapfbehälter* or somatocyst—the exact equivalent of a phyllocyst—betray themselves as compound structures formed by fusion of bract and bell, which he distinguished accordingly as *Deckglocken* (i.e. bract-bells) in contrast to simple *Schwimmglocken* or nectocalyces. As can be seen in Metschnikoff's

figures of *Galeolaria* ('*Epibulia*') or Chun's of *Mugiaeae* (Text-figs. 2 and 3), the somatocyst arises from the small gastral cavity of the young Planula close to the base of the larval nectocalyx, between the latter and the apical pole, exactly where the cap-shaped bract of a larval Physophore takes its origin. On the strength of these relations Schneider—as I think on ample grounds—homologized the endodermal canals of the two structures, thereby establishing an important common feature of Calycophore and Physophore larvae. The identity of the two structures was subsequently recognized by Woltereck (1905) and Moser (1924, p. 25), and used to support their argument that the larval bract, and not the pneumatophore, of Physophores corresponds to the larval bell of Calycophores.

Unfortunately Schneider shared with the last-named authors the same fixed idea as to the primitiveness of Calycophores, and all three missed the real significance of his identification. The simple inference was, of course, that the independent primary bract of the Physophore, already verging on disappearance, had become secondarily fused with the nectocalyx in the Calycophore. Instead he tortuously interpreted the independence of the bract in Physophores as due to a secondary breakdown of the Calycophore 'bract-bell', by which the bell became the pneumatophore, and the somatocyst the bract! He then proceeded to re-classify the Calycophora according to the dominance or degeneration of the bract-bell, broke up Chun's nicely ordered sequence of Mono-, Di-, and Polyphyids, based on the number of their bells, and drew the great man's thunders on his head as the author of 'kein System der Siphonophoren, sondern die Carricatur eines Systems' (1898 a, p. 305). Nevertheless, although Schneider's systematic adventure was ill-conceived, Chun never adequately met the morphological case which prompted it, as Schneider bitterly complained (1898), and I revive it now in the full belief that it is unassailable. I interpret it as showing that, in the earliest days of their history, Calycophores as well as Physophores possessed larval locomotive bracts, probably before nectocalyses had come into existence. With their increasing precocity the first or larval bract was transformed into a transitory gelatinous shield over the budding

area, and the locomotive function in Physophores was handed over to its successors, while in Calycophores the precocity of the primary nectocalyx rendered all locomotive bracts superfluous, and the primary bract was incorporated in the nectocalyx, which took over the protective function itself (cf. the hydroecium in Text-figs. 5 and 12). The bract being subapical, and anterior to the nectocalyx, the effect of their fusion was to provide the nectocalyx with an anterior pyramid of jelly as the functional apex of the young colony, in place of the larval apex which, as we saw earlier, had meantime been absorbed.

As evidence of the original independence of the somatocyst-bract, I have reproduced another neglected figure, also of Metchnikoff's (1874, Pl. vii, 16), which represents a larval Calycophore, fished at Villefranche, and provisionally identified as *Praya inermis* (?) (Text-fig. 6). The gelatinous dome over the somatocyst is seen to be incompletely fused with the nectocalyx. Bigelow regards Metchnikoff's species as *Sphaeronectes truncata*. There seems to be no ground for Moser's suggestion that this larva may be a detached cormidium (1924, p. 16).

If my assumption is correct that the original larval form of Siphonanths was an Actinula, as it still is in Disconanths, these bracts assume a new significance. They are neither modified polyps nor modified medusoids, but represent the persistent tentacles of the original Actinula larvae more fully adapted to the locomotive and other functions which we have seen they discharge in the young pelagic colonies.

Now the Actinula is merely a Planula with precocious adult characters, or, to be more precise, a Planula provided with additional yolk so that it develops some at least of the future polyp tentacles as well as a mouth before its liberation. Apart from the little four-tentacled larva of *Coryne Van Benedeni*, we are acquainted with only two types of Hydroid Actinula, the Tubularian (or Corymorphine), with an equatorial ring of tentacles (i.e. the future 'aboral ring' of the Hydranth with a considerable rudiment of the stalk), and the Myriotheline, with long tentacles scattered all over its body (Text-figs. 29-33). In both cases the tentacles are locomotive, mainly ambulatory

perhaps, but in *Tubularia* at any rate capable of swimming. The larva of *Myriothela* has been little studied since Allman (1875) described its remarkable history. I give here a short account of this history, for in various respects in which Siphonanths differ from Chondrophora, *Myriothela* shows unexpected points of agreement. [See Postscript, p. 193.]

Myriothela is another of the solitary or monogastric Gymnoblasts, but unlike *Corymorpha* and its allies, it is firmly attached by one side of its short stalk to rocks or large stones. Its body is very extensible, and closely studded with short knobbed tentacles, but, unlike any other Hydroid, it lies more or less prone on the face of a rock, or on the underside of a flat stone, and there stretches and probes about with its long proboscis for passing prey. It has peculiarly branched Coryniform blastostyles behind, presumably the vestiges of a once fully colonial life. They bear adelo-codonic gonophores, each of which, when female, liberates a single large egg, the fertilization and development of which take place outside the gonophore. But, instead of being sent adrift, as in Siphonanths, the egg, still enclosed in its membrane, is seized by a specialized tentacle (or dactylozooid) near by, and held aloft during the whole of its subsequent development. In this position the embryo from the beginning develops freely outside the gonophore on its own resources, and to that extent resembles the egg of every Siphonanth, and differs from those of Chondrophora and the Tubularian Hydroids (including *Corymorpha*), which are nursed within the parent gonophore until the Actinuloid characters are complete.

In the first years of the Plymouth Laboratory the late Sir William Hardy, then a young man fresh from Cambridge, paid several visits with the object of working out the development of *Myriothela*, and I have pleasant recollections of helping him in the search for specimens. Unfortunately he gave up this intention on learning that Korotneff was engaged on the same problem, a task he never completed. Nevertheless Hardy made the discovery (1898, fig. 13) that *Myriothela* is not limited to the budding of blastostyles, but produces little clusters of polyp-buds in the region immediately behind the blastostyles, though

they develop by a peculiar method and break off as in *Hydra* and *Tiarella* (Text-figs. 54-7). [See Postscript, p. 193.]

The larva before hatching has an oval body bearing short blunt tentacles except at the narrow oral end, which is closely beset with several rows of tubercles, forerunners of the adult series of short capitate tentacles (Text-fig. 31). This end grows rapidly, making the body spindle-shaped after hatching (Text-fig. 32). The larval tentacles become elongated and definitely capitate, while additional ones arise in the oral extension among the short adult tentacles, possibly by the enlargement of some of them. The aboral extremity develops a terminal sucker, which is apparently invaginated. After a free life of some days the larva attaches itself by its sucker,¹ and the long larval tentacles are withdrawn (Text-fig. 33). A remarkable developmental feature is the precocious origin of the hollow larval tentacles in an involuted condition (Allman, 1875). [See Postscript, p. 193.]

It would seem, therefore, that in *Myriothela* there is only one diffuse set of tentacles, as in *Coryne*, of which the larval are merely an aboral selection precociously developed for larval purposes. There is thus a close correspondence between the larval tentacles of *Myriothela* and the larval and paddling bracts of *Siphonanths* both in their aboral position, locomotive function, and precocity.

The sharply defined circlets of the Tubularian Actinula are much less closely comparable, although there also the aboral tentacles develop before the oral. When the larva of *Pelago-hydra* has been found, it may well provide a bridge between these two extremes. *Conaria*, with its vestigial pair of tentacles and internal complexity, is clearly too specialized for comparison (cf. p. 120).

9. NECTOSOME AND SIPHOSOME (Text-figs. 34-5).

Haeckel's distinction between the locomotive fore-body (nectosome) and the nutritive and reproductive hind-body (siphosome) is well based. The former carries the float, necto-

¹ So Allman states (1875); but his figure (my Text-fig. 33) is not convincing, and Sars is emphatic that in *Myriothela arctica* the larva attaches itself by several posterior tentacles, and not by its sucker.

calyces and paddling bracts, the latter the polyps and gonopalpons (= blastostyles), as well as various sterile palpons and stem-bracts when present. Each zone has its own centre of proliferation in the ventral tract, the two being separated by a slight gap.

In the larval stage the two zones correspond essentially with the hydrocaulus and hydranth of the primary polyp of a Hydroid colony, but the divergent modes of budding and the varying relations of gonophores to stem and hydranth prohibit any rigid homology. Nevertheless it is remarkable that the caudine 'float' of *Pelagohydra* is exactly equivalent to the nectosome, and carries an equipment of locomotive tentacles and gonophores, the theoretical predecessors of paddling bracts and nectocalyces. These tentacles, so alien to the stalk of an ordinary fixed Hydroid, will doubtless be shown in time to be the persistent tentacles of an Actinuloid larva (cf. *Myriothela*, p. 146). Their diffuseness, and the presence of gonophores among them—both caudine—also point away from the Corymorphine type towards *Myriothela* and the Corynoids.

(a) Nectosome.—Although paddling bracts and nectocalyces are both characteristic of the nectosome, it is important to note that they are alternative organs and rarely (*Nectalia*) function together. In the development of Agalmids the bracts come first and act as larval organs of locomotion, but they atrophy when the nectocalyces develop—a fact which strongly suggests that bracts were the earlier locomotive organs and are here in course of replacement. In *Nectalia* they are specialized for steering, and have ceased to paddle (p. 175). When nectocalyces are especially precocious, as in *Halistemma rubrum*, the larval bracts disappear very quickly or even fail altogether (cf. p. 141). This precocity of replacement reaches its climax in Calycophora (cf. p. 143).

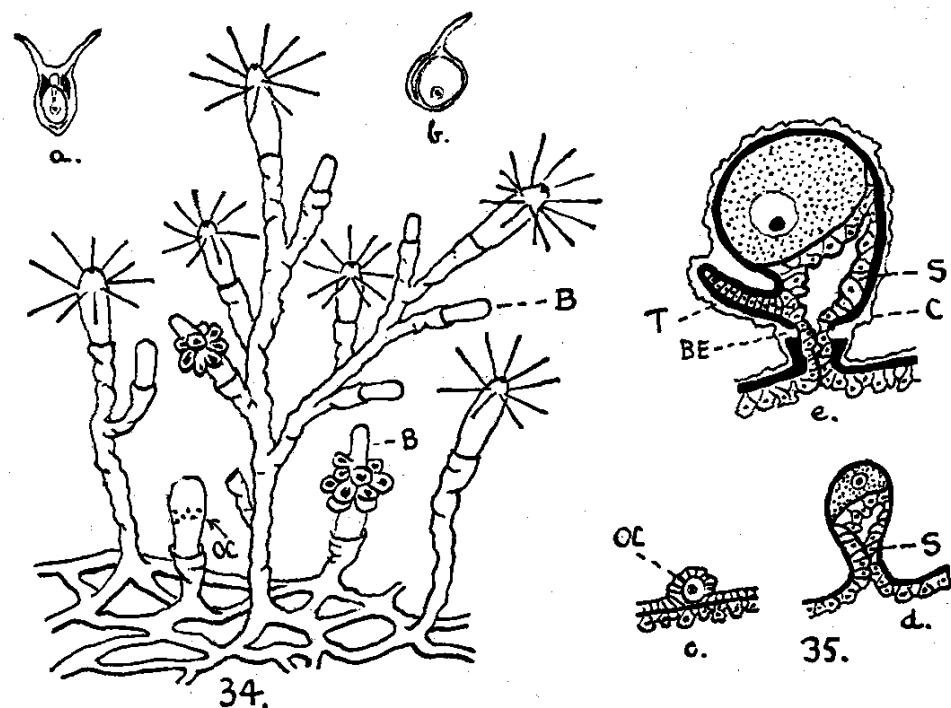
On the other hand paddling bracts persist throughout life in *Athorybia* and *Anthophysa*, and in the former Chun (1897 b) discovered rudimentary medusoid buds in front of them. These have been generally regarded as vestigial nectocalyces, but, with *Pelagohydra* in mind, one may tentatively claim them as obsolescent Hydroid gonophores, which in other families

have been converted into nectocalyces. Chun traced their development, but thought description unnecessary, and indicated no distinctive features. They urgently need a closer examination from this standpoint. In *Anthophysa* they have disappeared altogether.

(b) *Siphosome*.—When the larva of an arborescent Hydroid has fixed itself and grown into the primary polyp or oozoid, its budding zone for new polyps lies below the hydranth proper, between it and its stalk of fixation, exactly as the budding zone of a Siphonanth lies between the primary 'polypite' and its locomotive nectosome. From this zone in the growing Hydroid new polyps arise as radial or lateral buds, usually all alike and fertile, producing their own gonophores (e.g. *Syn-coryne*), but occasionally dimorphic, the terminal polyps of branches remaining permanently as sterile gastrozooids, the secondary subterminal polyps being specialized from the outset as mouthless blastostyles or 'gonozoids' (e.g. *Dicoryne*, Text-figs. 34-5). The latter is the condition in all Siphonanths, with the possible exception of the Calycophora, in which Chun's identification of a blastostyle is disputed (Schneider, 1898, 116; Moser, 1925; versus Chun, 1897 a). With the doubtful reservation of that sub-order, each cormidial group consists in the simplest cases merely of a gastrozooid (the siphon or polyp) and a gonozoid (the gonopalpon and its gonophores), though complicated in many cases by the addition of bracts or palpons or both.

Thus, in spite of the rarity of blastostyles in Gymnoblasts, there is no sharp difference between Siphonanths and Hydroids as regards their polymorphism. In their essential constitution the cormidia of Siphonanths, morphologically and physiologically, represent the trimorphic reproductive branches of an arborescent colony of the *Dicoryne*¹ type, in each of which a mouthless blastostyle and its gonophores are nourished by a

¹ In spite of its name *Dicoryne*—like *Podocoryne*—is not a Corynid in the systematic sense, but belongs to the *Hydractinia*—*Eudendrium*—*Bougainvillea* group, with a single whorl of tentacles above the gonophores and a bare hypostome. The only Corynid with blastostyles in these waters is *Tubiclava* and that is not arborescent.



TEXT-FIGS. 34 AND 35.

Dicoryne, its blastostyles and locomotive sporosacs. *B*, blastostyle; *BE*, breach in ectoderm; *C*, cuticle; *E*, egg; *OC*, oocytes in blastostyle; *S*, spadix; *T*, tentacle, with chordoid axis.

Fig. 34.—Generalized diagram of a typical colony, based on *Dicoryne conybeari* (combined from Allman, 1871, and Ashworth and Ritchie, 1915). In *Dicoryne conferta* the blastostyles have pointed tips, but polyps and branching are much the same in both species. Above, two ciliated sporosacs: (a) *Dicoryne conferta*, bi-tentaculate, usually containing two eggs, (b) *Dicoryne conybeari*, uni-tentaculate, usually with one egg.
 Fig. 35.—Development of sporosac on blastostyle of *Dicoryne conybeari* (Ashworth and Ritchie, l.c.): (c) oocyte in ectoderm, (d) outgrowth of spadix, (e) ripe sporosac with tentacle, ready for liberation.

terminal polyp. The fact that in most groups the cormidia include additional elements, such as bracts and palpons, in no way weakens the comparison, for, in contrast to Hydroids, Siphonophores have had to face a far greater variety of novel conditions of life, and to meet them by corresponding modifications of form and structure. Primary and secondary functions of the bracts have been discussed above. Palpons are no less variable in type, and doubtless play different parts in different families. They may serve as tactile, and even as prehensile organs in *Physophora* and *Epibulbia*, as supplementary organs for circulating the food-stream in others, or as ampullae for storage of fluid during sudden contractions of long stems. These are all special problems awaiting settlement by observation, and in creatures far more difficult to capture without injury and to observe than Hydroids.

The outstanding difference between the reproductive branches of Hydroids and Siphonanths is in their arrangement—a perpetual forking in Hydroids, a linear succession in Macrostelia, and a cyclical multiplication in Brachystelia. We are now in a position to give consideration to these points.

10. CORMIDIAL BUDDING IN MACROSTELIA.

Hitherto the uniserial, metamerised stem of the Calycophora has been regarded as primitive (Haeckel, pp. 7–9), and the derivative nature of the other types has been taken for granted. Phylogenetic value has even been given to the frequent detachment of the cormidial segments in Calycophora as free-swimming ‘Eudoxiae’. Schneider (1896) saw in this phenomenon a recapitulation of the process by which free-swimming Siphonophores first arose from highly polymorphic sessile ancestors, while Moser (1925) regarded it as older still, a step towards the evolution of ‘true Medusae’ out of her fantastic ‘Urmedusen’ (cf. p. 117, *supra*).

It is not irrelevant to note the steps by which Schneider reached his strange conclusion:

- (i) The pneumatophore arose as a modification of the larval nectocalyx of Calycophora (*l.c.*, p. 577);

- (ii) Therefore all Physophores, including Cystonects and Chondrophores, were derived from Calycophora (p. 611);
- (iii) Phylogenetically, therefore, only the 'simply built ancestral Calycophora' need be considered ('Die übrigen sind, weil von den Calycophoren ableitbar, auszuschalten', p. 632);
- (iv) Within the Calycophora the most ancient types alone exhibit the detachment of polymorphic cormidia as Eudoxiae (p. 653);
- (v) All other Siphonophores have 'lost' this habit (*ibid.*);
- (vi) Therefore the detachment of cormidia is not a newly acquired feature, but was inherited from polyp-stock ancestors (*ibid.*)!

Needless to say the whole argument is invalidated by its basal assumption, and by the fact that the Physophorid groups which were excluded from consideration contain the very forms whose cormidia are simplest in constitution and exhibit a polymorphism no greater than that of many existing Hydroïd stocks. Schneider made no attempt to show how the independent lateral branches of the ancestral Hydroïd came to be transformed into the single metamerie series of the modern Calycophore. Let us now examine this problem.

Each tetramorphic cormidium of *Sphaeronectes*, according to Chun (1897, my Text-figs. 12–14), makes its first appearance on the stem as a single pro-bud, which subsequently divides up into its four components—bract, gonophore, tentacle, and polyp (provisionally I follow the traditional treatment of the 'tentacle' as a dactylozooid). But, as soon as the first pro-bud has arisen, it is carried backwards by elongation of the stem, and a second pro-bud arises in front of it. The same process is repeated indefinitely, and each pro-bud in turn begins to resolve itself into its heterogeneous components. A continuous succession is thus kept up, and the stages of differentiation can be followed by glancing along the series from the youngest pro-bud to the fully constituted polymorphic groups at the end of the chain (Text-figs. 12–14). The succession of developing cormidia thus resembles the stream of proglottides from a *Taenia* scolex, or the chain of buds in a *Salpa* stolon, but with this

difference, that in these cases the buds, as they leave the stolon, are all alike and share the same fate, whereas in the Calycophore each soon begins to sprout into its heterogeneous elements, first polyp and tentacle distally, then gonophore and bract at its base. It is in fact the most condensed and complicated type of budding in the animal kingdom, and implies the existence of an internal machinery of differentiation without parallel in other cases. Even in *Doliolum* the pro-buds, as they leave the stolon, appear to be all identical, and their ultimate differentiation seems to be dependent on the positions to which they are carried by their attendant phorocytes. There is no possibility of epigenesis in the formation of the cormidial buds of Calycophores.

It is true that Chun's account was disputed by Schneider, who claimed that the gonophore-bract bud arises independently of the polyp bud, but his figures of *Abyla* (1896, figs. 15 and 18) are by no means decisive, and in any case the duplicity of the gonophore bud requires explanation. To Schneider himself it was just another form of his 'bract-bell' (cf. p. 142), which in the nectosome he thought was eventually dismembered to form the pneumatophore and larval bract of *Physophorida*; but I doubt if any one else could imagine that a bract-bell, once consolidated, could freely resolve itself into its original components. Moreover the bract-bell is a sterile nectocalyx, and, however easy the transformation may be of a gonophore into a nectocalyx, there are serious obstacles against the conversion of nectocalyces into gonophores.

Nothing like this condensation of the budding process occurs in any *Physophorid*. With the exception of the siphon-tentacle pair, all the buds arise from separate rudiments wherever their origin can be followed. When the cormidial tufts are restricted to definite 'nodes' along an elongated stem, they are usually too crowded for exact determination, but in *Cystonects* which lack bracts and palpons, as well as in various 'Brachysteles', the primary independence of trophozoids and gonozoids is easily verified (cf. Haeckel, Pl. xxiv).

Moreover outside the Calycophora the restriction of buds to a single longitudinal series is not absolute. In *Forskalia* each

polyp is embraced at its base by a pair of bracts, which implies the existence of a triserial budding tract with lateral as well as median buds. The same is true of various short-stemmed Agalmids, the cormidia of which have been carefully described and figured by Bigelow (1911). In *Agalma okeni* (= Haeckel's *Crystallodes*) and *Stephanomia amphitridis* there are three or four pairs of bracts in each cormidium springing from the stem on either side of a median series of siphons, pallions, and gonozoids (cf. Text-fig. 26). In *okeni* the bases of the bracts in any one cormidium lie in the same transverse plane (l.c., xvii, 9 and 13); in *amphitridis* in a pair of oblique rows, the most dorsal bract being distal, the most proximal ventral (xviii, 2). This arrangement is explained by a section of Bedot's (1888, Pl. iv, 28) through the stem of *Agalma clausi*, in which the ventral half of the rather stout triangular stem is much less muscular than usual. The pedicels of the bracts are seen to arise from the sides of the non-muscular ventral half at various distances from the ventral edge, the most dorsal lying just within the muscular zone. They are clearly lateral buds, and appear to have been formed successively in pairs near the ventral edge, and then pushed dorsally in turn by successive increments of transverse growth. The obliquity of the rows in *amphitridis* would follow from a larger element of longitudinal growth.

The remarkable carapace which surrounds the siphosome of *Agalma 'eschscholtzii'* (= *Agalma haekeli*, Bigelow) was described and beautifully figured by Haeckel (xviii, 8) as consisting of bracts arranged in a 'continuous spiral'. In view of the admittedly close relationship of this to the foregoing group of species it is highly probable that its bracts were attached to the stem by similar segmental groups of pedicels with bilateral symmetry. The illusion of a spiral arrangement would readily result from their larger numbers, five or six pairs in each cormidium, especially if combined with an obliquity of the rows. There is no ground for regarding the stem itself as spirally twisted, except slightly upon contraction.

The course taken by the combined processes of budding and growth in Macrostelia can now be summed up. In Physophorids

the bracts, when present, are arranged in lateral pairs on either side of a median series of polyps and gonodendra. In Calyco-phores the bracts are median, one to each cormidium, so that the triserial budding of Physophorids is reduced to uniserial in Calycophores. Moreover the buds in Physophores are separate from the start, whereas in Calycophores all the buds of each cormidium arise by subdivision of a single mother- or pro-bud, in which the various bud-rudiments or determinants have been, as it were, condensed. Budding in Calycophores is therefore more concentrated and less normal than in Physophores, so that, if one has been derived from the other, it is the Calycophore method that has been derived from the Physophore, and not vice versa.

But, while this difference is a point to bear in mind, the subsequent course of events is the same in both groups. Whether uniserial or triserial, the buds of each cormidium, as soon as formed, are immediately carried downwards by a marked excess of longitudinal over horizontal growth of the body in the zone of their formation, and a new set of buds promptly arises in their place, to be carried back in the same way by the ever-lengthening and scarcely broadening body.

This surely is no primitive state of things. The frequent use of the term *stolo prolifer* in connexion with the formation of this chain of buds has been greatly misleading, for the series differs radically from a *Salpa*-chain and similar proliferations in the fact that it is the parental body that extends and carries the buds along, and not a simple series of successive constrictions from a proliferating prominence. We have to think of the lengthening process as something quite distinct from the budding process. The body lengthens and carries the buds onwards for its own needs, which are clearly to spread its fishing tentacles and mouths through as great a zone of depth as it can, in order to increase its chances of catching scattered and elusive prey.

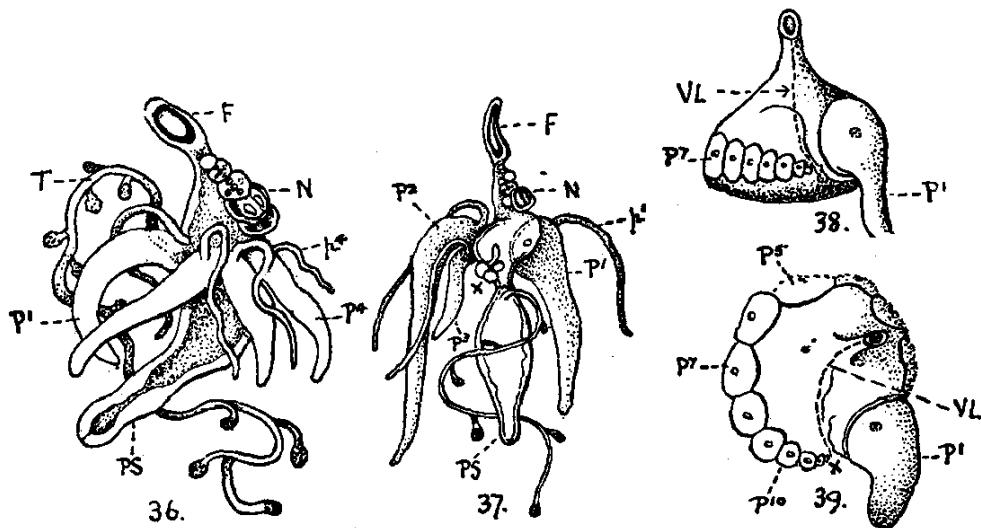
It is almost exactly the principle of long-line cod-fishing. With eight men in a boat, each lowering a separate 50-fathom line with a baited hook at every yard, the lines would soon be hopelessly entangled and the fishing ruined; but let each man lower his line in turn, after fastening it to the end of his prede-

cessor's, the result is a single free line of 400 fathoms with 800 hooks, each of which has an equal chance of catching a fish. So here the 'metameric' succession of cormidia, each attached to its predecessor, ensures more efficient fishing than 8, 16, or 24 cormidia separately suspended in a whorl round the Siphonophore body. The latter is the archaic method of the Brachystele, and of its human counterpart—good enough for shallow waters and the whiting fisherman, but with obvious limitations. If Claus and Haeckel had been fishermen instead of philosophers, they would never have dreamed that an oceanic Siphonophore would give up its Macrostele fishing-tackle for a hook-and-liner's Brachystele. Yet that is their theory, and in the next chapter we will examine it.

As an appendix to this section, to illustrate the nicety of a Siphonophore's adaptations for fishing, let me add this vignette from Claus's account (1879) of his marvellous '*Agalmopsis*' (*Lychnagalma*, Haeckel, Pl. xvi) *utricularia* from Messina. Each tentacle is buoyed up in a more or less horizontal position by a graduated series of tiny, but relatively large, floats, one beyond each battery of nematocysts (*sacculus*) in the middle of each lateral branch, and from each float no less than eight terminal stinging filaments radiate. Thus, as its discoverer relates: 'These filaments stretched out on every side (and at various levels) constitute in effect a kind of net spread all around the colony and ensuring the capture of every creature that penetrates its meshes.' How little we can understand such complicated little creatures as these until we have taken the measure of their special adaptations!

11. GROWTH AND SYMMETRY IN BRACHYSTELIA (Text-figs. 36–47).

On the current theory which we owe mainly to Claus (1860, 1878) and Haeckel (1888), the short-stemmed forms of Physophorid (Brachystelia) have been derived from long-stemmed Macrostelia (which includes all Calycophora as well as many Physophorids) by a secondary shortening and broadening of the stem. The tendency of the cormidal appendages to be disposed in whorls or a continuous spiral is attributed to a twist of the



TEXT-FIGS. 36-9.

Physophora hydrostatica. Larval and Young Colonies. *F*, float; *N*, nectocalyx; *P¹-P¹²*, palpons (or their facets) in order of formation; *PS*, protosiphon; *p*, palpacle; *T*, tentacle; *VL*, ventral line, dotted; *X*, budding point.

Fig. 36.—Larval colony with four palpons, right-dorsal aspect. (Haeckel, 1869.)

Fig. 37.—Similar stage from left-ventral aspect. (Huxley, 1859, but with the missing protosiphon and tentacle restored after Haeckel.)

Fig. 38.—Ventral, and 39, aboral view of siphosome of a later stage with twelve palpons, all removed except the first (*P¹*). The nectosome is truncated. (Based on photographs of Bigelow's, 1911.)

stem round an imaginary central axis. 'That they', says Haeckel, 'are often radially disposed depends wholly upon a secondary spiral twisting of the stem' (l.c., p. 9).

This theory of a twisted stem was originally held to apply to the nectosome of *Macrostelia* as well as to the siphosome of *Brachystelia*, until Chun showed that in well-preserved Agalmids and *Physophora* the stem bearing the swimming bells is perfectly straight, and that their biserial arrangement is produced by the bells bending alternately to right and left from their anchorage in the mid-ventral line (1898, p. 324, figs. 1-3). Even the great tiara of *Forskalia* is built up in this way.

The similar-looking swimming column of the Calycophore *Hippopodius* seems at first sight to be an exception to this rule, since its nectocalyces are demonstrably arranged upon a spiral axis (Haeckel, l.c., Pl. xxix). But this axis is not a part of the original stem, since, as was shown earlier, the whole of the aboral region atrophies. Here each new bell arises on the foot-stalk of its predecessor, and the series of out-growing stalks constitutes the spiral axis or 'Schein stamm', as Chun called it (1896 b, fig. 11). Lacking a float to keep it upright, this composite bell-stalk bends completely over from the weight of its pendent nectocalyces, and twines round the siphosome for support—a peculiarity which points strongly to the conclusion that the absence of a pneumatophore in Calycophora is a case of secondary loss, not of primitive simplicity. In *Physophores* the budding point moves upwards with the growth of the stalk of the pneumatophore; in Calycophores the nectocalyces are recruited from below.

But a true exception to the rule is provided by the Brachystele Rhodaliidae ('Auronectae', Haeckel), in which the nectocalyces, instead of mounting above one another along the stem of the pneumatophore, range themselves round its base to form a corona. As they all arise from the ventral budding tract, and the corona is interrupted dorsally by the aurophore (Haeckel, Pl. iv, 16; Bigelow, xxiii, 6 and 7), it is clear that new nectocalyces join the corona from each side of the ventral line, and that the diameter of the stem is increased pari-passu. Here at

any rate the corona is no product of a spiral twist of the stem, but of symmetrical bilateral budding and transverse growth of the body wall from the ventral line, the oldest bells being dorsal, the youngest ventral. If the same method of growth applied to the whole body, the cormidial buds below would also be arranged in parallel coronas of gonodendra and siphons. Actually they are arranged in a continuous dextro-tropic (clockwise) spiral, (Haeckel, fig. 17; Bigelow, xxiii, 11), the formation of which can best be studied in *Physophora* and *Discolabe*.

In *Physophora* (also *Discolabe*, Haeckel, Pl. xix-xx) the normal type of nectosome is combined with an asymmetrical reniform siphosome, which bears a single, or an imperfectly double, whorl of tentaculate palpons around its margin and, below this, two parallel whorls of gonodendra and siphons. The siphosome has been regarded as an inflated spirally twisted stem. The best case for this view was presented by Claus (1860, 1878) and illustrated by exact figures of two specimens from above and below. 'Der sack-förmige Polypenstock', he says, 'auf einen einfachen in Centrum verwachsenen Spiralbogen zurückzuführen ist.' The siphosome in his quaint first drawing (1860) has the outlines of a flounced crinoline split on the ventral side by a furrow (Claus's 'Naht') which contains the budding line on its right edge. Each flounce corresponds to a cormidium, consisting typically of a palpon above, a gonodendron below it, and a siphon lowest of all. He compares the regular succession of these trimorphic groups with that on a Diphyid stem. 'Assume', says Claus, 'a severely shortened and greatly widened stem, on which the groups of appendages are closely squeezed against one another, then the similar types of appendage will arrange themselves in rows, each forming its own circle.'

Claus ignored the fact that the appendages of a Calycophore arise as a single longitudinal series: bract, gonophore, tentacle, polyp; bract, gonophore, tentacle, polyp, &c. The spiral winding of such a uniserial stem, after suppression of its internodes, would merely change its direction from longitudinal to horizontal. No amount of 'squeezing' would transform its single polymorphic series into homogeneous parallel coronas as we see

them in a *Physophora*, 'each type forming its own circle'. Moreover the theory is at variance with the actual mode of development.

In the first stage the larva is monogastric, with no secondary siphons or gonodendra. It floats by its pneumatophore, its nectocalyces are developing but not yet functional, and its first palpons develop one after another to form the first corona. Haeckel (1869) reared *Physophora* from the egg to this stage, saw the first palpon arise on the ventral side, and move sideways to the right; and saw a second, third, and fourth palpon arise one after the other in the same place, each pushing its predecessor farther up the right side until the oldest reached the dorsum and protruded through the median dorsal cleft of the provisional larval bract (l.c., figs. 21 and 23). At this stage his oldest larvae died, each possessing a half-ring of palpons on its right side, and none on its left. He laid stress on the fact that the larval tentacle, arising as usual in the ventral line, remained in that position, while the palpons moved successively away from it. It is remarkable that no larva of *Physophora* with a complete ring of palpons has yet been found. Haeckel fished one from the sea which was almost identical with the oldest specimen he reared (Text-figs. 24 and 25), and the larva figured by Huxley was in the same stage of development, completely destitute of palpons on the left side. His drawing (1859, Pl. viii, 2), from the bare side, is the only one yet published which shows the condition of the stem. The siphon and its tentacle had clearly broken off during capture (a frequent experience with these sensitive creatures—see Sars, 1877), and Huxley's figure shows the jagged line of fracture. In my copy (Text-fig. 37) I have restored them from Haeckel's data, placing the tentacle on the ventral side of the siphon near its base.

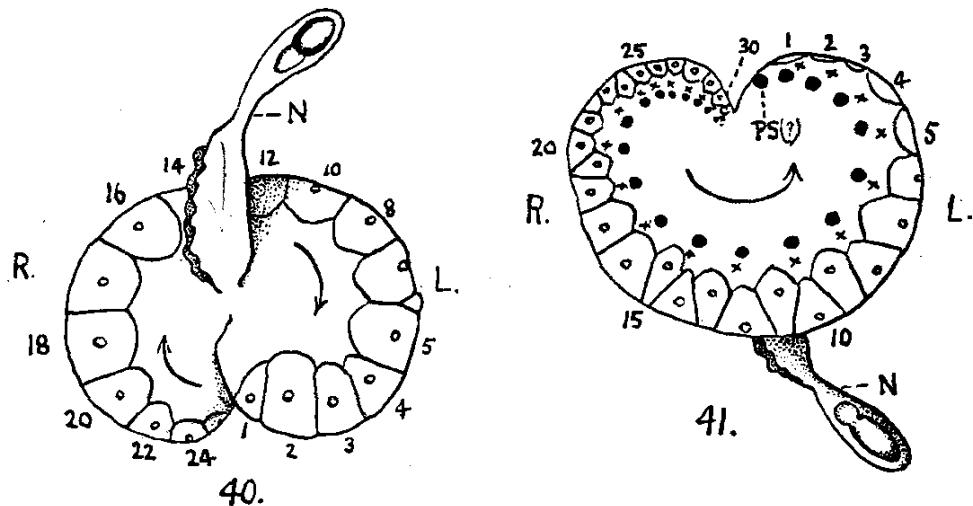
It will be seen that the stem of the siphosome retains its vertical position, but is dilated in the zone of the palpons, and tapered below to form the neck from which the protosiphon is suspended. If the stem as a whole had been 'twisted', the tentacle base would now be out of sight. It is asymmetrically bent above towards the dorsal side, which now

carries the first and stoutest palpon, but this is just what would follow from a predominant growth of the right side simultaneously with the proliferation of the palpons. A continuance of the same onesided process of proliferation and growth would bring the dorsal palpon round to the left side, and ultimately into close proximity to the ventral starting point.

In a later stage photographed by Bigelow (1911, Pl. xvi, my Text-figs. 38 and 39) from the 'Albatross' collection, the stem has fully attained its discoidal character and is surrounded by an equatorial ring of some 10–12 palpons, which increase regularly in size in dextral sequence from the budding zone. Secondary siphons and gonodendra have arisen beneath the ring of palpons, but their exact number and relations were not described.

To this stage, however, some of Kölliker's young colonies clearly belong. Their sizes ranged from $\frac{1}{2}$ in. to $2\frac{1}{2}$ in. in length, exclusive of their long tentacles. They possessed a 'full crown' of seven to ten palpons, mostly eight or nine, and two to five siphons on the underside of the conical siphosome. His figure (1853, Tab. v, 1) shows nine palpons and three siphons. Immature gonodendra were observed clearly in the larger specimens. Whether the protosiphon persists or not is left uncertain, but these data are sufficient to show that the larval whorl probably includes at least six palpons, possibly one or two more, before the secondary siphons and gonodendra begin to appear.

The final stage described and figured by Claus (1878) and Sars (1877) is that described at the head of this section—an asymmetrical reniform disc, fringed around its convex margin by parallel horseshoe-shaped cycles of palpons above, siphons below, and gonodendra between the two, all of them interrupted by the ventral groove, which now clearly divides the disc into prominent right and left lobes. The right (nascent) lobe begins ventrally with a crowded line of young buds curved around its apex; the left (senescent) lobe ends opposite this apex in a blunt prominence carrying the oldest palpon. The upper surface of this lobe is definitely higher than that of the right lobe (Sars, l.c., figs. 1–4; Claus, fig. 3), a circumstance which explains a striking feature in Gegenbaur's excellent figure of a living colony (1860; Taf 30, fig. 32), in which the oldest palpon is seen to end



TEXT-FIGS. 40 AND 41.

Physophora hydrostatica. Siphosome of adult colony after removal of all appendages (after Claus, 1878, simplified). *N*, nectosome with float; *p* (1-31), palpon-facets numbered by age; *PS*, proto-siphon (?); *R*, right; *L*, left. Arrows show the one-sided direction of growth (dextral) from ventral line. Siphons ●●; Gono-dendra ××

Fig. 40.—Upper surface, showing marginal series of palpon-facets. The youngest (*P* 27-31), and those of a lower series, are invisible from above.

Fig. 41.—Lower surface, diagrammatically extended to show the full series, as well as the points from which the siphons and gono-dendra arise.

the series abruptly at a higher level than the younger palpons in the whorl. The earlier development of this feature has been traced above from Huxley and Bigelow's figures (my Text-figs. 36-9).

Neither in Claus's nor in Sars's figures is there any indication of any further extension of the coil than this. In other words, the buds of a *Physophora* colony form three parallel, ever-widening, but uncompleted rings, one above the other, the ends of which in each case approach one another, but never meet. Proliferation and growth broaden each ring, and bulge it on either side to a reniform shape, but the distal (oldest) end is not produced into a spire.

Although the cycles of gonodendra and siphons run parallel courses around the discoidal stem below the palpons, there is a numerical peculiarity to be noted as regards the palpon cycle, to which both Claus and Sars have already drawn attention, but which Haeckel dismissed as an 'accident' (p. 258). In the more regular of the two prepared specimens which Claus figured (figs. 3 and 4; my Text-figs. 40-1) the palpons, as marked by their facets of articulation, form a single marginal row round the greater part of the left (senescent) lobe, but a double row round the whole of the right (nascent) lobe, except close to the budding centre. Sars also figures a double row in the same lobe (l.c., Tab. V, figs 1-6), without defining its extent. In each case the extra row consists of small triangular facets on the lower side of the large pentagonal marginals, and alternating with them. The upper row of the right lobe is continuous with the single row in the left lobe. Siphons and gonodendra are present in equal numbers, about twenty of each, but the total number of palpons is about thirty, of which rather more than half (actually seventeen) form the marginal series of large facets. In the densely crowded initial part of the sequence next the budding zone, the siphons and palpons appear to be equal in number, so that their numerical disparity in the disc, for which no explanation has yet been given, is probably not due to any inequality in their rates of proliferation. It should be noted, therefore, that the difference (about eight to ten, but exact numbers cannot be given) corresponds closely with the number of palpons in the

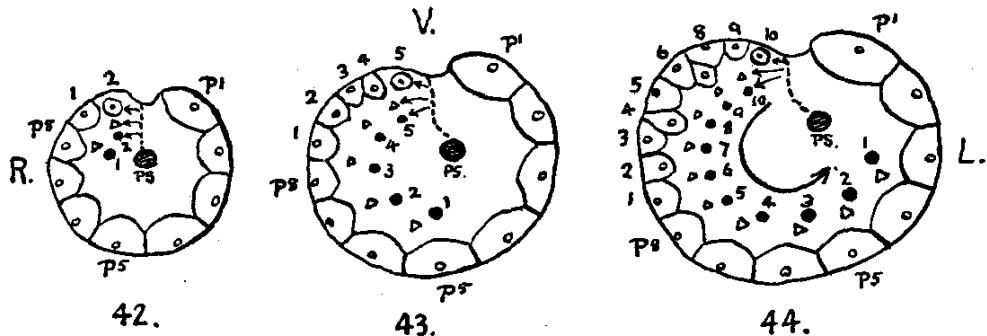
larval whorl which, as shown above, is probably completed before the appearance of gonodendra and siphons. As all additions are made from the ventral line, an important conclusion follows. When the larval circlet of palpons has been completed, the under surface of the disc must be free of all appendages except the protosiphon, which has been pushed to the left by the preponderant growth of the right side. Consequently the trimorphic groups ('cormidia'), which then begin to appear, will not have equal freedom of movement for their members. The gonodendra and secondary siphons, as they leave the budding zone, will have an open space before them, but their palpons, following those of the larva around the margin, will find their line of advance already occupied by their predecessors. Thus the one-sided dextral growth which accompanies their proliferation carries the gonodendra and siphons freely into unoccupied territory, while their palpons, pressing in single file against the rear of their predecessors in the right (nascent) lobe, are squeezed, as they grow, into a zigzag double series round the margin (Text-figs. 42-4). The variability of their arrangement described by Claus is doubtless due to different degrees of pressure in different individuals, consequent upon inequalities of nutrition and growth.

In any case it will be seen that Haeckel's statement that the cormidia of Physophoridae preserve a 'perfectly ordinate' character is incorrect. The gonodendra and siphons certainly keep and move together, but, in their rotation round the disc, the earlier pairs of these must gradually push past the palpons which were budded with them, and, on entering the empty region of the left lobe, must eventually come into a new alignment with the larval palpons already present around its border. Thus the arrangement of appendages in the siphosome of *Physophora* is not the result of the spiral twist of an ordinate Macrostele stem, but of one-sided (dextral) proliferation and growth from three successive zones of the budding line. According to Haeckel the peripheral margin of the disc, to which the cormidia are attached, is the ventral median line of the twisted stem (p. 265). On the contrary, the cormidial line is drawn by the succession of larval palpons at right angles to the stem, as a horizontal ring around it, the stem itself remaining

straight and untwisted. Gonodendra and siphons follow, tracing two more lines parallel with the first. Therefore the whole three-fold cormidial sequence is at right angles to the stem, not parallel with it.

Some new questions arise when we pass from the more familiar *Physophora* to Haeckel's '*Discolabe quadrigata*' from the Indian Ocean, which competent authorities have regarded as generically, and even specifically, identical with the almost ubiquitous *Physophora hydrostatica* (Schneider, 1898, p. 126; Bigelow, 1911, p. 292). If these identifications could be accepted, *quadrigata* would furnish an additional or fourth stage in this summary of *Physophora* development, for the cormidial coil, which forms a single ring in *Physophora*, is produced in *Discolabe* into a typical two-whorled spire beautifully drawn by Haeckel (Pl. xx, fig. 12). But neither Haeckel nor his successors noticed that this spire has a sinistral (counter-clockwise) coil, instead of the dextral (clockwise) coil that has characterized every *Physophora* hitherto described, adult or larval. The astonishing thing is that in his text Haeckel referred explicitly to 'figs. 9–13' on this plate for confirmation of his statement that 'the spiral turning in the siphosome of all *Discolabidae* (= *Physophoridae*) seems to be dexiotropic' (p. 258). Yet of these five figures all but one (fig. 13) show sinistral ('laeotropic') coils! (This is but one of many similar lapses from accuracy which disfigure Haeckel's 'Challenger' Report when he deals with matters of Right and Left, Dorsal and Ventral, Dexiotropic and Laeotropic. They are in part, if not always, traceable to the 'promorphological' orientation of Siphonophores which he set up in his youth (1869) and continued in his 'Challenger' Report, with the mouth above, and the aboral extremity below, thereby turning the natural Right into Left, and Left into Right, in complete disharmony with his illustrations, which are always the right way up. In these the artist was wiser than the philosopher.)

The single dextral specimen represented in Haeckel's fig. 13 was a small colony, so similar to Bigelow's photograph copied in my Text-figure that I have no hesitation in claiming it as a representative of the same species, *Physophora hydro-*



TEXT-FIGS. 42-4.

Physophora hydrostatica. Oral surface of denuded siphosome in successive stages of unilateral (dextral) growth and cormidial proliferation. Ventral side (*V*) uppermost. (Original diagram.) Young palpon, \odot . Gonodendra, $\triangle\triangle\triangle$. Siphons, $\bullet\bullet\bullet$. Ventral Line in hilum of reniform disc, - - -.

Fig. 42.—Early post-larval colony with two cormidia (1, 2). Larval palpons (*P* 1-8) already surround the disc. They are recruited by the cormidial palpons, while the siphons and gonodendra at a lower level are carried past them.

Fig. 43.—Stage with five cormidia (1-5). Increased pressure on the marginal palpon-facets. The siphons and gonodendra continue to advance.

Fig. 44.—Stage with ten cormidia (1-10). The cormidial palpons round the margin are squeezed into a double row. Their siphons and gonodendra nearly surround the disc. The protosiphon (*PS*), displaced to the left by the preponderant growth of the right side, will soon head the procession of siphons in the left (senescent) lobe (cf. fig. 41).

statica. It would appear that Haeckel mixed up two distinct species in his account of *Discolabe quadrigata*—a true *Physophora* with dextral coil (fig. 13) and a new form with counter-clockwise spire, to which the name *Discolabe quadrigata* may be provisionally restricted (figs. 9–12). Possibly the ‘*Dicymba*-like’ young colony from the South Atlantic, represented in Haeckel’s Pl. xix, fig. 8, which also shows a sinistral sequence of palpons, may be an early stage of this type.¹ Following Haeckel’s account in other respects, the revived genus may be distinguished by its quadri-serial nectosome, its sinistral siphosome terminating below in a true spire, and by its single series of marginal palpons and their facets.

The extension of the *Physophora* ring into a continuous spire involves no change in its theoretical interpretation, and but minor changes in the form of the colonial body. Upon reference to Haeckel’s Pl. xx it will be seen that in the sinistral *Discolabe* (figs. 9–12) the nascent line of palpon facets is visible almost to its origin, whereas in the dextral *Physophora* (fig. 13; also Claus, 1878, iii, 3, &c.) it is completely hidden within the deep groove of the disc by the overhanging senescent lobe. In other words the ‘senescent’ lobe, which is on the Left side and elevated in *Physophora*, is on the Right side and depressed in *Discolabe*, thus enabling the older palpons to turn the corner of the lobe and move inwards on its lower face, where the spire is continued (figs. 10 and 12). The reduction of growth-pressure on the marginal row of palpon facets, which must result from this extension, probably explains the simplicity of the series in *Discolabe*, as compared with the tendency towards duplication proximally in *Physophora*. Incidentally Haeckel pointed out that the appendages of the inner coil are older than those of the outer, and gradually

¹ The other larvae on this plate (figs. 5–7) are apparently touched up copies of the author’s original figures of *Physophora* (1869, figs. 15, 20, 22, and 23) and of very doubtful validity. The statements about them on p. 261 flatly contradict his original statements as to ‘ventral tentacle’ and ‘dorsal cleft’ without any explanation. Lacking corroboration, both should be ignored.

diminish in size. This means that they undergo degeneration, with the loss of their articulating facets, as they turn the ventral corner of the senescent lobe (Text-fig. 45).

A third type of Brachystele is seen in *Anthophysa*, already referred to as a connecting link between Cystonects and Physonects in the structure of its huge float which, with its pericystic outgrowths, entirely fills the stem (Text-fig. 45). This is a stout conical vesicle gradually expanding below into a boat-shaped disc with its long axis dorso-ventral. An extension of the ventral region forms the actual floor of the disc, from which a median row of siphons depends, the most dorsal of which is doubtless the original protosiphon. In all these features *Anthophysa* shows significant resemblances to *Physalia*. Above, however, below the apex of the pneumatophore, it is surrounded by a great corona of paddling bracts, supported at the ends of a series of muscular ridges which radiate, with varying degrees of obliquity, from the ventral budding cone of the nectosome. Below the bracts is a second oval corona of much less numerous hermaphrodite gonodendra. Large numbers of small non-tentaculate palpons accompany the gonodendra, and also extend across the floor of the disc in groups that alternate with the siphons (Bigelow, 1911, xxiii, 5). The ventral line above the youngest siphon is marked by a crowded series of young cornidial buds, five or six abreast (Haeckel, Pl. xi, 9).

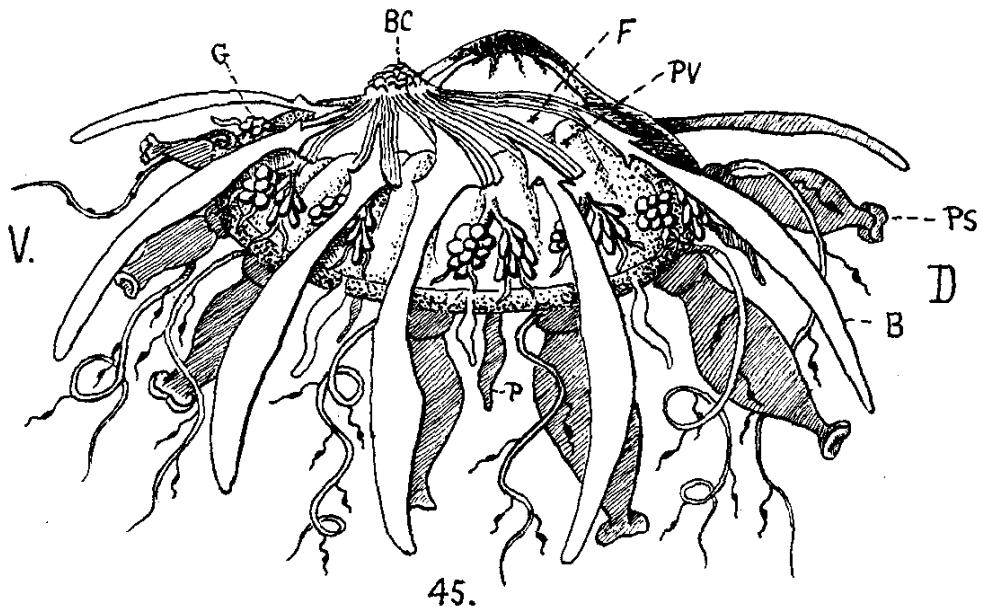
The corona of bracts arches over the whole colony, as in its close ally *Athorybia*. The ridges which bear them are muscular folds of ectoderm and mesogloea, each traversed by a fine canal of endoderm continuous with that of the bract (Bedot, 1904, i, 13–15; Bigelow, 1911, xx, 7 and xxiii, 3). The course of this canal has not been described, but from Bigelow's figure it would seem to run directly into the body through the distal part of the ridge. The uppermost ridges are longest, and extend towards the dorsum, the middle ridges run to the flanks, and the lowest and shortest, which are of course the youngest, support the ventral bracts (Haeckel, xii, 7–9). They are arranged in bands of four to six or more, separated by bare intervals, and the number of bands corresponds with that of the gonodendra below them. The bracts accordingly are four to six times as numerous

as the bands and the gonodendra, and these on each side correspond in number with the secondary siphons.

From this equality in their numbers the bands (or groups of bracts), the gonodendra, and the secondary siphons might be expected to form the same number of parallel, vertical series, and this alignment is actually shown by the younger zooids of each type, i.e. those nearest the budding line; but further dorsally the siphons lag behind this alignment, probably because of the protosiphon in front of them, and come to alternate with the others, their place being taken by the alternating groups of palpons (Bigelow, xxiii, 5; my Text-fig. 45). Apart from this minor dislocation the co-ordination of the appendages of nectosome and siphosome is the more remarkable as the buds are derived from at least two different centres of proliferation. It implies the existence of a common factor of co-ordination, which we shall show to be contained in the common mode of growth.

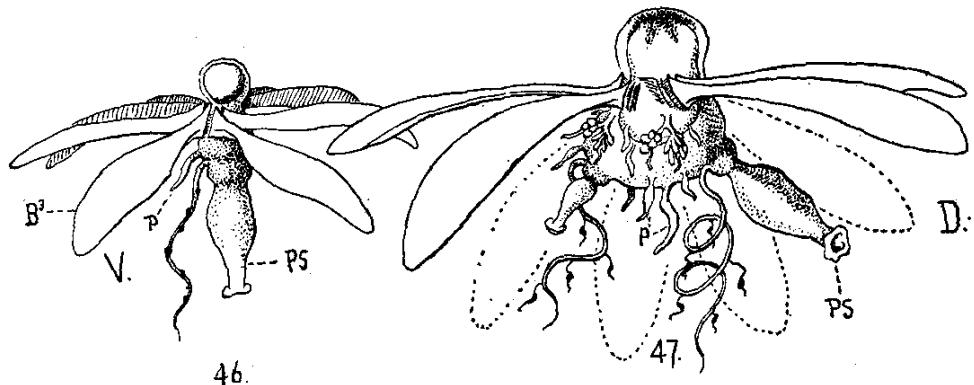
Haeckel misunderstood the distribution of the palpons, thinking that they formed a separate corona between the bracts and the gonodendra—a mistake which Bigelow corrected. He also likened the cormidial composition ‘to that of *Physophora* and the other *Discolabidae*, the cormidia being ordinate and arranged symmetrically in a flat spiral line which is twisted around the flat and broad base of the shortened vesicular stem’. The symmetry is clear, but the cormidia (following Bigelow’s elucidation) are not ordinate, but ‘dissolved’; the gonodendra form a ring, not a spire; and the straight line of the siphons (which Haeckel himself noted) neither accompanies the ring nor is ‘twisted’ round the stem. Surely *Anthophysa* is no type to be invoked in support of the theory of a twisted stem.

The explanation here submitted is essentially the same as that applied above to the case of *Physophora*, but simpler because of the complete bilateral symmetry of *Anthophysa*. The corona of bracts is obviously produced by bilateral proliferation and growth from the ventral line, the ectodermal ridges leaving a persistent record of the direction of their growth after each proliferation. Taking for example a case in which each band of bracts includes four ridges, the first or larval stage will be



TEXT-FIG. 45.

Anthophysa formosa. A large colony schematically represented from left side. (Based on Bigelow, 1911, but with omission of numerous palpons between and below the gonodendra, reduction of bracts to one from each band, and relative reduction in size of all siphons and palpons. Original.) *B*, bracts; *BC*, budding cone of bracts ('anterior blastocrene'); *F*, float; *G*, gonodendra (hermaphrodite); *P*, palpons; *PS*, protosiphon; *PV*, pericystic villi and septa; *D*, dorsal; *V*, ventral.



TEXT-FIGS. 46 AND 47.

Anthophysa formosa. Hypothetical larva and young colony to show the probable course of development by successive increments of ventral proliferation and ventro-lateral growth. Lettering as in fig. 45.

Fig. 46.—Larva as in *Athorybia*: four pairs of paddling bracts attached ventro-laterally. Protosiphon only, followed by the first median palpon.

Fig. 47.—Next stage with a cormidial siphon ventrally, in line with the protosiphon dorsally, two pairs of lateral gonodendra midway, and two pairs of bract-bands (each with four bracts) over the enlarging float, together with many palpons.

marked by the development of four bracts on each side (Text-figs. 46-7). An interval of growth follows, predominantly from the ventral side, and the basal ridges are extended centripetally (towards the 'cone'), thereby increasing the muscularity of the bracts. Then a new batch of bracts is proliferated on the ventral side of the first, and alternating processes of proliferation and growth are repeated, each new period adding an additional band and four more bracts to the corona on each side.

Simultaneously with these processes in the nectosome, after the first or larval stage, the cormidial centre proliferates a lateral pair of gonodendra and a median siphon, followed by an interval of growth, which carries all three appendages dorsally—the gonodendra laterally and the siphon obliquely backwards. During this period an indefinite number of palpons¹ is produced on either side, and these, according to the growth gradient in which they occur, are carried away, some more or less transversely, others backwards, either obliquely or in the middle line after the last-formed siphon.

Thus every zooid of each class, cormidial and locomotive, arises as a separate bud from the ventral tract, and takes part in a general concerted movement towards the dorsum with complete bilateral symmetry—bracts above, gonodendra and siphons, intermixed with palpons, below. The effect of the combined processes of ventral budding and lateral ventro-dorsal growth of the body-wall is to bring about a zonary distribution of the different kinds of zooid almost identical with that of a *Velella* or *Porpita* colony, but with bracts in place of tentacles above, gonopalpons (= 'blastostyles') with their gonophores in the middle, and siphons below—nectocalyces being absent in both cases. *Anthophysa* is thus almost unique among Siphonanthae, both in the completeness of its bilateral symmetry and in the extent to which it rebuilds a radial arrange-

¹ Bigelow states that 'New ones in various stages of growth are to be seen in various regions' (l.c., p. 298), and in *Dromalia* attributes the formation of whole cormidia to the presence of secondary buds near the bases of siphons far from the ventral line (p. 308). Such exceptions to the 'law' of Siphonanth budding would be of first-class importance if fully substantiated.

ment of its zooids—in both respects recalling the Corymorphine *Branchiocerianthus*.

But, although I cannot demonstrate it, the real climax of this series will probably be found in the rare Cystonect ***Epibulia***, described and figured in Haeckel's 'Monograph' (1888, Pl. xxii). The trunk of the siphosome is described as 'short, wide, and bag-shaped', and the 'ventral line' of appendages as 'circular or rather spiral'. But Haeckel admits that he was 'unable to examine closely the form of the central trunk and the attachment of the cormidia', and adds that it is 'probably similar to that of the Anthophysidae, Discolabidae and Nectalidae'. 'All I could observe', he says, 'was that it represented a shortly conical or ovate bladder, coiled up in a spiral, with a single dextrotropic turning.' This is essentially the same description as he gave of the siphosome of *Physophora*, so that a similar explanation of it is to be expected. But there are some differences.

On Plate xxii he figures various larval stages attributed to '*Cystalia*', which is now generally regarded as merely the young monogastric stage of *Epibulia*. In fig. 4 a larva is drawn from the right side to which a 'corona of buds (palpons)' is attributed. The half-corona of six palpons shown reveals a steady increase in the size of the palpons from venter to dorsum, and the other half doubtless showed the same sequence. If the whole corona were the product of a one-sided proliferation, as in *Physophora*, some of the larger palpons of the left side would undoubtedly have been visible near the base of the ventral tentacle. It is, therefore, probable that the whole corona is formed by a symmetrical proliferation on both sides as in *Anthophysa*. This inference is confirmed by the structure of the later stages (figs. 5 and 6), in both of which a crowd of young buds is drawn on the ventral side, and the largest palpons are seen laterally and dorsally, with obvious bilateral symmetry. Similarly, there can have been no kink or hilum in the 'ovate bladder' bearing these appendages, as there is in *Physophora*, or Haeckel would have noticed it, and would not have described the 'ventral line' as 'circular'.

The inference is accordingly that the cormidal buds, as well

as the palpons, are proliferated equally on both sides of the true ventral line, and, by their movement dorsally at right angles to this line, form bilaterally symmetrical rings, as do the nectocalyces of *Rhodalia* and the bracts and gonodendra of *Anthophysa*. It is thus possible, even probable, that *Epibulia* possesses a complete biradial symmetry, which differs from that of *Anthophysa* in having a basal ring of siphons around the protosiphon like the peristomial ring of secondary polyps ('blastostyles') of *Disconantha*.

Whether this be so or not, I cannot but think that a perfect biradial symmetry is the primitive condition of Siphonanths, and that all the other conditions which in various degrees have seemed to be leading up to it, are in reality so many deviations or declinations from it. In the case of *Anthophysa*, for example, there is a manifest peculiarity in its obliquely extended float amply sufficient to account for the mid-ventral multiplication of its siphons. In effect the colony floats like a *Physalia*, with its ventral side largely horizontal instead of vertical, and the proliferation of its siphons has been affected accordingly. *Epibulia* on the other hand retains the primitive vertical orientation, conducive to radial symmetry; but a symmetry progressively built up, by proliferation and growth from the ventral line, exactly as in *Branchiocerianthus* (fig. 48).

As cited above, Haeckel also included **Nectalia** among his Brachysteles with a spiral corm, but from lack of exact data this can be neither confirmed nor denied. Its outstanding feature, however, is the unique differentiation and symmetry of its bracts. These are few (eight) in number, of three different sizes, and arranged around the body with a quasi-cruciform symmetry. They constitute a corona which is 'raised and subhorizontally expanded in the quietly floating corm, whilst they form a closed bilaterally compressed calyx in the rapidly swimming animal' (p. 250). There is a pair of short leaf-shaped bracts in the plane of the nectocalyces (i.e. right and left of the budding line), a pair of long sword-like bracts at right angles (i.e. dorsal and ventral), and a quartet of intermediate-sized bracts interradially placed between the four perradials.

(Haeckel wrote before Chun (1898 b) had shown that the pairs

of nectocalyces in a biserial column were not dorsal and ventral, as was then generally believed, but right and left (cf. p. 157), so that the terms 'sagittal' and 'frontal' in his account need correction. The 'lateral compression' he speaks of is really a compression in the sagittal plane, which bears the long bracts, while the short ones are right and left, at the ends of the longer axis, i.e. the colony is broader from side to side than from front to back.)

It will be realized that an appendage in the middorsal line looks like a breach of the law of ventral budding, which is even aggravated by the bract being a member of a diagonal pair in the sagittal plane. Yet precisely the same relations of the four perradials were observed by Bigelow (1911) in a younger colony of the same species, the only other specimen which has been adequately described. These relations must therefore be accepted as described.

Haeckel's description of the siphosome is almost identical with that he gave of *Physophora*: 'the trunk of the siphosome is shortened, vesicular, and horizontally expanded in form of a spiral bladder' (p. 260). For the *Discolabidae* it was: 'vesicular, much shortened and inflated, and coiled up spirally in a subhorizontal direction . . . as in the *Nectalidae*' (p. 258). He adds a significant contrast with the condition in the *Agalmidae*: 'The trunk of the latter (i.e. *Discolabidae* and *Nectalidae*) possesses therefore permanently about the same shape which the trunk of the former (i.e. *Agalmidae*) exhibits only in the state of the strongest contraction' (p. 258). On the other hand he gives a separate figure (xiii, 3) of 'the trunk alone after detachment of the appendages', and draws it as an upright spindle-shaped vesicle bearing a straight vertical series of some fifteen to sixteen 'buds of siphons and palpons' along the ventral line! No conflict could be greater, and the labelling of his drawing of the full contracted colony (fig. 2) prohibits any sure interpretation which would reconcile one figure with the other. In fig. 2 the nectosome is seen to be contracted with a dextral twist above a sinistrally twisted coil bearing vertical stripes. This might well be his 'spiral bladder' if he had not marked the stripes 'nb', which means 'nectocalyx buds', which they cannot possibly have been! No bract attachments are marked as such in either figure.

Schneider (1898, p. 124), convinced of the systematic affinities of *Nectalia* with Agalmidae by various details of structure, cut the Gordian tangle by throwing over Haeckel's words and pinning his solution to the very dubious fig. 3, which, for my part, I imagine must have been not the drawing of an actual preparation, but a diagrammatic sketch of what Haeckel thought the sinistral coil of fig. 2 would look like if 'untwisted'. Schneider interpreted the apparent whorls of bracts, palpons and siphons as a superficial consequence of the spiral twisting of an Agalmid stem, shorter and more inflated than usual, exactly as his master Claus had interpreted the structure of *Physophora* forty years before, except that Schneider assumed the stem of *Nectalia* to retain its Agalmid flexibility and to display the whorled appearance of its appendages only on contraction.

Schneider's theory, though favourably regarded by Bigelow on systematic grounds, raises more puzzles than it solves. The development of the bracts in diagonal pairs recalls the arrangement described above (p. 153) in the case of *Agalma okeni*, &c.; and the marvellous carapace of Haeckel's *Agalma 'eschscholtzii'* shows what can be accomplished by cormidial bracts suitably fixed. If it were possible to eliminate all the lower bracts of that species, and to differentiate the topmost series by contrasts of size on a radiate plan, *Nectalia* might be its next of kin. But Bigelow's specimen vetoes any such ideas.

As we have seen, the process of budding and growth in *Macrosteles* carries the cormidia downwards as fast as they are produced, and the newest cormidia are those at the top of the series. Haeckel's specimen of *Nectalia* possessed eight bracts and four siphons. Bigelow's young colony possessed only two siphons, yet it displayed the four perradial bracts in the same form and in the same positions as in Haeckel's older specimen possessing two additional cormidia, and the four new bracts in Haeckel's specimen were small and undifferentiated. Clearly the four perradial bracts in a young colony like Bigelow's are not carried downwards with an increasing number of cormidia as they should be upon Schneider's Agalmid hypothesis. In other words the bracts of *Nectalia* are precormidial in position, and

presumably homologous with the bracts of the nectosome of *Athorybia* and *Anthophysa*.

As regards their symmetry, Bigelow shows that the small pair are situated in line with the nectocalyces and above the level of the blastocrene of siphons, and that both pairs are supported by the usual muscular pedicels. It is therefore probable that the cruciate symmetry shown by the bracts is explicable in the same way as the cruciate symmetry of nectocalyces in a quadriserial nectosome, of which both the Physophoridae and Nectalidae furnish examples (*Discolabe* and the *Sphyrophysa* of Agassiz), viz. by adaptive bendings of their pedicels from the ventral budding line. Fixed in this way, and not subject to the perpetual shift backwards of cormidial bracts, their differentiation presents no special difficulties. Haeckel's lively account of the marvellous swimming powers of *Nectalia*, and its skill in avoiding obstacles, renders it probable that the long bracts, which he compared to 'lee-boards' in a sailing boat (mistranslated as 'swords', p. 254), may be a sensitive mechanism adaptive to that end.

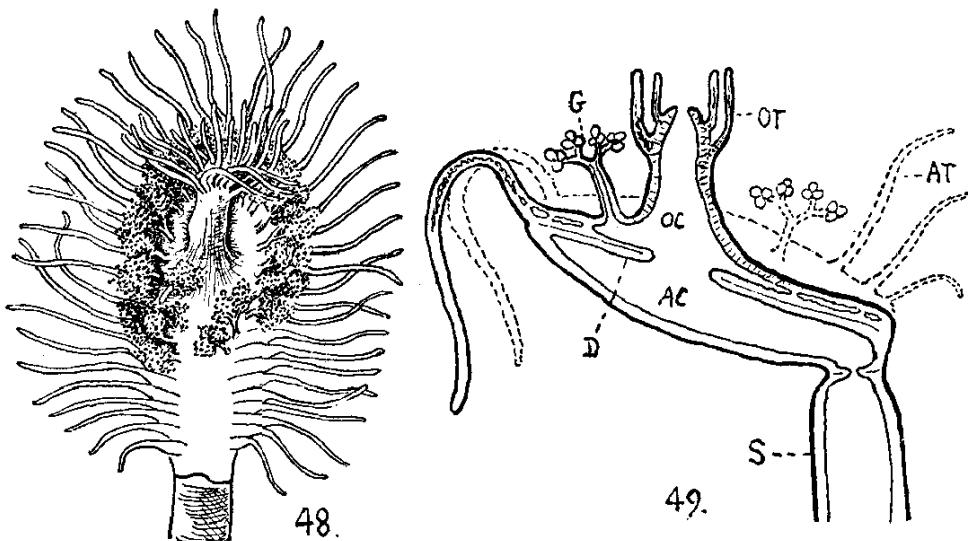
Bigelow's specimen, in spite of his careful study, was too small, and its small appendages were too crowded, to throw light on the problem of the siphosome; but indirectly, by helping to clear up the nature of the bracts, it has shown that in all probability the siphosome will ultimately prove explicable on the same lines as those of *Physophora* and *Anthophysa*.

12. GENERAL CONCLUSIONS (Text-figs. 48-57).

The advantage of an occasional stock-taking of our knowledge lies in the fact that, in addition to clearing the shelves of dusty relics, it serves to define the nature and extent of the gaps, so that efforts can be made deliberately to fill them up. The history of Siphonophores, necessarily proceeding piecemeal, and often based on scanty or ill-preserved material, has been rich in hasty theories, doctrines, and generalizations, but these have been adequately dealt with in my earlier chapters (§§ 1, 2, 5, 10, and 11). Here I will sum up the more general results of my survey, referring to particular chapters for explanatory matter and details of evidence.

Relations have been established between Siphonophora and Anthomedusae which are certainly closer, and probably firmer, than any previously advanced. Woltereck's larva of *Velella* (§ 5) contained evidence (in its mesogastric septum and subsequent aboral plexus) of an intimate relationship of Disconanthae with the Corymorphine group of Gymnoblastic Hydroids, and incidentally reveals *Pelagohydra* as something very near the ancestral stock—a pioneering effort of that stock to achieve a free-floating existence. But *Corymorpha* and *Pelagohydra* are non-colonial monogastric forms, and presumably only side twigs of the sessile colonial stock that gave rise to Siphonophora, while *Tubularia*, apparently their closest colonial relative to-day, is in several respects too specialized to illustrate adequately its original characters. On this I will add some remarks farther on (p. 187).

On the other hand, the gap between Disconanths and Siphonanths, which Schneider admitted to be 'himmelweit', has been materially reduced, negatively by removing the grounds on which the Calycophora have so long been regarded as primitive, and positively by showing the assimilation of the Brachystele group to *Corymorpha*'s next-of-kin, *Branchiocerianthus* (Text-figs. 48–9), owing to their common bilateral mode of growth from one side. This assimilation means that the short-stemmed Siphonanths, with their buds arranged in whorls over the sides of the body, are more primitive than the long-stemmed forms, in which the buds form a single ventral series along a greatly attenuated stem. The different symmetries of Disconanth and Siphonanth are thus no longer prohibitive of close relationship, as seemed probable when my study began (§ 5). Nevertheless, anatomical divergences between Disconanths and Siphonanths remain as regards the structure of the float, the storage of nematocysts, and the simple or ramified coelenteron; the polymorphism of Siphonanth cormidia closely recalls that of the reproductive branches of certain Gymnoblast colonies; and an affinity with a diffusely tentaculate stock of that group is suggested by various details in the structure and life-history of *Myriothela* (§ 8). Let us take these points in order.



TEXT-FIGS. 48 AND 49.

Branchiocerianthus (Monocaulus) imperator, deep-water Corymorphine with ventral proliferation and bilateral symmetry. *AC*, aboral chamber; *AT*, aboral tentacles; *D*, diaphragm; *G*, gonophores; *OT*, oral tentacles; *S*, stalk.

Fig. 48.—Oral view of horseshoe-shaped series of gonophore-clusters and aboral tentacles recruited from below (Mark, 1898).

Fig. 49.—Diagrammatic sagittal section of disc, showing diaphragm partly fused with peristome (original, after Miyajima, 1900, modified).

The float of Disconanths differs from that of Siphonanths in being composed of concentric chambers, produced below into fine tubular 'tracheae', and in lacking a recognized gas-gland. That of a Siphonanth is a simple vesicle, except for the secondary outgrowths of its gas-gland (§ 1). The latter, as suggested by Korschelt and Heider (1890, p. 44), could readily be derived from the invaginated 'Fussplatte' or sucker of an Actinula larva, especially if, as in *Myriothela*, the habit of fixation by this glandular disc was being given up (§ 8). In such a case, in tidal waters, the larva could easily fill its sucker with air, and float away like a Minyad on its adventurous voyage, carrying with it its inherited cargo of potentialities, and using its tentacles as paddles. But the arenicolous Corymorphines have no sucker or adhesive disc, being rooted in sand or mud by a multitude of fine rootlets. In the great *Monocaulus imperator* of the 'Challenger' (= the *Branchiocerianthus* of Mark and Miyajima) these are concentrated round a terminal caudal bulb, and in all Corymorphines (*Hybocodon*?) the normal chitinous perisarc is replaced by a soft thin pellicle, apparently subject to periodic ecdysis and renewal. If the rounded base of a Corymorphine Actinula, while still floating, were to undergo invagination, the chitinogenous ectoderm, being now inverted within the body, would presumably in due course secrete a thin chitinous vesicle produced into everted rootlets with a similar chitinous lining—the two primary features of the Disconanth float. Periodic withdrawals of the epithelium from the vesicle, keeping pace with the general growth, would result in a succession of ring-like chambers around the primary cyst, together with corresponding annulations upon the inverted rootlets, as on the so-called 'tracheae' of the float. The eight 'radial chambers' with which Haeckel complicated the structure, have been shown by Bigelow (1911) not to exist. Thus the two kinds of float may have arisen independently in these two ways, although it is equally true that the simpler float of Siphonanths (apart from its gas-gland) may be the result of a secondary simplification of the Disconanth float, though this is not the simpler explanation.

The second difference in regard to the storage of nematocysts

is bound up with differences in the arrangement of the tentacles in the two groups. Like the common possession of a float, the mere existence of special stores of nematocysts in the two groups marks some kind of relationship, though the differences in detail are profound. No Hydroid polyp has a compact basal store of nematocysts comparable with the basigaster of Siphonanths, though the zones of nematocysts in the Actinula of *Tubularia* are suggestive (Lowe, 1926), and no Hydroid colony has a central reserve like the centradenia of Disconanths. In Siphonanths each polyp has its own heavily armed and highly extensile tentacle, while the Disconanth polyps have no tentacles of their own, and the aboral wreath of the colony, in spite of the huge centradenia serving it, consists of relatively feeble structures, barely differing from the tentacles of Hydroids. Until this puzzling resemblance and difference has been explained, we cannot say with any confidence whether the tentacles of either type are modified Hydroid tentacles or dactylozooids. It looks as if the two conditions were divergent modifications of some unknown tertium quid. I can offer no explanation, but there is plainly here a promising field for a crucial piece of research, which should be associated with a comparative study of the distribution and, if possible, of the migrations of the different kinds of nematocyst, on the lines so well begun by Weill (1934).

The third difference as regards the septation of the hydranth and the plexiform coelenteron of the aboral or caudine region is not fatal to the possibility of close relationship. When present, these characters naturally have a high systematic value, although in Hydroids, owing to lack of anatomical information on many forms, systematists prefer to use external characters more or less associated with them. That their absence does not preclude close relationship is readily seen by comparing *Pennaria* with *Tubularia*. Moreover, the aboral plexus in its origin was clearly associated with the formation of a pseudo-notochordal axis for the support of large polyps on exceptionally long upright stems, probably at a time when the hard perisarc was still restricted to short basal cups on a retiform stolon. The loss of the upright attitude, as in *Myriothela* and *Hypolytus*

(fig. 56), or suspension upside down from floating weeds as in *Tiarella*, would remove this function and might well result in complete loss of the endodermal complexity. The same argument applies to Siphonophores. In Disconanths the inherited plexus has been retained and even extended for the better nourishment of the massive tissues around and below the float; but in most Siphonanths no such reason exists, and a secondary return to simplicity may have ensued. The massive body of the Rhodaliidae (Haeckel's 'Auronectae') is the one exception, and it is certain that the canalization of the coelenteron in that group is quite different and independently acquired. There is a sequence in the group from complete simplicity in *Archangelopsis* to almost complete canalization in other forms, and even in these the aboral region may remain as a large undivided hypocystic cavity (Bigelow, 1911, xxi, 7). On this character, therefore, we are again presented with the same alternative as in the case of the float: the Siphonanth condition is directly derivable from that of the simpler non-Tubularian type of Hydroid, or may be derivable from that of Disconanths, or of Corymorphines, by a secondary simplification.

The last of our differentiating points yields evidence of a more decisive character. In general the mere number of polymorphic types is of little moment for tracing relations, because nectocalyces and palpons are obviously modified gonophores and polyps, and could be derived from those of either Hydroids or Disconanths. Bracts also can be excluded, since, as I have tried to show, they are neither polyps nor nectocalyces in origin, but special modifications of persistent larval tentacles (§ 8). But the position of nectocalyces may be crucial. The cormidial nectocalyces of certain Calycophores are obviously modifications of their own gonophores, provoked by the need of extra locomotive power for their specialized 'Eudoxiae', while all those of the nectosome, being produced as buds from the larval body (oozooid), must represent the gonophores of pre-Siphonophore (i.e. Hydroid) ancestors, since no Siphonophore, whether Disconanth or Siphonanth, produces gonophores on the oozooid. Like the oozooid of Salps and Doliolids, it remains permanently sterile, and the sexual gonophores are all produced by its off-

spring, the secondary budded polyps and gonopalpons. Moreover, as the nectosome corresponds to the hydrocaulus of a Hydroid, when a stalk can be distinguished, and not to the hydranth proper (§ 9), this means that the Hydroid ancestors of Siphonantha, unlike Tubularia and Corymorpha, produced their gonophores on their stalks, and not on their hydranths. This condition in the oozooid is actually represented in *Pelago hydra*, the locomotive tentacles and gonophores of which suggest the immediate precursors of paddling bracts and nectocalyces; but for the nearest colonial type with diffuse tentacles and caudine gonophores we have to look away from the Tubularian towards the Coryniform Hydroids, from some unknown stock of which the long-stalked and highly specialized Tubularians doubtless arose. A direct relationship between the two groups is indicated independently by the great similarity of the medusae of Corymorpha and Pennaria to the 'Sarsia' of Syncoryne.

A similar conclusion is reached from a study of the polymorphic tufts of Siphonanths which have been termed 'cormidia'. The linear strings of these in Macrostelia are clearly secondary modifications, due to the excess of longitudinal over transverse growth (§ 10), while their more or less radial distribution in Brachystelia assimilates them to the reproductive branches of an ordinary arborescent Hydroid. Omitting Calyphora, in which important points are still uncertain, and in which simplifications of structure have evidently played a great part (§ 9), the typical and minimum constitution of a cormidium is a combination of polyp, gonopalpon (= blastostyle), and gonophores. This trimorphic combination is exactly comparable with the branch of a Dicoryne colony, consisting of a terminal polyp, a subterminal blastostyle, and its gonophores. There may be an extra polyp or blastostyle on the branch, as there may be extra polyps and some palpons in the cormidium, but the combination stated is essential and constant. In both cases the polyps themselves are sterile. This condition of pronounced trimorphism is adumbrated in Disconanths, but is not found in Tubularia, or in any of the colonies, like Pennaria, which possess the Tubularian type of hydranth, with gonophores above

an aboral circlet of tentacles. All consist simply of polyps and gonophores. Thus, as in the case of the float, an origin from Disconanths is possible, but it is equally possible from Hydroids themselves, of a type less elaborate in structure than the Tubularians.

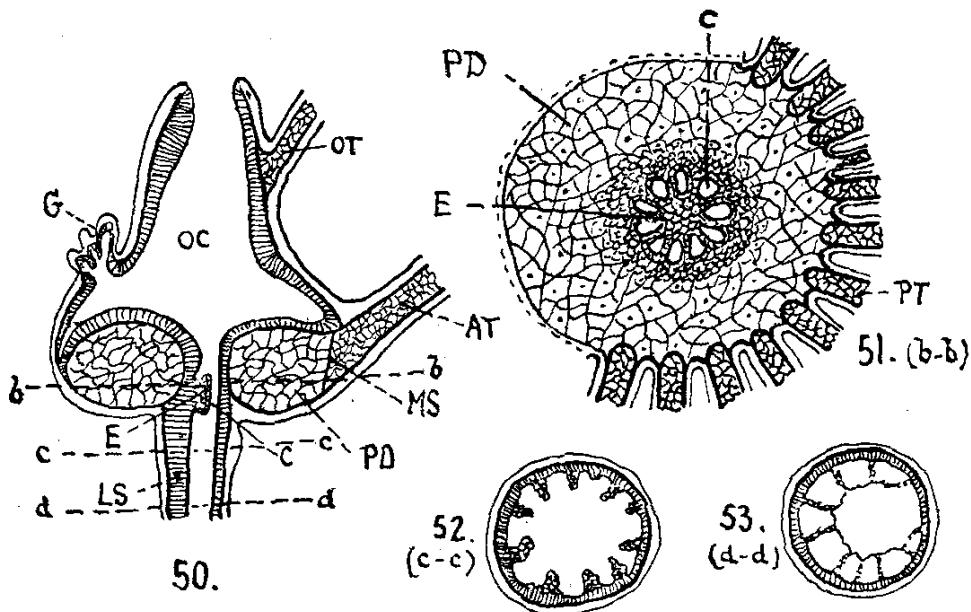
From these various considerations it seems to follow that, although the gap between Disconanths and Siphonanths has been substantially reduced, the possibility of a diphyletic origin of Siphonophores has not been entirely excluded. The sharpest distinction that remains is that of their symmetries—radial budding and growth in one group, one-sided (ventral) budding and growth in the other; but, as a similar contrast separates *Branchiocerianthus* from *Corymorpha* without affecting their relationship, the separation at their origin may be no wider than that between one genus of a family and another. I have already indicated in my earlier chapters various points in Siphonophores themselves that can only be cleared up by new investigations, but for the settlement of this problem what we most need is more information, or more precise information, on the development and anatomy of certain Hydroids on which the solution of the problem of affiliation seems to depend. These requirements seem to be mainly as follows:

(a) the structure and development of the larvae of *Corymorpha*, *Hybocodon*, *Pelagohydra*, & *Coryne Van Benedeni*, Hincks (1868, fig. 4) (= *pusilla* of Van Beneden).

(b) the presence or absence of gastric diaphragm and caudine endochord and plexus in *Acaulis* and *Hypolytus*, and their mode of development in *Corymorpha* and *Tubularia indivisa*.

(c) the anatomy and complete development of *Myriothela*, with special reference to possible traces of diaphragm, endochord and plexus; gastrulation, and any evidences of a ventral non-muscular line and of bilateral symmetry; fixation of larva by sucker or tentacles. [On this, see Postscript, p. 193.]

My reasons for specifying so many non-colonial forms will appear from the following considerations. The specialization which attends the integration of bud-communities leads quickly



TEXT-FIGS. 50-3.

Tubularia indivisa. Sections after Grönberg, 1898, showing deviations from Corymorphine structure. *AT*, aboral tentacle; *C*, one of the short canals; *E*, endochord; *G*, gonophores; *LS*, longitudinal septa of stalk; *MS*, Mesogloea between parenchyma of dia-phragm and aboral tentacles; *OC*, oral chamber; *OT*, oral tentacles; *PD*, parenchyma of diaphragm; *PT*, parenchyma of tentacles; *SP*, sieve-plate formed by remnants of the longitudinal canals opening into the single hydranth cavity.

Fig. 50.—Vertical section of hydranth, showing fusion of diaphragm with basal wall (N.B. Mesogloea between parenchyma of dia-phragm and aboral tentacles); obliteration of aboral chamber; and reduction of endochord and stalk-canals.

Figs. 51, 52, and 53.—Transverse sections through *bb*, *cc*, and *dd*.

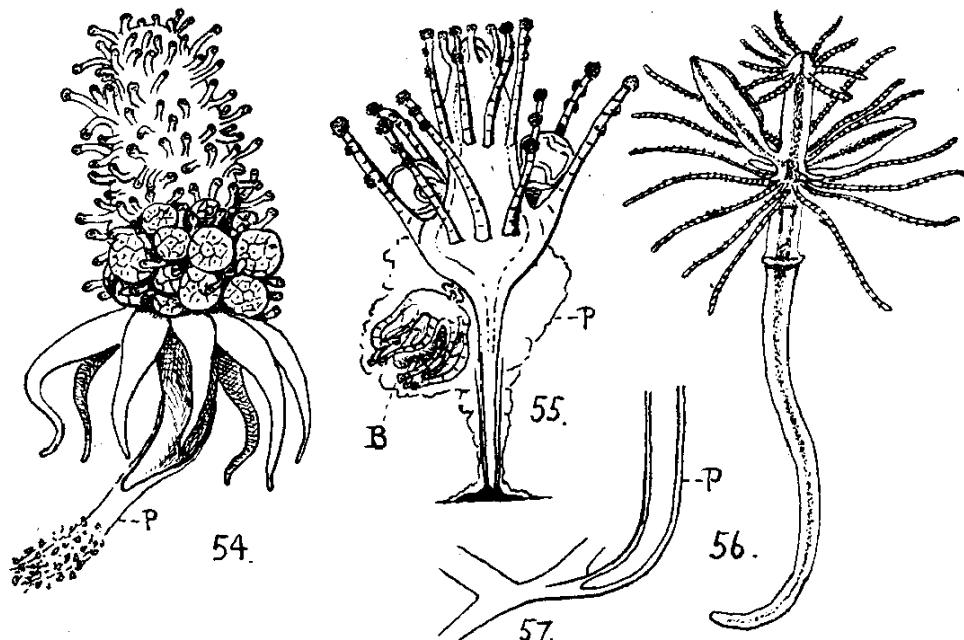
to the obliteration of earlier characters if they are not essential for the tasks of the various buds. Organisms, therefore, which have dropped out of the colonial race, at different levels, may reveal more completely some of the stepping stones of their advance. We are apt to think of Tubularians as the climax of Gymnoblast evolution, and, so far as hydranth structure is concerned, that is manifestly true. But there is good reason to regard the structure of both hydranth and stalk as built up by a succession of definite additions and subtractions. The original position of Hydroid gonophores, as of polyps, was admittedly on a creeping stolon, and stages in their subsequent ascent up the side-walls of the polyps are seen in such simple forms as *Clavatella*, *Podocoryne*, and *Clava*, in the last of which they reach the zone immediately below the tentacles. In *Coryne* they just invade the tentaculate zone, and in the Corymorphines and Tubularians they pass on to the oral face of the hydranth, encircled by an equatorial whorl of specialized tentacles, unfortunately named 'aboral', but probably the lowest of the oral series (cf. *Tiarella*, Text-fig. 55).

Now in *Pelagohydra* both endochordal axis and peripheral plexus are enormously developed, thereby constituting its 'float', but the hydranth is perfectly simple with diffuse homogeneous tentacles, as in *Clava* or *Coryne*, and the gonophores are limited to the float, which clearly represents the Tubularian stalk. It is thus impossible to imagine the sessile forebears of *Pelagohydra* as solitary *Tubularias* or *Corymorphas*, owing to the basal position of their gonophores and their simple heads. There must have been—and may still be—a tribe of tall, simple, naked, polyps rising from a creeping stolon, with gonophores on their basal stalks, supported only by an endochordal axis; and this tribe was presumably ancestral not only to *Pelagohydra*, but to all the Tubularians with a similar internal axis. The presumed existence of such a tribe cannot be dismissed as mere phantasy, for in several other primitive Gymnoblasts (*Gemellaria* and *Clavatella*), with tall and slender naked stems, the hydranth is known to be supported by a corresponding differentiation of the endoderm of the stem, the narrow axial cavity being sur-

rounded by two specialized layers of an endodermal parenchyma (Allman 1871, Pl. vii, 5, and xviii, 11). After *Pelago hydra* broke away, the gonophores must have continued to climb, and eventually entered the tentaculate zone, thus completing the handsome but heavier structure of the Tubularian head. Apparently to meet this additional strain, the perisarc of the basal cups then extended upwards over the stalks, and the Tubularian character was fully attained.

But evolution clearly has not halted there. The simple unbranched stalks of the great *Tubularia indivisa* have been followed by the sparsely branched stalks of the smaller *Tubularia larynx*, and these by the full arborescent branching of the monopodial *Pennaria*—the sequence being also one of increasing number and diminishing size of the individual polyps. In the latter genus the composite structure of the Tubularian head has been fully retained, but the original endochordal axis has been completely replaced by the firm, light, perisarcal tubing of other forms, almost exactly as a cartilaginous tube first stiffened, and then replaced, the notochordal axis of early vertebrates.

This view of the evolitional sequence derives strong support from Grönberg's investigations of the structure of the Tubularian stalk. In his Ray Society Monograph (1871) Allman attributed to *Tubularia* the same structure of the stalk as in *Corymorpha*, and figured a cross section showing an axial endochord surrounded by a ring of peripheral canals. But Grönberg, using the method of serial sections, has shown (1898) that this condition prevails only in the colonies with large unbranched polyps (*Tubularia indivisa*), and in them only through a very short region at the apex of the stalk (Text-figs. 50–3)—so short that in effect the endochord and canals together constitute merely a kind of sieve-plate between the cavities of hydranth and stalk. Below this level the endochord disappears, and only the side-walls of the canals persist for a short distance as a series of low free septa. These quickly degenerate into mere ridges, one cell thick, the edges of which are connected with those of their neighbours except for one or two irregular gaps. Farther down the ridges gradually disappear. In the smaller, but more arborescent, species (*Tubularia larynx* and *coronata*)



TEXT-FIGS. 54-7.

Various Monogastric Hydroids with intertentacular gonophores. *B*, bud ready for detachment; *P*, perisarc.

Fig. 54.—*Acaulis primarius*, Stimp. After G. O. Sars (1873).

Fig. 55.—*Tiarella singularis*. After F. E. Schulze (1876).

Fig. 56.—*Hypolytus peregrinus*. After Murbach (1899).

Fig. 57.—The same, showing the caudal extremity in its tube.

there are no canals at all—merely an occasional septum or cross-bar ('Bälkchen') which divides the lumen of the stalk with all the irregularity of vestigial structures.

Thus, as Grönberg correctly argued, *Tubularia* cannot be regarded as ancestral to *Corymorpha*, but the latter, in the structure of its stalk, indicates the ancestral type from which the *Tubularia* series has been derived, the new features being the perisarcal tubing and the atrophy of the original endochordal axis. Moreover, these characters lead directly to *Pennaria* which, with apparently no trace of endochord or plexus, has undergone further colonial integration by discarding the last relics of the creeping stolon, and carrying all its buds as out-growths of the primary polyp body.

Without *Corymorpha* the structure of *Tubularia* would be unintelligible, and no one would suspect the secondary simplification which has led to *Pennaria*. But it does not follow, as Grönberg appears to have believed, that the ancestors of *Tubularia* were necessarily non-colonial, like *Corymorpha*. Many reasons, as well as the examples cited above, render it probable that *Corymorpha* was itself derived from a primitive polyp-community differing from that of a *Gemellaria* or *Clavatella* merely in details. Very little is known of the development of any *Corymorphine*. E. T. Browne's promised drawings of *Amphicodon* (*Hybocodon*?) seem never to have been published (Browne, 1895).

Of the other monogastric Hydroids, *Acaulis* (Text-fig. 54) is probably a *Corymorphine* which has developed a long prehensile proboscis on the lines of a *Myriothela*, just as various *Myriothelines* of deep water show remarkable modifications for limicolous or arenicolous existence on *Corymorphine* lines (see Bonnevie, 1898). Sars obtained his specimens from muddy ground off Lofoten in 40–100 fathoms. It would appear to live immersed to the level of its large extensile aboral tentacles, which doubtless radiate over the surface and guide its proboscis to approaching prey. Attachment to the mud appears to be no longer by rootlets but by the adhesiveness of its loose perisarcal sheath. In view of its diminished stalk, a knowledge of its internal structure would be of much value.

Hypolytus (Text-fig. 56) is found in the eel-pond at Woods Hole, adhering to blades of *Zostera* by the whole length of its perisarcal tube, which can be deserted and renewed. It has obvious affinities with *Corymorpha* and *Tubularia*, but its tentacles have a more primitive aspect, and only additional knowledge of its internal structure can settle its history. Judging from Murbach's figures, which include no sections, it would seem that endochord and plexus have disappeared even more completely than in *Tubularia*, but the diaphragm may be represented by the 'deeply pigmented band' below the tentacles, for which Murbach 'found no adequate explanation'.

Tiarella (Text-fig. 55) is an obscure little Hydroid, interesting from its production of free buds like *Myriothela*, which F. E. Schulze found for a few weeks one year attached to *Cystosira* drifting about the Bay of Muggia near Trieste. He referred it with considerable hesitation to the Pennariidae, but it has three equidistant whorls of tentacles, all capitate, so that Corynoid affinities are equally possible, and its perisarcal sheath is essentially Corymorphoid.

After this lengthy discussion the evolutional situation may be summed up in few words. There are indications of a Myriotheline relationship of Siphonanths which needs to be reconciled with the Corymorphine affinities of Disconanths before a common origin can be firmly assured. *Pelagohydra*, Siphonanths, and Disconanths may in fact be independent pelagic offshoots from three different types of Gymnoblastic Hydroid, the larvae of which failed to attach themselves but succeeded in keeping afloat until their gonophores ripened. *Pelagohydra* absolutely, and Disconanths to some extent, may be said to have survived by the adaptive aggrandisement of their oozooids, at the expense of their colonies, while Siphonanths, by precocious budding, elaborated the colony at the expense of the oozooid. The latter tribe somehow acquired a new feature, their one-sided mode of gastrulation, which predetermined a bilateral symmetry. Growth in width at first compelled a whorled arrangement of their buds, but the divergent forms it assumed suggest great instability (*Brachystelia*). Some of these then turned it to real use by suppressing all growth in

width for greatly increased length, and thus trailed a long line of prehensile buds behind the locomotive fore-body (*Macrostelia*). Evidently their free embryonic life, peculiar gastrulation, and precocious budding have been distinctive factors in Siphonanth evolution.

13. SYSTEMATIC.

From the systematic standpoint the following scheme sums up the more definite results of the present study. Its main feature is its reversal of the order in which Chun arranged the principal groups (1897). In detail I go back to Eschscholtz's (1829) tripartite division into *Chondrophorae* (Chamisso, 1821), *Physophorae*, and *Calycophorae* (Leuckart, 1854), which was broken up by Haeckel, but have combined Haeckel's *Disco-nantheae* and *Siphonantheae* with it to mark the major gap between the *Chondrophorae* and the remainder. All the feminine terminations, however, which originally marked the '*Siphonophorae*' and its subdivisions as '*Medusae*' (Chamisso) or '*Akalephae*' (Eschscholtz), have been changed to the simpler and more conventional neuter plurals.

Haeckel claimed his '*Physonectae*' to be synonymous with Eschscholtz's '*Physophorae*', but in fact he applied the term to a mere section of that comprehensive group, which is here revived under the nearest possible approach to the original designation, viz. *Physophorida*. As a title for one of its sections '*Physonectae*' is undesirable, both from its liability to confusion with the historic ordinal name and from its failure to convey any distinctive meaning in contrast to '*Cystonectae*'. I therefore propose to substitute the title '*Amphinecta*', which emphasizes the outstanding difference between the surviving sections. Both possess a similar unchambered float (i.e. they are *Physophorida*), but one lot swim with the bladder alone (*Cystonecta*), the other with both bladder and special appendages, i.e. bracts or nectocalyces (*Amphinecta*). In both these sections, pending the establishment of definite lineages, I have provisionally employed Haeckel's descriptive terms *Macrostelia* and *Brachystelia* in his sense.

SIPHONOPHORA

Floating bud-communities of Gymnoblastic Hydromedusae.

I. DISCONANTHA.—Oozooid with a large chambered air-float and an aboral ring of tentacles (dactylozooids?). Secondary polyps (blastozoooids) non-tentaculate, ranged around the oozooid with radial symmetry, and bearing Anthomedusan gonophores ultimately detached. No bracts, palpons, blastostyles (s.str.), or nectocalyces. Larva an Actinula with a mesogastric diaphragm (Conaria). = Order CHONDROPHORA: including *Porpita*, *Porpema*, *Velella*.

II. SIPHONANTHA.—Colonies bilaterally symmetrical, the oozooid with a mesosomatic budding tract in the mid-ventral line, which divides the colony into a locomotive nectosome and a gastro-genital siphosome. Polymorphism to various degrees, but always with palpons, gonopalpons, or nectocalyces. Polyps each with a single basal tentacle. Gonophores usually sessile on blastostyles (gonopalpons), together forming the gonodendra. Polyps and gonodendra usually associated in pairs (polyp below, gonodendron above), forming 'cormidia' with or without the addition of bracts and palpons.

A. PHYSOPHORIDA.—With unchambered float and ectodermal gas-gland. Oozooid either short and stout, bearing cormidia in whorls or spires (*Brachystelia*) or greatly attenuated, with cormidia more or less metamerie (*Macrostelia*).

(1) CYSTONECTA.—Float large with apical pore, usually with hypopycistic villi. Nectosome without locomotive or other appendages. Stem without bracts.

BRACHYSTELIA.—*Epibulia*. *Physalia*.

MACROSTELIA.—*Rhizophysa*. *Bathophysa*. *Pterophysa*.

(2) AMPHINECTA (= Physonectae, Haeckel)—Float closed, usually small with pericystic septa; but large, with incomplete septa in *Anthophysa*.

(a) *BRACHYSTELIA*.—*Anthophysa* and *Athorybia* (Nectosome with paddling bracts but no nectocalyces); *Nectalia* (with bracts and nectocalyces); *Physophoridae* and *Rhodaliidae* (with nectocalyces only).

(b) *MACROSTELIA*.—*Agalmidae*, with bracts in larva, nectocalyces in adult, and numerous stem-bracts, e.g. *Agalma*, *Stephanomia* (= *Halistemma* and *Agalmopsis*); *Foriskaliidae*; *Apolemidae*.

B. CALYCOPHORIDA.—No float (aboral region of larva aborted), but a subapical position assumed by one, two, or more nectocalyces, usually with a somatocyst. All *Macrostelia*, the cormidia usually detached as free-swimming sub-colonies ('Eudoxiae') with an anterior covering bract enclosing phyllocyst with oil-globule.

Stephanophyes, with a corona of four nectocalyces and slender palpons alternating with sessile cormidia (connecting with *Amphinecta*?); *Hippopodius*, with a turret of nectocalyces and sessile cormidia; *Galeolaria*,¹ *Praya*, and *Diphyes*, with two nectocalyces; *Muggiaeae* and *Sphaeronectes*, with one nectocalyx.

Although this classification is a mere statement of distinctive facts of structure, it suggests the course of Siphonophore evolution as a progress from passive flotation, through various combinations of flotation with active modes of locomotion, to a climax of purely muscular methods of swimming and colonial simplification in *Calycophorida*.

The Chondrophora and Brachystelia are essentially epipelagic, while the Macrostelia range through a great variety of depths, several Cystonects and Calycophores being definitely bathypelagic (cf. Bigelow, 1911; Bigelow and Sears, 1937).

¹ I must decline to substitute for this expressive name (*galea*, a helmet: cf. Text-fig. 5), so long imbedded in Siphonophore research, the barren and barbarous *Sulculeolaria* of Blainville, merely because some obscure Mollusc is also entitled to it. Who would ever confuse *Galeolaria* the Mollusc with *Galeolaria* the Siphonophore? Such useless applications of the law of priority severely handicap the progress of Zoology.

LITERATURE CONSULTED.

- Agassiz, A., 1865.—“North American Acalephae”, Ill. Cat., ‘Mus. Comp. Zool. Harvard’, **2**.
 —— 1883.—“Porpita and Velella”, ‘Mem. Mus. Comp. Zool.’, **8**.
 Agassiz, L., 1862.—‘Contr. Nat. Hist., U.S.A.’, **4**. Boston.
 Allman, G. J., 1871.—“Monograph Gymnoblastic Hydroids”, ‘Ray Soc.’
 —— 1875.—“Myriothela”, ‘Phil. Trans.’, **165**.
 —— 1888.—“Hydroidea (II)”, ‘Challenger’ Rep., **23** (Monocaulus).
 Ashworth and Ritchie, 1915.—“Dicoryne”, ‘Trans. Roy. Soc. Edin.’, **51**,
 1 (6).
 Balfour, F. M., 1885.—‘Comparative Embryology’, **1**.
 Bedot, M., 1884.—“Velella, Organe centrale”, ‘Rec. Zool. Suisse’, **1**.
 —— 1885.—“Rataria”, *ibid.*, **2**.
 —— 1888.—“Agalma Clausi”, *ibid.*, **5**.
 —— 1904.—“Siphonophores”, ‘Résultats Camp. Sci.’, Monaco, **27**.
 Bigelow, H. B., 1911.—“Siphonophorae Eastern Pacific”, ‘Mem. Mus. Comp. Zool. Harvard’, **38**.
 Bigelow and Sears, 1937.—“Siphonophorae of ‘Dana’”, ‘Rep. Dan. Ocean. Exp.’, **2**.

- Bonnevie, K., 1898.—“Myriothela of deep water, &c.”, ‘Zeit. wiss. Zool.’, 63.
- Browne, E. T., 1895.—“Hybocodon (?) Actinula”, ‘Trans. Liverpool Biol. Soc.’, 9.
- Chamisso and Eysenhardt, 1821.—‘Nova Acta Acad. Caes. Leop.’, 10, Pls. 24–33.
- Chun, C., 1887.—“Morph. d. Siph. (Pneumatophores)”, ‘Zool. Anz.’, 10.
- 1897 a.—“Bau d. Siphonophoren”, ‘Verh. Deutsch. Zool. Ges.’, 7.
- 1897 b.—“Siphonophoren”, ‘Ergeb. d. Plankton Exp.’, 2, K.b.
- 1898 a.—“Schneider’s System”, ‘Zool. Anz.’, 21.
- 1898 b.—“Knospungsgesetz d. Schwimmglocken”, ibid.
- Claus, C., 1860.—“Physophora”, ‘Zeit. Wiss. Zool.’, 10.
- 1878.—“Halistemma, Physophora, &c.”, ‘Arb. Zool. Inst. Wien’, 1.
- 1879.—“Agalmopsis utricularia”, ibid., 2.
- Dendy, A., 1903.—“Pelagohydra”, ‘Quart. Journ. Micr. Sci.’, 46.
- Eschscholtz, J. F., 1829.—‘System d. Akalephen.’ Berlin.
- Fewkes, J. W., 1882 a.—“Acalephs of Tortugas”, ‘Bull. Mus. Comp. Zool. Harvard’, 8.
- 1882 b.—“Acalephs of New England”, ibid., 9.
- 1885.—“Development, Agalma”, ibid., 11.
- 1888.—“Ploeophysa (= Anthophysa)”, ‘Ann. Mag. Nat. Hist.’, (6), 1.
- Gegenbaur, C., 1860.—“Physophora”, ‘Nova Acta Acad. Caes. Leop.’, 27.
- Grönberg, G., 1898.—“Tubularia, canals”, ‘Zool. Jahrb., Anat.’, 11.
- Haeckel, E., 1869.—“Entwickl. Siphonophoren”, ‘Utrechter Gesellschaft.’
- 1888.—“Siphonophorae”, ‘Challenger’ Report, 28.
- Hardy, W. B., 1891.—“Myriothela”, ‘Quart. Journ. Micr. Sci.’, 32.
- Hincks, T., 1868.—“British Hydroid Zoophytes”, ‘Ray Soc.’
- Huxley, T. H., 1859.—“Oceanic Hydrozoa”, ‘Ray Soc.’
- Kölliker, A., 1853.—‘Schwimmpolypen.’ Leipzig.
- Korotneff, A., 1884.—“Histologie”, ‘Mitth. Zool. Stat. Neapel.’, 5.
- 1888.—“Myriothela”, ‘Arch. Zool. Exp.’ (2), 6.
- Korschelt u. Heider, 1890.—‘Lehrbuch d. Entwickl.’, 1.
- 1910.—‘Lehrbuch d. Entwickl. Allg.’, 4, 2 (Budding, 526–77).
- Labbé, A., 1889.—“Myriothela”, ‘Arch. Zool. Exp.’ (3), 7.
- Lens and van Riemsdijk, 1908.—“Siphonophora”, ‘Siboga’ Exp., 38.
- Leuckart, R., 1853.—‘Die Siphonophoren.’ Giessen.
- 1854.—“Siphonophoren von Nizza”, ‘Arch. f. Naturgesch.’, 20.
- Lochmann, L., 1914.—“Entwickl. Galeolaria”, ‘Zeit. Wiss. Zool.’, 108.
- Loman, J. C. C., 1889.—“Amalthaea (Corymorphine)”, ‘Tijdschr. Nederl. Dierk. Ver.’ (2), 2.
- Lowe, E., 1926.—“Embryol. Tubularia”, ‘Quart. Journ. Micr. Sci.’, 80.
- Macbride, E. W., 1914.—‘Text-book of Embryology’, 1.
- Mark, E. L., 1898.—“Branchiocerianthus”, ‘Bull. Mus. Comp. Zool. Harvard’, 32.
- 1899.—“Correction”, ‘Zool. Anz.’, 22.

- McCrady, 1857.—“Gymnophthalmata, Charleston”, ‘Proc. Elliot Soc.’, 1.
- Metschnikoff, E., 1874.—“Entwicklung”, ‘Zeit. Wiss. Zool.’, 24.
- Moser, F., 1911.—“Glocken d. Siphonophoren”, ‘Zool. Anz.’, 39.
- 1912.—“Glocken d. Siphonophoren”, ‘Verh. Deutsch. Zool. Ges.’, 22.
- 1924.—“Larvalen Verhältnisse”, ‘Zoologica’, 28.
- 1925 a.—“Siphonophoren”, ‘Deutsch. Südpolar (“Gauss”) Exp.’
- 1925 b.—“Siphonophoren”, Kükenthal’s ‘Handbuch’.
- Miyajima, R., 1900.—“Branchiocerianthus”, ‘Journ. Coll. Sci. Tokyo’, 13.
- Murbach, L., 1899.—“Hypolytus and Corynitis”, ‘Quart. Journ. Micr. Sci.’, 42.
- Nutting, C. G., 1901.—“Alaskan Hydroids (Tubularia Harrimani)”, ‘Proc. Wash. Acad. Sci.’, 3.
- Sars, G. O., 1873.—“Norges Hydroider (Acaulis)”, ‘Vidensk. Selsk. Forh.’, Pl. V.
- Sars, M., 1877 (MSS., 1857).—“Physophora”, ‘Fauna Litt. Norvegiae’, 3.
- Schneider, K. C., 1896.—“Organization d. Siph.”, ‘Zool. Jahrb., Anat.’, 9.
- 1898.—“Systematisches”, ‘Zool. Anz.’, 21.
- Schulze, F. E., 1876.—“Tiarella”, ‘Zeit. Wiss. Zool.’, 27.
- Stechow, E., 1909 and 1913.—“Branchiocerianthus”, ‘K. K. Bayer. Akad. Wiss.’, 1 and 3 Suppl. Bd.
- 1919.—“Hydroids”, ‘Zool. JB. Systematik.’, 42.
- Totton, A. K., 1932.—“Siphonophora”, ‘Great Barrier Reef Exped., 1928–9’, Rep. IV.
- Vogt, C., 1852.—“Siphonophoren”, ‘Zeit. wiss. Zool.’, 3.
- 1854.—“Siphonophores de Nice”, ‘Mem. Inst. Nat. Genève’, 1.
- Weill, R., 1934.—“Nematocysts and Taxonomy”, ‘Trav. Stat. Zool. Wimereux’, 2.
- Woltereck, R., 1904.—“Entwick. Velella (‘Conaria’ larva)”, ‘Zool. JB.’, Supp. VII.
- 1905 a.—“Entwick. (‘Bipolaria’)”, ‘Verh. Deutsch. Zool. Ges.’, 15.
- 1905 b.—“Ontogenie (Pneumatophores)”, ‘Zeit. Wiss. Zool.’, 82.

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Three important memoirs on Myriothela were overlooked in the writing of this paper in 1943–4, viz.:

- Benoit, P., 1925.—‘Arch. Zool. Exp.’, 64.
- Manton, S. M., 1940.—‘Rep. Brit. Graham Land Exp. 1, 4’.
- 1941.—‘Jour. M.B.A.’, 25.

Benoit throws reasonable doubts on the normality of Hardy’s ‘buds’ (p. 145, supra), which were nevertheless seen by me at the time; and Manton, along with other things of interest, renders it almost certain that the larva attaches itself by a number of aboral (‘hydrorhizal’) tentacles, and not by a basal disc or ‘sucker’ (p. 146, supra).