INTRODUCTION

The question of the siphonophores has, at all times, preoccupied the most qualified scientists. Diverse concepts have been put forward and numerous ideas exchanged; but no single hypothesis has gained a unity of views on this subject in this group as to which is most primitive; thus the origin and phylogeny of the siphonophores remains very controversial.

On the one hand, the absence of palaeontological documentation - the siphonophores leave no fossil trace - constitutes a most regrettable gap in establishing an indisputable plan for the origin of the group. On the other hand, as these extremely delicate and vulnerable pelagic animals, that are generally collected in a fragmentary or mutilated state and which are moreover difficult to fix and preserve, the relative facts about their constitution and about their evolution have been so few and insufficient to establish a perfectly arranged line. Always, if one agrees with J. Hadzi (1918) that "all recent organization is a product of history" one can, with this thought, fill in the gaps and conceive the origin as to the evolution followed by the siphonophores to arrive at the differentiation of the actual group. In consequence of the following postulation and its support by knowledge of embryology and comparative anatomy utilisation of ethology, one can reconstruct the formation of the group and to establish the branching that allows the establishment of a sufficiently complete genealogical tree.

The study of embryology and comparative anatomy allows comparisons between the juvenile stages of the groups which, in the course of time, have evolved in diverse directions; while observations of the behaviour of living siphonophores[1] gives an understanding of the changes caused to these animals by a factor which I believe is predominant, which is a progressive tendency toward a more and more active release with respect to the ambient medium. The phylogeny of the group, on the basis of the traces that are left by the different representatives, the details used by an individual siphonophore to free itself from an originally sessile life, to develop into a passive floating life. In the genealogical relations of the siphonophores one finds a series of phenomena which, gradually, bring the organisms into life with their proper reactions and gives them independent movement in the ambient medium.

I. CONCEPTS ON THE ORGANISATION OF SIPHONOPHORES.

Is the siphonophore and individual or a colony?

The majority of authors consider it as a polymorphic colony formed by budding.

Two principle theories confront us:

On the one hand certain authors derive the siphonophores from a transformed medusa, in a state to give birth, by budding on the manubrium, to new medusae or to

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[1] W. Jacobs [1938] has published some remarks on this subject. Myself, I have made, in 1934, certain *n vivo* observations at the marine laboratory of Villefranche-Sue-Mer (France), thanks to a grant given to me by the Commission du Fonds National de la Recherche Scientifique de Belgique.

some polyps. This medusomorph theory is recommended notably by F.W. Eysenhardt (1821), Fr. Eschscholtz (1829), J.H. Huxley (1852, 1859), P. E. Müller (1971), E. Metschnikoff (1871, 1874), W. Fewkes (1880), F.M. Balfour (1885), E. Haeckel (1869-1888), B. Hatschek (1889), V. Franz (1924), F. Moser (1925), G. Bohn (1934), R. Legendre (1940).

One the other hand some authors think that the origin of such a colony is found in a floating colony comprised of hydropolyps which are modified, by a subdivision of work, and which possess the ability to produce medusae. This hydro- or polypomorph theory has been defended most notably by Lesueur (1813), H. Milne-Edwards (1840), C. Vogt (1848, 1854), R. Leuckart (1851, 1854), A. Kölliker (1853), C. Gegenbaur (1854), C. Claus (1878, 1885), A. Agassiz (1865), C. Chun (1882, 1897), E. Korschelt and K. Heider (1890), O. Hamann (1892), K. Schneider (1896), J. Hadzi (1918), H.C. Delsman (1923), E. Leloup (1929).

In summary, all participants in the polypo- or medusomorph theories base their reasoning on the study of the adult siphonophore. Meanwhile, Ed. Perrier (1881), Ed. Perrier and Ch. Gravier (1902), A. Lameere (1902, 1929) and F. Woltereck (1904, 1905) sought an explanation for the origin of siphonophores by considering the larval stage. A. Lameere and F. Woltereck estimate that a siphonophore is the result of a union, at the aboral pole, of a medusoid and polypoid individual (meduso-polypomorph theory). Ed. Perrier 9(1881), Ed. Perrier and Gravier (1902) though that the siphonophore is a product of tachygenesis: its ramified bodies arising from a single fixed form that buds laterally all sorts of hydromedusae. For these latter authors, the development of siphonophores shows the larvae of hydroids budding off some medusoids before having attained the polyp form.

A. Medusomorph Theory.

T.H. Huxley (1852) considered a siphonophore as a medusa on which the organs are multiplied, dissociated and distributed on the individual as an adaptation to diverse functions (polyorgan theory). It is necessary to take into account that T.H. Huxley considered the polyps and medusae as the organs of an individual that constitutes the hydroid colony.

The other authors mentioned considered the siphonophore as an individual colony arising as buds from a medusa whose elongated manubrium became the stem.

According to F.W. Eysenhardt (1821) the float of a siphonophore is derived from the recurved umbrella of a medusa. The float of *Physalia* arose by the union of several medusae.

Fr. Eysenhardt (1829) ranked the siphonophores amongst the "medusenartigen Strahlthiere" [medusa-like radiate animals].

According to E. and L. Metschnikoff (1870, 1871), P.E. Müller (1871), W. Fewkes, (1880), E. Haeckel (1888) and B. Hatschek (1889), the siphonophores arose from a medusa with a very long manubrium bearing buds of some polymorphic individuals like *Sarsia siphonophora* or *Lizzia*.

For E. Metschnikoff (1874) the float was formed by the refolding of the umbrella and the stolon represents a manubrium. The gastrozooids were derived from the manubrium, the tentacles from the marginal tentacles, the bells and the bracts from the umbrella: these are the products of the multiplication of organs of the initial medusa which are dispersed and distributed on the stem. In contrast, the fertile

medusae of the cormidia are budded from the initial medusa of which they have the quality.

E. Haeckel (1888) gave rise to the medusome theory. The siphonophores are colonial organisms composed of individuals of three generations or less. The siphonula is a subdivided medusa. The float arises by the glandular invagination of the exumbrella at the apical pole, the gastrozooid represents an exumbrella manubrium and the tentacle is the displaced unique marginal tentacle. The manubrium of the siphonula, the primary individual, buds and gives rise to the second generation individual, the cormidia with their bracts, their gastrozooids and their dactylozooids. The swimming bells arise from the umbrella dislocated and dispersed from the initial siphonula.

B. Hatschek (1889) complimented the theory of Haeckel. The swimming bells represent the sterile medusoid formations, deprived of a manubrium and having the quality of an individual siphonula.

F. Moser (1925a) has summarised, as follows, these concepts as the "Ursiphonophor" theory. The siphonophores evolved inn the alternation of generations sense into the form of a colony. Its organs are on the point of arising as individuals. The siphonophores are of medusae (heteromedusae) with bilateral symmetry, with a manubrium (stem) of exumbrella (oral) origin. On the stem buds of secondary gastrozooids with their basal tentacles and of sexual medusiform bells (protomedusae) as well as other forms, bracts, palpons, etc... The sexual bells become detached from the trunk, either individually or as eudoxids, with other appendages, before the sexual organs reach maturity. The release of the sexual products gives rise to the heteromedusae.

In 1934, G. Bohn reported that in siphonophores "the medusae are budded from the polyps and from even some highly complex colonies".

D. Damas (1936), whilst describing an aberrant medusa, considered that the origin of the Chondrophores "must be sort amongst the Anthomedusae (medusae of gymnoblasts, following the old terminology)".

For R. Legendre (1940) "the siphonophores are some floating hydromedusan colonies composed of polymorphic individuals".

B. POLYPOMORPH THEORIES.

H. Milne-Edwards (1840) described, with regard to the Physophores, that he had "the conviction that they are not simple animals, but aggregations of a great number of individuals born from buds and living united together in the manner of a composite polyp".

For R. Leuckart (1851, 1854), C. Vogt (1847, 1854) and A. Agassiz (1865) the siphonophores are colonies of highly polymorphic polyps which detached from the bottom and became planktonic.

According to E. Korschelt and K. Heider (1890) a larval hydroid could fix itself to the water surface, due to surface tension, and give rise there to a suspended colony.

Ed. Perrier (1881), Ed. Perrier and Ch. Gravier (1902) comment that the physalids are floating colonies of polyp-"Hydraires".

C. Chun (1897) based on the errant polyps such as *Nemopsis gibbesi* MacGrady, as well as the graptolites, which, according to their discovery in palaeontology, sometimes posses a central float. He wondered if it could not make the descent of siphonophores from pelagic colonies of hydroids.

A. Goette (1907) made to derive the siphonophores from pelagic hydroids.

J. Hadzi (1918) thought that the siphonophores arose from benthonic gymnoblastic hydroids as temporary vagabond larvae (actinulae) of which only the transitional individual is polypoid while all the secondary individuals are medusoid.

H.C. Delsman (1923) considered the adult porpitid as a polyp suspended at the water surface with its head towards the base and which, on the inside of its tentacular ring around the buccal mouth, carried a large number of sister polyps, products of medusae.

C. MEDUSO-POLYPOMORPH THEORIES.

A. According to Ed. Perrier (1881) and Ed. Perrier and Ch. Gravier (1902), a sessile colony of hydroid polyps can be transformed into a floating colony by the precocious appearance of a gas-secreting apparatus in some planulae of hydropolyps carrying them towards the deep sea. Some floating planulae are maintained at the sea surface by adapting a part of their organism to conserve in their tissues a certain quantity of gas. Some such planulae then transmitted this property to their descendants, but these evolved in two different ways. On the one hand, the gas-secreting apparatus or aerifer could evolve a sufficient volume to ensure the flotation of the colony (*Physalia*, *Porpita, Velella*). On the other hand, it is poorly formed, and development tends to accelerate more and more the locomotory individuals are budded directly on the planula. Always, under the influence of whatever cause (abundant nourishment, for instance) the buds are developed to the detriment of the feeding bodies and the youngest bud, by embryological acceleration, becomes a perfect individual before those that have produced it. For these authors, a siphonophore deprived of swimming bells is made up in the following way: a planula develops from the egg and is transformed into a hydroid polyp which, very soon, becomes able to bud off some medusae; these medusae at a premature developmental stage lose their reproductive capacity and become the locomotory individuals, the swimming bells, capable of towing the colony. A moment slows, the development of the polyp starts up according to its usual rhythm and the primitive hydropolyp gives rise to a pelagic colony which buds off some groups of individuals, simple or transformed, polymorphic, feeding and fishing (gastrozooids) or protective (palpons, bracts) or reproductive (gonozooids).

B. A. Lameere (1902, 1929) brought back the organisation of the siphonophores to that of the siphonula: "The siphonula is morphologically an association of three individuals of a hydroid colony: a polyp, a tentacle and a medusa: but physiologically the siphonophores are medusoid".

R. Woltereck (1904, 1905), on the basis of a study of the *Conaria* larva of the chondrophores, of which he recognised the narcomedusan nature. He considered the siphonophores as a planula producing two individuals united by their aboral poles: a polymorph, the primary polyp and a medusomorph, the terminal medusa. For this author the egg has given rise to an aboral stolon which differentiates into a terminal organ and into a circumpolar zone of proliferation, budding off some secondary and tertiary zooids.

For W. Garstang (1946) the siphonophores represent budding communities of gymnoblastic Hydromedusae.

D. PERSONAL THEORY

In a work of 1929 I have insisted on a comparison of the *Ratarula* larval stages of the Chondrophorids and the *Siphonula* of other physophorids as well as the *Actinula* of tubularid hydropolyps. At that time, when I did not have a knowledge of the work of Hadzi (1918), I concluded, like that author, that physophorid siphonophores represent colonies of gymnoblastic hydropolyps related to the Tubulariids, of which the polypoid larvae have adapted themselves for a pelagic life.

In the present study, I give the reasons for that theory strengthened by some embryological, anatomical, and ethological facts and rally the opinions of Ed. Perrier (18881), C. Claus (1885), E. Korschelt and K. Heider (1890), C. Chun (1897), Ed. Perrier and Ch. Gravier (1902), J. Hadzi (1918) and H.C Delsman (1923) to my choice.

Before passing on to the theoretical interpretation, there is reason to summarise the general facts known actually and relatively on the modes of development of the different groups of siphonophores.

1. Embryological development of Physophorids.

Recalling briefly the different stages that the physophorids show in the course of their ontogenetic evolution.

Immediately one establishes that there are two modes of development according to whether the larvae possess one or two zones of proliferation.

A. - Siphonophores characterised by one zone of budding, possessing a primitive structure, although already very evolved: these are the Chondrophorids and the Cystonectids.

a) **Chondrophoridae**.

At the present time, one is still ignorant of the phenomena of maturation and fecundation of the genital products as well as the first bathypelagic embryological stages.

a^1) Velellidae

The youngest larva of *Velella* is known as the *Conaria* (E. Leloup, 1929)

Spherical, with octaradial symmetry, transparent, it comprises three superimposed parts (fig. 1A). The superior part contains the monothalamic rough outline of the float surrounding the two endodermic crests, the external one, vertical, roughly shaped like a collar, and the internal other, horizontal, roughly limb-shaped. The inferior part, vesicular, will become the primary gastrozooid. Under the pneumatophore, a mid region, characterised by a thick centripetal proliferation of nematoblastic ectoderm, constitutes the cone. This larva normally is bathypelagic.

The active formation of gas provokes the inflation of the pneumatocyst of the *Ratarula* stage (fig. 1B). The larva becomes bipolar, ovoid, with a secondary bilateral symmetry, with an apical and inferior pole. The simple incomplete float becomes globular, oval; it starts to spread horizontally. The limb defines it. Its pressure throws back the collar toward the exterior, and under this feeble prominence the primary tentacle appears. C. Chun (1888) has observed the "young *Rataria*" with a simple pneumatophore and four tentacles, either disposed "partially bilaterally", or presenting a large central tentacle surrounded by three smaller ones. This larva starts to entrain itself towards the surface.

The larva continues to elongate in a horizontal plane; it becomes elliptical at the *Rataria* stage. The float increases more and more (fig. 1C); the first chamber acquires a floor and a second chamber is formed. An apical crest, membranous, leaf-

like, precursor of the sail, begins to appear; it is bilobed at the apical pole that is closed by the fusion of the surrounding tissue. The sub leaf-like crown is accentuated. The number of tentacles increases; always few in number, the remainder deployed in a single circle. The endodermal canals of the collar, of the limb and of the cone multiply progressively. The larva continues its movement of ascent.
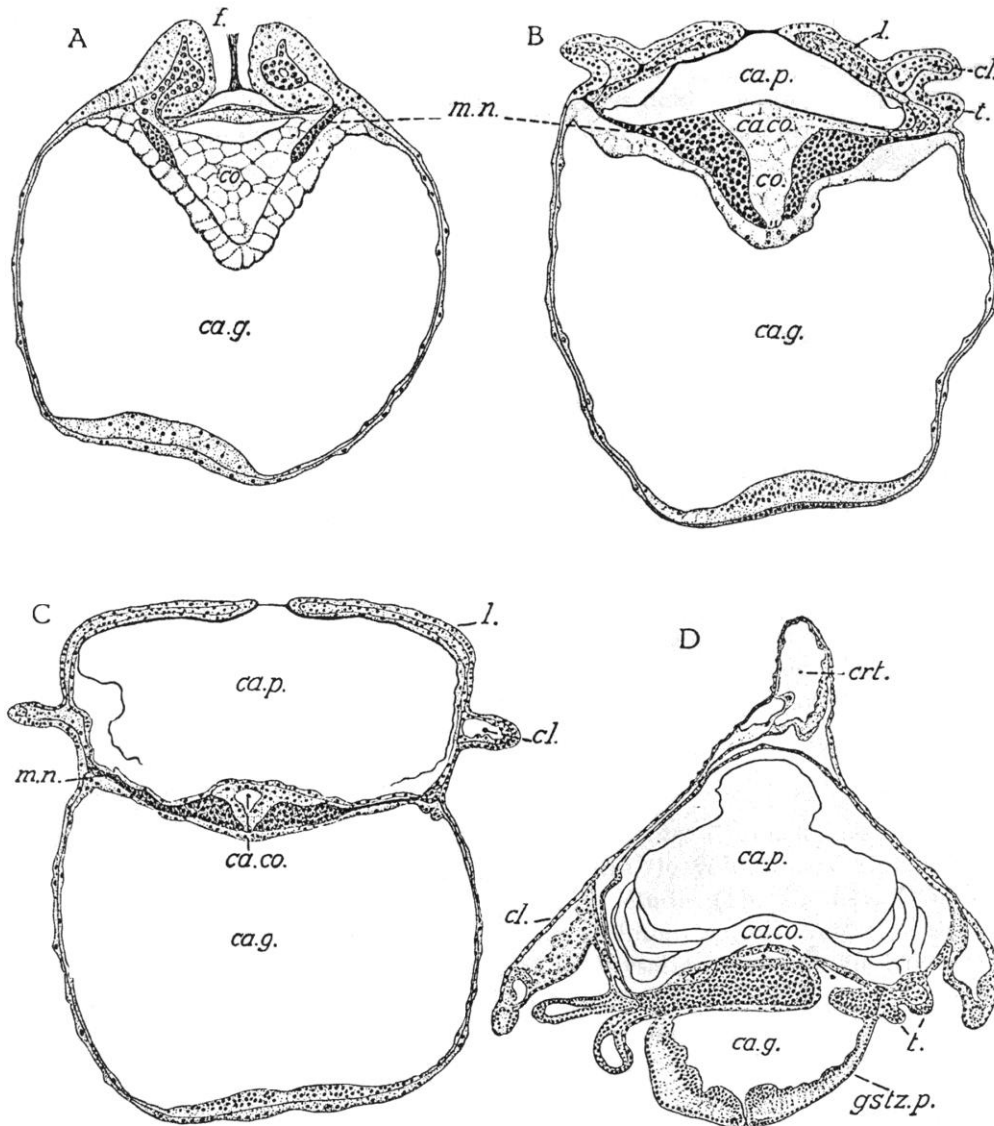

Fig. 1 - Stages in the development of a Chondrophoridae
A: Conaria stage. - B: Ratarula stage. - C. Rataria stage. - D. Young Velella.
ca.co. = cavity of cone. - ca.g. = gastrovascular cavity. - ca.p. = cavity of pneumatophore.
- cl. = collar. - co. = cone. - crt. = pneumatophore crest. - f. = float or pneumatophore.
- gstz.p. = primary gastrozooid. - l. = limb. - m.n. nematoblastic mass. - t. = tentacle.

The young *Velellas* (fig. 1D) arrive at the surface. Because of the inequalities of growth in their various parts, their shape becomes a parallelogram. An internal cartilaginous crest extends and progressively reduces the leaf-like crest, which is no longer interrupted by the apical pore. The sail is precise; it is placed diagonally and subject to torsion into an S. The pneumatophore is complicated, the number of chambers increased, the secondary external openings and stigmata appear; the aeriferous tubes are formed. The internal cnidoblastic mass becomes the central mass.

According to the animal's growth, all the parts of the gastrovascular system become increasingly complicated. The sub-leaf-like crown spreads horizontally under the float; it is limited externally by the crown of peripheral tentacles and internally by the base of the central gastrozooid. The tentacles, fishing and defensive, are in two, then several rows. Between these tentacles and the eating gastrozooid and reproductive blastozooids appear. They have a narrow distal part and a proximal swollen one, where the bunches of gonophores are inserted. They detach themselves immaturely, become free and constitute the small unisexual medusae: the *Chrysomitra.*

a^2) **Porpitidae**

At the outset, the porpitids show the same stages of development as the velellids. The studies of H.C. Delsman (1923) have shown that the porpitids also pass through the *Conaria* stage (fig. 10). But beyond this stage the embryos of *Porpita* and *Velella* evolve differently (E. Leloup, 1931).

The *Conaria* of porpitids is transformed into the *Disconula* larva. On its upper part the *disconula* posses a circular limb, slightly curved, and limited at its periphery by a collar. The inferior face carries the appendages; a primary central gastrozooid and a circle of eight peripheral tentacles. The chitinous float is comprised of two chambers; the central chamber opens to the exterior by the open terminal pore and the second chamber has eight extensions, each provided with a secondary pore, a stigma. The float lies on the compacted cnidoblastic mass. With all these organs, the disconula has acquired the characters of the adult *Porpita*. Beyond this time, the disconula increases in size without modification except for the multiplication of these organs, becoming the adult *Porpita*, with a circular float, without crest, with a constantly open apical pore.

The *Disconula* can easily be compared to a *Ratarula* of *Velella*, if one takes into account that certain of its organs are more evolved. The internal organisation of the *Ratarula* differs in two instances: the float only possesses a central chamber and the tentacles are less developed.

b) Cystonectidae

One knows few facts about the development of the bathypelagic cystonects *Rhizophysidae* and *Epibuliidae*. By contrast the voluminous siphonophores *Physalia*, surface dwelling organism, has been well studied (T.H. Huxley, 1859; Yo. K. Okada, 1932) and it allows an easy interpretation of what happens in the two other families. One presumes that *Physalia* leads a bathypelagic life during the first stages of its existence, because the planula has not yet been found. The simplest stage is the Cystonula (fig. 2A). It consists of a vast, superior, ovoid, pierced float situated at the extremity of a gastrozooid (inferior) of which the other extremity is provided with an orifice. Separated from the float, by a narrow part, this gastrozooid has an aboral swelling where the tentacle is inserted, the fishing filament.

Whereas the gastrozooid grows slowly, the float is developed in an exaggerated manner (fig. 2B, 2C, 2D). Its longitudinal axis executes an invertional motion; instead of resting vertically, it is progressively inclined and arrives at its horizontal position. In this position the float carries, at one end, the primary gz4, which resembles a short appendage and, at the other end, it has the apical pore, which disappears by fusion of the surrounding tissue (fig. 2D). In this case the morphological summit no longer corresponds to the physiological one; these summits are found on two perpendicular axes.
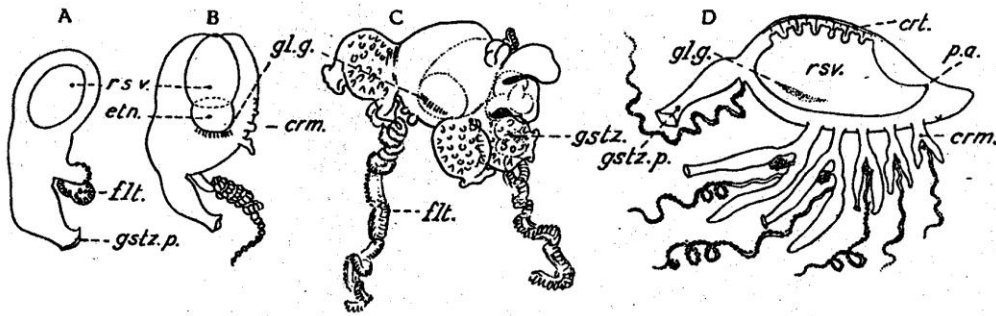
Figure 2. Development of physaliid Cystonectidae
(after Y. Delage and E. Hérouard, 1901 and Yo K. Okada, 1932)
Larvae of Physalia
A. Cystonula stage - B. Start of the appearance of the cormidial buds.
C - During the development of the cormidial buds. - D. At the moment of formation of the dorsal crest.
crm. = cormidium. - cyz. = cystozooid. - etn. = funnel. - flt. = tentacle. - gl.g. = gas gland. - gstz. = gastrozooid.
gstz.p. = primarry gastrozooi. - p.a. = apical pore. - rav. = reservoir.

Morphologically, above the primary gastrozooid; physiologically under the pneumatophore, there are formed the successive groups of cormidia. Each cormidium contains a long terminal peduncle with a mouthless cystozooid provided with a tentacle. A gastrozooid provided with a buccal orifice is inserted on the peduncle above the tentacle; it carries at its base a ramified gonozooid. The blastostyles produced by medusoid budding which, one believes, are detached at maturity, at least for the females.

One sees that the abnormal elongation of the float causes in *Physalia* an overturning in the orientation of the siphonophore and in relation to its different parts.

But it is easy to suppose that the float stays normal in that its apical pore is closed. In this case, the narrow portion of the *Cystonula*, which is found under the pneumatophore, elongates considerably (fig. 3). It becomes the centre for the formation of the very simple cormidial appendages, gastrozooids with their tentacles. On the siphosome, between each secondary gastrozooid, are formed the ramified gonozooids of which the free mouthless blastostyles support basally the sexual buds.

On such an extension is found according to whether it is joined vertically to the formation as in a rhizophysid where the siphosome remains stretched out with these cormidial elements separate, or in the epibuliids where the siphosome stays short and vesicular with the cormidia inserted in a helix.

B. - Amongst the Physonectidae there exist two zones of proliferation. Their embryological development has been well followed (E. Metschnikoff, 1874).

a) The voluminous egg, rich in deuteroplasm, is fertilised after its release. In undergoes a total and equal segmentation; it is transformed into a full morula. By secondary delamination, this morula acquires a layer of small peripheral cells, ectoderm, and an internal mass of large cells full of deuteroplasm, primitive endoderm. This primitive endoderm produces a continuous and peripheral layer of plate cells, definitive endoderm. The ectodermal cells are garnished with vibratile cilia. This free larval planula (fig. 4A) elongates and becomes bipolar, oval or pyriform. The nutritive reserves serve for the growth of the larva; the primitive endoderm disappears and a central cavity is constituted, the gastrovascular cavity, soon uniformly covered by the definitive endoderm.
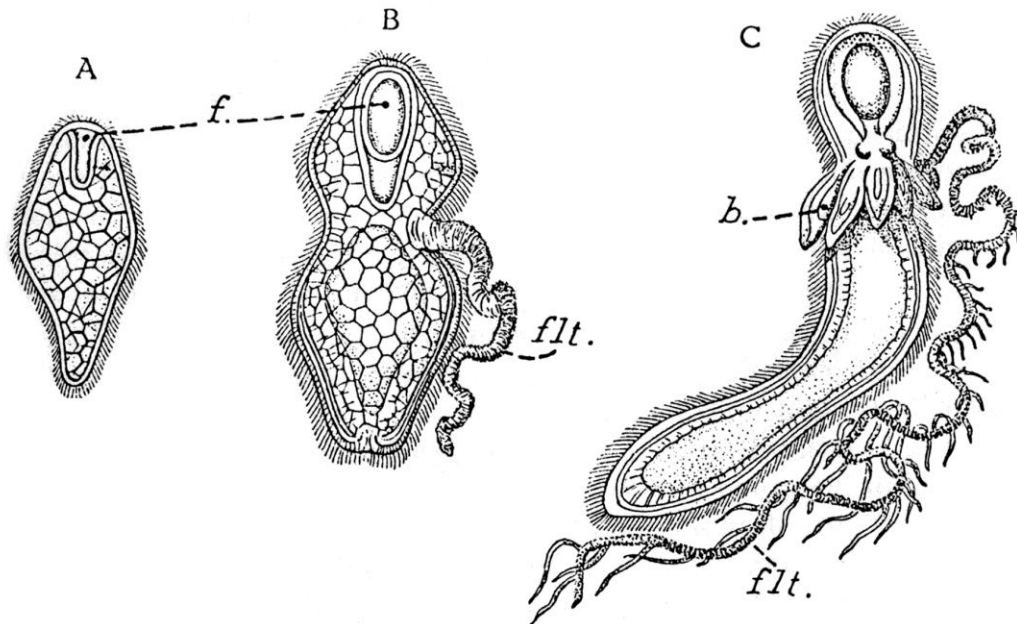
Figure 3. Larval forms of epibuliid Cystonectidae, Cysralia monogastrica
(after E. Haeckel, 1888)
A. Planula with float (f). - B. Ctsyonula stage, with tentacle (flt).
C -Older larva with proliferation of buds (b) of tentacules.

This planula, which resembles those of other hydrozoans, does not attach itself.

At one of the poles of the larva, the ectoderm thickens to form a nodule which becomes hollowed by a cavity, and is transformed to become the float of the organism (fig. 4B). Under the float, an annular transverse constriction separates the two parts of unequal size: an aboral superior region which entirely becomes the pneumatophore, and an oral inferior region of which the strongly pigmented extremity is perforated and which becomes the primary gastrozooid. At the level of the constricted part of the larva, this gastrozooid is provided with a thick ectodermal swelling, rich in nematocysts. At this place the wall of the body is evaginated as a digitiform bud which is considerably elongated and which becomes the caducous tentacle (fig. 4C).

This is the *siphonula* larva (fig. 4D).

In the course of development, the region of the float does not vary in the majority of siphonophore: while in *Physophora hydrostatica* (E. Leloup, 1941) the apical pore is closed and it forms a secondary lateral external pore.

The tentacle of the primary gastrozooid degenerates occasionally. The median zone in between the float and the gastrozooid undergoes a great change; it becomes a generative zone. It elongates considerably and is changed into a sort of stolon which starts to bud off all the members of the colony. On the side where the tentacle is developed are formed all the buds of the swimming bells and cormidia.

On finds two distinct zones of budding. One superior, immediately below the pneumatophore gives rise to the swimming bells (nectosome), by an identical process by which results in the medusae of the hydropolyp colonies. The other, inferior, part produces the cormidia (siphosome). Each cormidium arises from a unique bud. The primary unique bud is elongate and becomes the siphon or gastrozooid. Having its terminal opening, this gastrozooid shows two superimposed secondary buds: one

median, the future tentacle, and the other basal. The latter is divided into two tertiary buds: one superior which produces the bract, and one inferior which becomes the blastostyle, carrying the bunches of fertile medusoid gonozooids, and proliferating in their manubria the mass of genital products.

The budding process heightens toward the base, the oldest buds are the most inferior; it is independent of the two generative regions.
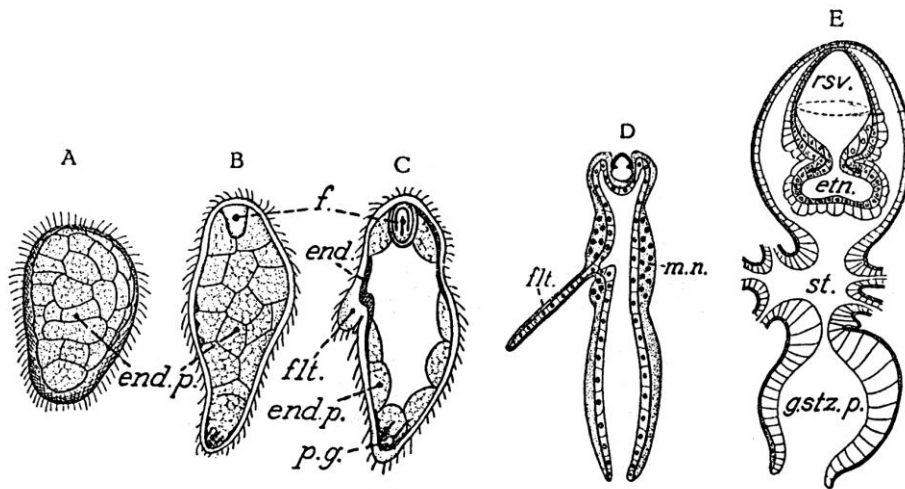

Figure 4. Developmnt of Physophoridae
A-C: Halistemma pictum (after E. Metschnikoff, 1974). E: Agalma (after R. woltereck, 1905).
A. Young planula with the aboral pole turned toward the base. - B. Larva with the debut of the pneumatophore.
C. Larva with the formation of the tentacle. D: Schematic Siphonula, morphological type.
E: Older larva with proliferation of stolon.
cnd. = definitive endoderm. - wnd. p. = primitive endoderm. - etn. = funnel. - f. = float. - flt. = tentacle.
gstz.p. = primary gastrozooid. - m.n. = nematoblastic mass. - pg. = pigmented zone. - rsv. = reservoir. - st. = stolon.

The stolon is subjected to torsion. In the nectosomal region, it is effected in one sense, and in the siphosome in the opposite sense; such that, during a contraction of the stolon, all the appendages appear to be disposed into a helix and orientated in all directions.

As far as the *siphonula* stage, the larva is covered in vibratile cilia and swims with the pneumatophore turned toward the front.

But in proportion that the pneumatophore is developed and that the stolon is formed and progressively differentiated, the embryo straightens by 90°. Instead of being moved horizontally, it is positioned vertically: its anterior part, with the pneumatophore becomes superior; the gastrozooid, instead of being posterior, becomes inferior. The ectoderm looses its ciliary covering and the colony, supported by the pneumatophore, floats passively with its greatest axis vertical. The float plays the role of a parachute which retards the descent of the larva and which gives it a vertical position in the water.

When the contractions of the swimming bells are sufficiently powerful to accomplish the movement of the colony, it advances itself with its greatest axis more of less horizontal and its float directed toward the front.

In the Physonectidae, the physiological summit corresponds to the morphological summit.

b) Always, this type of development can undergo some modifications. The embryonic organism forms an apical, larval caducous apparatus destined to sustain the colony in the midst of the water up to the time that the pneumatophore is sufficiently developed; for example in *Agalma sarsi* Kölliker, 1853.

At the aboral pole of the planula appears a circular fold of ectoderm. This fold increases in a continuous fashion and the mesogloea proliferates there, so that the ensemble forms a type of cap covering the aboral pole. The gastrovascular cavity there envelops an endodermal diverticulum, simple or bifurcate, the somatocyst. This apical organ not only protects the larva but, with the decrease in the density of this larva, contributes to its flotation (fig. 5A).

Moreover, the secondary and temporary bracts appear equally, they arise from an early proliferation of the siphosome (fig. 5B).

But when the pneumatophore attains a sufficient size, the apical organ and the secondary bracts degenerate and disappear.

C. - In summary, if one compares the development of the Physophorids deprived of a nectosome for the entire course of their existence, the Cystonectids and Chondrophorids, with that of the Physophorids provided with a nectosome and siphosome, the Physonectids, one ascertains that all these siphonophores pass from the beginning of their ontogeny through the same stage, the *Siphonula.*

In effect, in the Cystonectids, the first stages of development of the Physalids, Cystonectids, is easily comparable with the siphonula. On the other hand, E. Haeckel (1888) has described and figured, with regard to *Cystalia monogastrica*, some larval forms of the Epibuliids that agree with the siphonula (fig. 3).
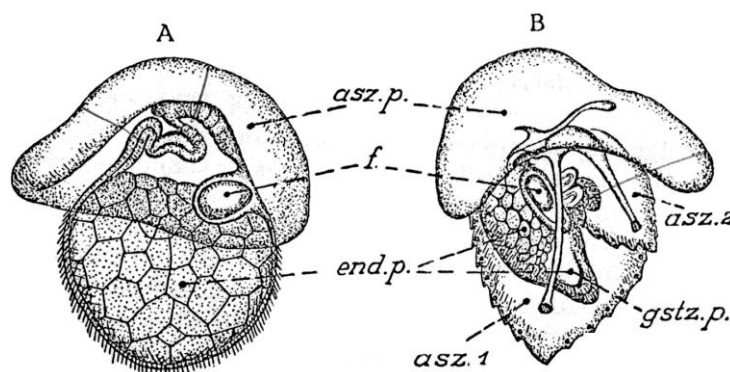

Figure 5. Two stages in the development of Agalma sarsi Kölliker 1853.
(after E. Metschnikov, 1974).
A: Larva with apical organ (primary bract) and pneumatophore. - B: More advanced larva with two secondary bracts.
asz. = secondary bracts numbered according to their order of appearance. - asz.p. = primary bract.
end.p. = primary endoderm. - f. = float. - gstz.p. = primary gastrozooid.

In addition, the Chondrophorids pass through the *Ratarula* stage. In 1888, C. Chun described the reason how the stage arises from a bilateral siphonula; the two larval stages can be homologised for all their constituent parts. Only the *Ratarula,* instead of lengthening vertically, spreads out in the horizontal sense; its middle part, which gives rise to the stolon in other Physophorids, undergoes growth in the horizontal plane. The pad of nematocysts proliferates towards the interior where it constitutes an organ peculiar to the Chondrophorids, the internal cnidoblastic mass. The complication of the gastrovascular system derives from the faculty, in an organism that achieves a relatively large size, of subdividing its internal organisation in order to assure the nutrition of all the parts of the body.

2. Embryonic development of the Calycophorids.

Deprived of a float, the Calycophorids appear to be made up in a different way than the Physophorids. However, one can easily homologise the various structures present in these two groups.

The development of the fertilised egg of Calycophorids is identical to that of the Physophorids, as far as the *Planula* larva (fig. 6A). After this stage the processes differ and lead to the formation of a special larva, *Calyconula*. (L. Lochmann, 1914; C. Chun, 1897, F.S. Russell, 1938).

Like the siphonula, the bipolar calyconula shows an annular constriction. This oblique girdle separates two distinct regions which will undergo different destinies.

At the basal end, one sees the appearance of the primary gastrozooid provided with its retractable tentacle (fig. 6B, 6C; 7B, 7C). This gastrozooid follows the same development as in the Physophorids. But the essential peculiarity of the calyconula resides in the fact that its apical part atrophies and disappears without forming the float (fig. 7C). The anterior mass of primitive endodermic cells degenerates without leaving any trace. To compensate for the absence of a float, a medusoid nodule appears above the tentacle of the primary gastrozooid. This nodule is transformed into a modified medusa, the larval bell, deprived of a manubrium and tentacles, showing a large subumbrella cavity, a very large orifice, a velum, a circular canal to which the four radial canals are joined, which, at the top of the subumbrella unite to form the pedicular canal. This pedicular canal enters into the superior part of the gastrovascular cavity of the primary gastrozooid. Soon, the anterior part of the wall of the pedicular canal gives rise to an endodermic diverticulum which ends in a cul-de-sac and is directed towards the apical pole of the larva, forming the somatocyst of the bell.

At the end of the calyconula stage one can consider two modes of development are derived one from another. It is necessary to distinguish the embryology of the calycophorids with regard to rounded bells and a slowly active life (Prayomorphae) and those calycophorids with prismatic bells and a very active mode of life (Diphyomorphae).

a) Development of the Prayomorphae.

The primary larval bell enlarges and forms a rounded, gelatinous mass, being a real hydrostatic apparatus that aids the suspension of the animal in the ambient medium (fig. 6E, 6F). Because of the resorption of the apical part of the primary endodermic mass, the somatocyst[2] at first more or less parallel with the longitudinal axis of the larva, is placed perpendicular to it and extends the axis of the subumbrella of the bell (fig. 6F). The region under the larval bell begins to bud.

The cormidia arise at the zone of proliferation situated slightly above the position where the peduncle of the bell is inserted onto the gastrozooid (fig. 6E). It is

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[2] According to the classic authors, the somatocyst or oleocyst of the bells of calycophores replaces the pneumatophore of other siphonophores as the organ of floatation. But M. Rose (1931) has shown that the somatocyst plays no hydrostatic role. This organ contains "a special physiological liquid, an actual secretion at pH always distinctly acid and which serves in the digestion of ingested prey." Moreover (M.Rose, 1939), the oleocyst of certain diphyid siphonophores often presents "some drops of a oily liquid that has a great analogy with the 'oil of copepods' from which it appears to be derived" and which includes infusorian ciliates.
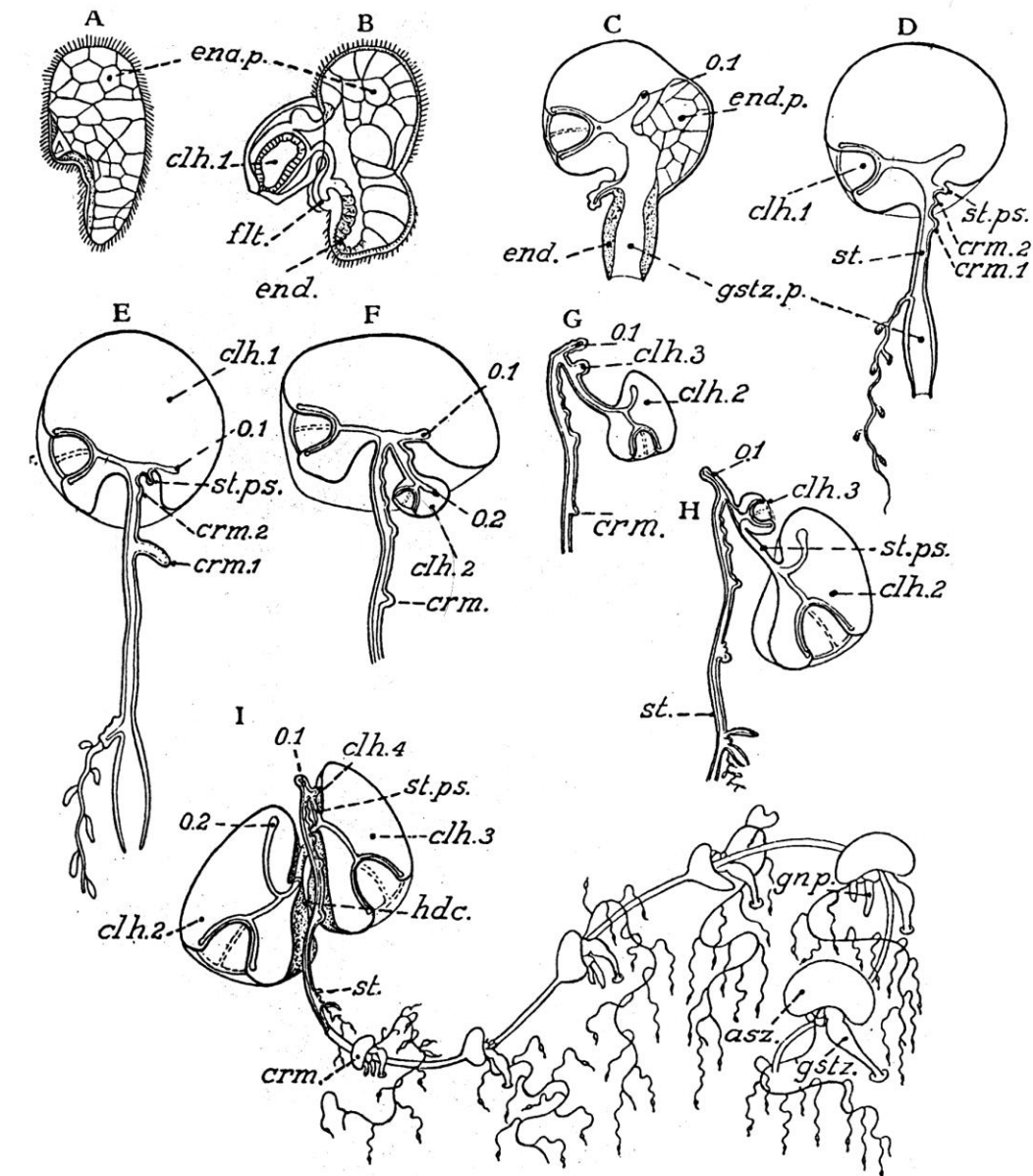
Figure 6. Morphological type of prayomorph Calycophorides.
Successive stages of development (after Y. Delage & E. Hérouard, 1901).
A: Embryonic form of the primary nectophore. - B: Formation of the endodermic cavity.
C: Formation of the primary gastrozooid. D: Formation of the stolon, with some cormidial buds and
stolon of nectosome. E: Growth of stolon and some buds. F: Formation of the second nectophore
representing the first permanent nectophores. - G: Colony after the loss of the primary nectophore.
H: Formation of the third nectophore representing the second permanent nectophore. - I: Developed colony.
asz. = bract. - clh. nectophores numbered according to their order of appearance.
crm. Cormidia numbered according to the order of their appearance. - end. = definitive endoderm.
end.p. = primitive endoderm. - gnp. = gonophore. - gstz. = gastrozooid. - gstz.p. = primary gastrozooid.
hdc. = hydroecium. - 0. = oleocysts numbered according to their order of appearance.
st.ps. stolon of pseudonectosome.

formed on the opposite side to the insertion of the larval bell, the dorsal side; there is
a succession upwards with the youngest being the highest.

The cormidia are liberated (*Eudoxia*). In certain species they are detached with
the gonozooids generally immature; they lead a free life and their gonocytes ripen.
These eudoxids assure a very extensive dissemination of the sexual products.

Generally their bracts are expanded, and their endodermic canal is a simple diverticulum or is ramified, provided with a large drop of oil, the phyllocyst, which assumes the role of floatation. Sometimes the cormidia develop a sterile gonophore, contributing to the motion of the whole colony, but which also serves for the locomotion of the eudoxid when it is liberated (*Ersea*).

Equally on the dorsal side, above the budding zone of the cormidia and at a level where the gastrovascular cavity bifurcates into the peduncle of the bell and into the somatocyst, a bud is developed (fig. 6E, 6F); it develops into the second bell of the organism, the first definitive bell. The peduncle of this bell is elongate. But, at that moment, the zone of proliferation of the nectophores is not able to enlarge towards the superior part of the larva. In effect, the umbrella mesogloea of the larval bell constitutes an amorphous, unchangeable mass and the peduncle of the first definitive bell pushes downwards. The second definitive nectophore arises at the base of the peduncle of the first (fig. 6G), its peduncle pushing back toward the base of the first and also each new bell repels the peduncle of the preceding bell.

In this way a more or less long stem is formed which bears at its distal end the first definitive bell and, laterally, some identical bells arising successively opposite or sub opposite, the youngest being the most elevated (pseudonectosome) (fig. 6I).

Then when the contractions of the definitive swimming bells become sufficient to ensure the locomotion of the colony, the first larval bell is detached. Its somatocyst remains at the level of the siphosome: it represents the morphological summit and acts the role of the physiological summit (fig. 6G, H, I).

In certain species, according to how a newly formed bell acquires certain importance, the oldest adult bell falls as, in an adult Prayomorph siphonophore, the normal number of bells remains almost constant.

The other part of the stem of the pseudonectosome coils into a helix around the stem of the siphosome, which represents the longitudinal axis of the colony. The latter, by its contractions, presses down on the mesogloea of the swimming bell. This mesogloea, increasingly, forms two wing-like extensions that encircle the constantly moving stolon: thereby forming a gutter, the hydroecium, which is present for all the height of the bell and which shelters the stolon (fig. 6I).

In the siphonula, the gastrovascular cavity proceeds from the siphosome to the nectosome following the same axis. In the calyconula this axis is altered at the level of the somatocyst vestige of the larval bell, and it proceeds in a inverse direction into the gastrovascular cavity of the nectosome.

b) Development of the Diphyomorphae.

The development of the Diphyomorphs is identical to that of the Prayomorphs as far as the formation of the bipolar larva, the calyconula (fig. 7A, 7B).

In the Diphyomorphs the primary bell becomes greatly extended. The growth is so rapid that the remainder seems to be dorsal appendage of the bell. Progressively, its attachment peduncle is disengaged from the rest of the larva. It soon forms a larval organism in which the two parallel parts are joined by a median, transverse peduncle (fig. 7C). The primary bell is provided with a sufficiently powerful velum, as well as a sufficiently voluminous oleocyst, oblique with regard to the longitudinal axis, and inserted onto the peduncle above the point where the four gastrovascular radial canals unite.

The peduncle is connected to the embryonic bodies of which the two ends experience different destinies. The oral part is transformed into a primary gastrozooid

with a tentacle. At the aboral end, the endodermal mass remains undifferentiated and it progressively disappears without giving rise to a float.

The peduncle that joins the embryonic bodies to the larval bell comprises a lateral extension of the primary gastrozooid. The diverse centres of formation for the parts of the adult siphonophore are found to be concentrated at this level.

On the superior wall a rounded bud appears, which will form the second swimming bell, and on the inferior side the zone of proliferation for the cormidia is formed. The latter elongates toward the base and forms the stolon.
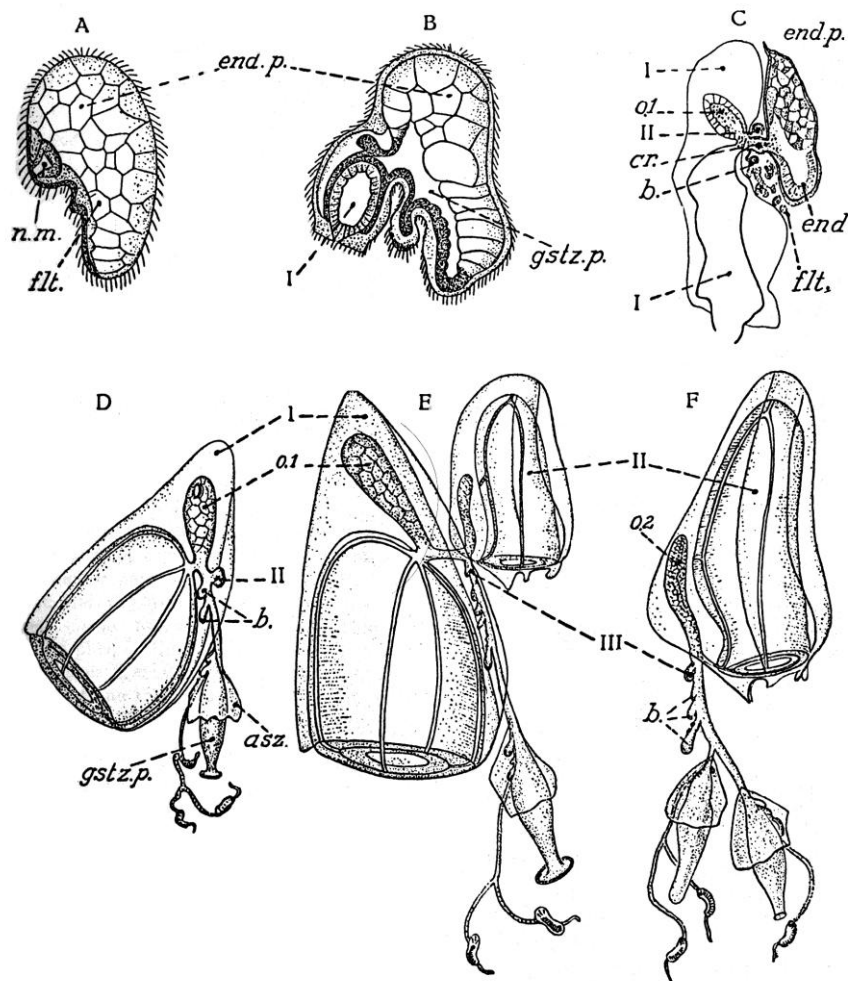
Figure 7. Development of diphyomorph Calycophorids
Sulculeolaria quadrivalvis Blainville.
A, B: after E.Metschnikoff, 1874. - C-F: after L.Lochmann, 1914.
A: Very young Calyconula larva with the buda of the nectophore (n.m.) and a tentacle (flt.). - B: Older larva.
C: Longitudinal section of a larva showing the separation of the substance of the Calyconula and the closed bell,
as well as the disappearance of the aboral part of the planula. - D: Stage with a primary larval bell (I) with the
budding of the first adult definitive bell (II), the anterior nectophore. - E: Stage with two bells (I & II) with the
budding of the second adult bell, the first posterior nectophore (III). - F: Stage with one adult definitive nectophore.
asz. = bract. - b. = buds of cormidia. - c.r. = vanal between the body of the larva and the first swimming bell.
crm. = cormidium. - end. = definitive endoderm. - end. p. = primitive endoderm. - flt. = tentacle.
gstz.p. = primary gastrozooid. - n.m. = medusoid nodule. - o. = oleocysts numbered according to
their order of appearance. - I, II, III. = nectophores numbered according to their order of appearance.

At this larval stage there is only the larval bell (fig. 7D). This is perfectly developed, as a conical, powerful swimming bell capable of carrying along the primary gastrozooid and the stolon in full evolution. Imperceptibly, the gastrozooid is displaced along the stolon, which elongates along the long axis of the apical oleocyst

of the swimming bell. In contact with the stolon, the inferior half of the wall of that bell is hollowed as a gutter, the hydroecium.

This freely swimming larva is formed by a colony that offers little resistance to forward motion. At this stage the top of the larval bell with the oleocyst represents the physiological summit; the morphological summit is situated immediately above the bud of the second swimming bell.

The first swimming bell, primary larval bell, no longer undergoes change. In contrast, the bud of the second swimming bell rapidly develops (fig. 7D, 7E); it produces an elevated umbrella, a simple gastrovascular system, a hollow hydroecium on the lateral part of the inferior face, and a lateral oleocyst parallel to the major axis of the bell. This second bell soon shows all the characteristics of the first definitive heteromorph bell, the anterior (or superior) bell of the adult siphonophore.

One now has a larval stage with two bells (fig. 7E) comprising, on the one hand, the rounded conical larval bell, with a lateral hydroecium and an apical somatocyst, and on the other hand, the superior definitive nectophore of the colony, which is elongated, prismatic, with a latero-inferior hydroecium, a somatocyst parallel to the nectosac and prolonged apically the stolon. These two bells are united by a peduncle which arises by the elongation of the stolon comprised, at the stage of the larval bell, between the base of the oleocyst of the first swimming bell and the bud of the second bell.

At this stage, the peduncle is found more or less perpendicularly between the base of the oleocyst of the primary bell and the base of that of the second. Soon, close to the first bell, slightly laterally, one sees a bud, the beginnings of the third swimming bell, the second heteromorph bell, the first posterior (or inferior) definitive bell of the adult siphonophore.

The second swimming bell, superior definitive bell, enlarges. At a certain moment the larval bell is detached. The rupture is made above the point of union of the stolon, the oleocyst and the peduncular canal of the second swimming bell, in such a way that the young superior nectophore entrains within itself the stolon (fig. 7F). This nectophore becomes the only locomotory apparatus of the colony; its form and structure allowing more rapid motion than could be achieved with the massive larval bell. The latter, isolated, moves about for some time, then stops and dies.

The third swimming bell, the first definitive posterior bell, is formed with or without an oleocyst. Endowed with more or less important contractions, it aids in the movement of the colony.

Then, at the base of the peduncle of the primary inferior bell, the second inferior bell is developed. Similarly at the base of the second inferior bell will be formed the third. Thus, each inferior bell is budded at the base of the preceding bell and presses it back such that each colony of Diphyomorphae is usually only composed of a single posterior bell and a single anterior bell, which appears to remain throughout the whole life of the colony.[3]

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[3] Always, in certain colonies (*Sulculeolaria quadrivalvis*, see Leloup, 1935), 2, 3 or even 4 posterior adult bells adhere together to the common trunk. On the other hand it is generally admitted that only the posterior bells are replaced. But C. Chun (1885) showed that "both nectophores of the Diphyidae show a continual renewal by reserve nectophores of identical shape". Further, C. Chun (1885) for *Galetta turgida* (Gegenbaur, 1854), and L. Lochmann (1914) for *Lensia subtilis* (C. Chun, 1886) have shown that a posterior bell, provided with every short trunk, presents a replacement bell simply identical to the superior bell. However, the statements of these authors are too brief to establish them as an important fact.

In consequence, the budding zone of the swimming bells, that is to say the nectosome, is condensed to a very limited part of the stem. This progressive regression of the generative facility of the nectosome is made even to the point where in certain species, there is no longer a formation of posterior nectophores. Only the anterior nectophore persists and assures the movement of the colony (monophyism).

In the Diphyomorphae, the physiological summit is represented by the top of the superior bell; the morphological summit is situated at the apical part of the stolon at the junction of the oleocyst of the superior bell and the pedicular canals of the superior and inferior bells.

c) Comparison of the calyconula of Prayomorphae and Diphyomorphae.

The study of the two modes of development of the calyconula larva demonstrates that, in the Calycophorids, the apical part of the planula degenerates. With this, the position of the bud of the pneumatophore disappears. It cannot thus be a question of homologising the pneumatophore of the Physophorids with a given structure in the Calycophorids, and notably to the definitive superior bell as F. Moser (1925) claimed.

The larval bell of the Prayomorphs is homologous to the larval bell of the Diphyomorphs. In the two cases, it arises at the same place in the planula larva.

The first adult bell of the Prayomorphs is homologous to the anterior definitive nectophore of the Diphyomorphs. It is formed on the opposite side to that of the larval bell. In the Prayomorphs this bell is caducous, while in the Diphyomorphs it persists,

The replacements bells of the Prayomorphs, those which succeed the first adult bell, are homologous with the replacement or posterior bells of the Diphyomorphs. Thus, it is necessary to remark that, in the Prayomorphs, the peduncle of the first definitive bell is prolonged by the peduncles of the swimming bells that are successively formed, to constitute the pseudonectosome. In contrast, in the Diphyomorphs, the posterior bells are rapidly detached and the zone of replacement remains condensed.

3. Comparisons between *Siphonula* and *Calyconula* larvae.

The siphosome behaves in exactly the same fashion in the siphonula as in the calyconula. But, as the siphonophore becomes more active, one sees that the cormidia are detached more numerously. Before even their sexual products reach maturity, they abandon the mother colony to live independently (eudoxids). In consequence, when the siphosome produces new cormidia at its proximal end, it loses one at its distal end, so that as a result not only multiplying the chances of dissemination of the species, but also to lighten the colony and increase the possibility of speed. The production of eudoxids increases proportionally with the progressive abandonment of a passive life.

The pneumatophore is not found in the calyconula larva because of the degeneration of the aboral end of the planula.

The production of the nectosome is active in the siphonula, slow in the calyconula. In the calycophorids, their elements also arise successively from top to bottom; but a massive organ, the larval bell is developed before the appearance of the budding zones. From the start of ontogenesis, it prevents the nectosome from proliferating during the elongation of the siphosome, such that the generative centre has been forced back laterally. The zone of proliferation of the nectosome is divided into sections at the base of the somatocyst of the larval bell (fig. 6,7). The peduncle of

the following bell, first definitive bell, is a bud on the stem. It elongates and, on encountering the larval bell, can only expand laterally and in the opposite sense to the major axis of the colony; thus explaining the broken line which appears between the axis of the siphosome and the axis of the nectosome in calycophorid colonies.

The peduncle of the first definitive nectophore takes on a great importance and constitutes the origin of the pseudonectosome in the Prayomorphs; siphonophores with slow movement. In contrast, in the Diphyomorphs, with rapid movement, the production of the nectosome is made according to a more and more accelerated rhythm: one nectophore replacing its predecessor, which is detached, such that their number remains relatively limited. Also, in the, it does not form a pseudonectosome; the region of the formation of the nectophores remains compact, beneath the somatocyst of the anterior bell, and in a more and more restricted zone.

as R. Woltereck (1905) and F. Moser (1925) have reported, the apical bract of certain Physophorids is equivalent to the larval bell of Calycophorids; it represents it in outline.

C. Chun has attempted several times to demonstrate that the primary bell of the calycophorids is homologous to the pneumatophore of the physophorids. This homology has proven inexact. It is a question of an analogy, because the primary bell of the calycophorids and the pneumatophore both fulfil the same function, as a hydrostatic apparatus, but are formed in different embryonic regions.

In summary, the comparative embryology of the siphonophores tells us that a characteristic form of their phylogeny is represented in their ontogenetic development up to the siphonula stage.

The differences that come into play after the transformation of the siphonula result in a diversity of adult forms; these are the secondary modalities acquired by the siphonophores during their evolution, as progressive liberation, first to a passive pelagic life, and later to a slow active life.

The adaptation of the siphonophores to an active, rapid pelagic life has resulted in the fracture of the gastrovascular axis between the zones of formation, nectosome and siphosome, and the disappearance of the production zone of the pneumatophore; the appearance, the transformation and migration of the hydroecium; the concentration of the nectosome, the decrease in number and the shortening of the nectophores, the displacement of the posterior bells first opposing then sliding behind the anterior bell, the formation of eudoxids and the appearance of a prismatic structure.

II. ORIGIN OF THE SIPHONOPHORES.

A. Author's concepts.

The diverse concepts for the organisation of the siphonophores discussed previously rest particularly on the hypotheses relating to the origin of this pelagic group, this origin having been made the subject of numerous controversies amongst the specialists.

Some think that the siphonophores descended from a medusoid form, others believe they are derived from a hydropolyp form.

a) Among the subscribers to the medusoid origin, E. Haeckel (1888) joined the Chondrophores to the Trachymedusae, and the Cystonectids, Physophorids and Calycophorids to the Codonid Anthomedusae.

R. Woltereck (1905) believed that the siphonophores possibly arose from the "*Bipolaria*" larva. These *"Bipolaria"* relatively resembling the actual Narcomedusae, are the pelagic larvae of the ancestral polyp, real sacs of which the wall is composed of two layers, differentiated into two poles, the oral pole and the aboral pole (point of fixation). In the siphonophores, the aboral part is transformed into the proliferating stolon provided with a special terminal organ, or swimming medusoid, highly developed in the Chondrophorids and under which arise the blastostyles. From the Chondrophorids, R. Woltereck makes to derive the Calycophorids, deprived of terminal organs, with a recurved stolon and a secondary medusoid placed laterally. By contrast, in the Physophorids, the primary zooid looses its medusoid structure, the secondary zooid is transformed into a simple protective parachute by which is formed the third zooid, the pneumatocyst.

H.C. Delsman (1923) makes to derive the Disconects from Anthomedusae.

F. Moser (1925a) has reviewed in this way the idea directed from her works.

The primitive siphonophores was a larval form resembling the most primitive monophyids, but smaller and simpler; a small bell with radial symmetry, simple, borne on a medusoid bud carried at the aboral end, a simple cormidium, composed of a gastrozooid with basal tentacle and a genital organ, hanging on a small, short, exumbrella, stem = *Protomonphyes* of C. Chun. On the other hand the author mentions that the primitive siphonophore appears as a primitive medusa from which one can derive all the cnidarians, of which the Heteromedusae are the most primitive forms which, by regression of the bell and of the basal tentacle, give the polyps and for which the free pelagic life is primitive.[4]

b). The defenders of a polyp origin are more numerous..

Already in 1865, A. Agassiz wrote "I have already hinted at the similarity of the embryonic *Nanomia* …, when it consists of only the large polyp and the float, with the early stages of the fixed Hydrarium of Melicertum; where we have at first a single polyp, from which are derived, by budding, the branches and the other kinds of individuals of the community; supposing this community, instead of fixing itself, as it does, to remain movable, the base of the stem to expand into a float and become separated from the main cavity, we should have a siphonophore".

In 1884, C. Claus derived the siphonophores from a larval form resembling that of the planula larva of a *Hydractinia* or of *Polycoryna*, colonial hydropolyps which already showed polymorphism.

In 1892, O. Hamann derived the siphonophores from the Taeniolate hydropolyps which show some endodermic, longitudinal grooves in the gastrovascular wall of the hydranth.

For this author, the transitional form of the hydropolyps was liked to the actual hydroid. This form is developed, on the one hand, toward the Intaeniolates (*Hydrinae,*

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[4] I can only admit that the mode of primitive life of the coelenterates has been pelagic. Of others, E. Korschelt and H. Heider (1893), Ed. Perrier (1881), Ed. Perrier and Ch. Gravier (1902) have arrived at the same conclusion for all the primitive forms of ramified animals.

In effect the protoplasm was heavier than the ambient liquid medium, life ought to have developed in the depths of the sea. All the organisms that abandoned he deep and live in the plankton show special adaptations reducing their density, such as the extension of their horizontal surface, the production of droplets of oil, of gas, of abundant mesogloea, the formation of particular organs, floats, swimming vessels, etc. (Murray, J. and Hjort, T., 1912; Hesse, 1924). I consider, as prototypes for hydrozoan coelenterates, some simple hydropolyps, sessile, fixed at depth; these hydropolyps having acquired the facility to bud, to form some colonies; the medusoid forms are derived.

Campanularinae, Sertularinae) and, on the other hand, toward the polyps with longitudinal, endodermic grooves "of Taeniolated, such medusoid structures, from which comes the siphonophore".

In 1902, A. Lameere formulated a rational supposition that perfectly applies to the origin of the Calycophorids: "Supposing that the medusa appears at the right moment, not on the polyp, but even sooner, directly on the planula before that itself is fixed and changed into a polyp; the beating of the medusa entrains the larva, preventing it becoming sedentary, the swimming body remains pelagic, and we will have siphonophores.". This hypothesis is equal to the others, which consider the Calycophorids as the most primitive siphonophores; but does not explain the origin of the Physophorids which form the least evolved group.

For A. Goette (1907), the siphonophores were derived directly from the pelagic hydropolyps, such as *Margelopsis* and *Pelagohydra*, derived from a principle hydranth and reproductive medusae.

Concerning the pelagic hydranth of *Margelopsis stylostoma* described by C. Hautlaub (1904) and "which is apparently detached from *Tiarella singularis* F.E. Schulze", A.G. Mayer (1910) mentioned that "it is apparent that the Siphonophorae may have been derived from hydroid forms having a similar life history".
According to J. Hadzi (1918), the siphonophores were derived from species resembling *Margelopsis*. The actinula, polypoid and pelagic form, is transformed into a hydrosome which buds off some medusae is modified and remains in part sessile; primitively the gonomedusae are detached, following their enlargement, and become sessile. The siphonula is a polyp and the primitive bract a larval organ.

For J. Hadzi (1918), the siphonophores were derived from gymnoblastic hydropolyps living isolated and broken into a little consistent bottom (???); the solitary mode of life and the extension of the planktonic life of the larva (actinula) explained the passage into the pelagic mode of lie. The author has tried to demonstrate, in consequence of the adult form, that the Chondrophorids arose from solitary Tubulariids (*Corymorpha*) and the Siphonanths from simple colonies of Tubulariids *Myriothela*). In the Chondrophorids, the swimming part represents the basal, cauline, part of the hydropolyp of *Corymorpha*: the gastrozooid the hypostome; the internal zone of proliferation the intertentacular chamber. In the siphonanths, the distal extremity agrees with the hydrorhiza barely (or not) formed in the hydroid colony; the middle part, to the hydrocaulus where the secondary polyps are budded; the principle part, to the hydranth with the primary polyp.

The hydrorhiza of the polyp becomes a primitive, static organ, a parachute. On the hydrocaulus, there is formed the reproductive medusae and the secondary polyps (hydrosome). In the siphonophores, the medusa plays a primordial role. In effect, a part of the medusa carries the reproductive elements specialised for a locomotory function; they finally eliminate the primitive mode of passive floatation due to the larval bract; also forming a locomotory zone, the nectosome. This forms remains as that in the Calycophorids; but in the Physophorids there is added a pneumedusa, that is to say a medusa that penetrates, secondarily, to the distal extremity of the hydrosome. Under the nectosome, the siphosome is differentiated, a region comprising the polymorph and medusomorph organs brought together in separate groups, the cormidia. The terminal individual, the primary polyp with its reduced tentacular crown is maintained.

For A. Lameere (1929) "the siphonophores were descended from a gymnoblastic hydroid; they arose probably from Capitates of the group Corynides",

"from which the colony has been formed from a small number of polyps, but in which appears precociously some medusae".

In 1929, based on a study of the actinula larva, I put forward the idea that the Physophorids (Chondrophorids + Cystonectids + Physonectids) were derived from hydropolyps close to the actual Tubulariids. And moreover, verifying that in the Chondrophorids, the sexual products are borne on the manubrium of their medusa, I have concluded, without other precision, that the Calycophorids arose from gymnoblastic hydropolyps. This second hypothesis leaves to suppose a diphyletic origin of the group; is not to be retained, because, as I have previously seen, the calycophorids are related to the primitive physophorids.

For R. Weill (1934), the siphonophores of the Calycophorid-Physophorid group are joined to the true gymnoblastic capitate hydrozoans; that is to say with capitate tentacles provided with desmoneme cnidoblasts.

Describing an immature individual of a aberrant cladonemid medusa, *Oonautes hanseni*, D. Damas (19936) showed a special subdivision of the gastrovascular cavity, a subdivision that, in its general shape, recalled that observed in *Velella* (E. Leloup, 1929) and in *Porpita* (E. Leloup, 1931). This morphological fact made him search for the origin of the chondrophorids amongst the Anthomedusae; while, the author stipulates that *Oonautes hanseni* does not represent an intermediate form between the two groups. But, in nature, the conditions of existence govern the organisational form; in the case of *Oonautes* and of the Chondrophorids, it suggests a phenomenon of convergence evident in some coelenterate organisms which leads to the same way of floating life.

W. Garstang (1946) believed that the disconanths had some very close relations with the Tubulariids and especially *Corymorpha*, because of the actinula larva, of the aboral structure of its large axial polyp, of its ramified aboral, gastrovascular cavity and its aboral network of tentacles. For this author, the planulae of actual siphonanths developed, generally one per gonophore, beginning with the eggs stuffed with reserves. Very soon they are used for proliferation, so that the characters of the primitive actinuloid can be suppressed or retarded.

The siphonanths are joined to the Corynoids. The structure of *Pelagohydra* and of *Myriothela* suggests the possibility of a common origin through the intermediary of certain types of Gymnoblasts which have rise to the two lines of siphonophores.

B. Siphonophores and Tubulariid Hydropolyps.

On looking at the facts, with the actual state of our knowledge, one can express the opinion that siphonophores are derived from gymnoblastic hydropolyps of the Tubulariid family, without being able to state precisely either the species or the genus. The identity of their hydromedusae and the analogies of their cnidome stated already are in favour of bringing together these two groups.

It seems certain that the passage from the benthic fixed life to the free swimming planktonic life could be effected only during the larval period.

The siphonophores arose from an ancient polypoid form, tachygenic actinula, of which the actual living type is represented by the actinulae of *Turbularia*. To support this hypothesis, it is convenient to base it on the one hand, on the comparison of the larval stages of siphonophores and of tubulariid hydropolyps, and, on the other

hand, on the examination of the adult form of pelagic tubulariid hydropolyps actually known.

C. Actinula and Siphonula

Comparing, in the first place, the characteristic larva of the siphonophores (siphonula) with the free larval stage, temporary (actinula) of sessile Tubulariids at the adult stage, such as *Tubularia larynx* Ellis and Solander, 1786.

1. The actinula larva and its transformations.

In the subumbrella cavity of the fixed medusoid bud of *Tubularia*, the egg is transformed into the planula. After being released, this planula acquires an ovoid shape, develops some tentacles and is transformed into a polypoid actinula larva, which resembles an adult hydranth of Tubulariids.

This actinula, free swimming by means of its cilia, or is displaced to the deep with the hydrosome directed toward the base, in this latter case, certain proximal tentacles function like feet while the others are raised up.

Soon the actinula affixes by the aboral pole, it trunk elongates, it forms some roots, the beginnings of the hydrorhiza, and also directly becomes a hydropolyp.

Considering any actinulae at the moment when it is displaced to the depths of the sea and comparatively examining its structure with that of a hydropolyp adult.

Figure 8A shows a schematic longitudinal section of an actinula of *Tubularia larynx* slightly after its appearance. This larval form shows already the characteristics of the hydropolyp (fig. 8B). It is divided into three principle regions.
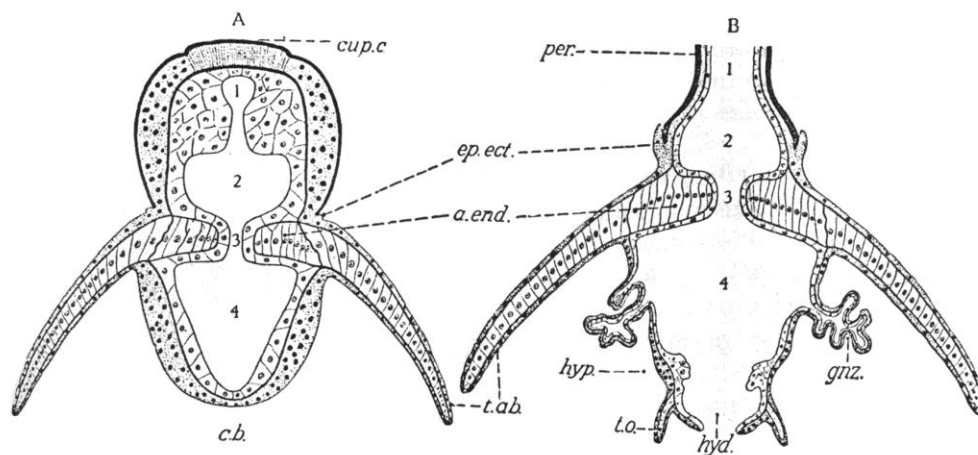
Figure 8. Semi-schematic longitudinal sections of the hydropolyp Tubularia larynx Ell. & Sol. 1786.
A: Actinula. - B: Distal extremity of young hydranth.
1, 2, 3, 4: Subdivisions of the gastrovascular cavity. - a.end. = endodermic ring. - c.b. buccal cone.
cup.c. = chitinous cup. - cp.ect. = ectodermal layer. - gnz. = gonozooid. - hyd. = hydrostome.
hyp. = hypostome. - per. = perisarc. - t.ab. = aboral tentacle. - t.c. oral tentacle.

A. - The cylindrical aboral part, limited below by the crown of aboral tentacles, showing a differentiated ectodermal layer and two endodermic layers.

a). Of one part, this simple prismatic ectoderm which covers the convex aboral part forms a circular zone limited by an annular, slightly deep groove. These very elevated

cells have acquired a glandular function; at their surface they produce a thin layer of chitinous substance.

On the bodies in the aboral part, the ectoderm is differentiated into two superimposed crowns. In the upper crown, the ectoderm is layered; the basal cells produce numerous nematocysts, and the peripheral cells secrete a chitinous lamella. The inferior crown, with simple cuboid epithelium, only contains some cells secreting chitin. It is limited below by a groove which brings to a halt the chitinous layer. The groove, bordered below by a thickened ectodermal swelling, surrounds the bases of the tentacles.

In the adult tubulariid, the apical glandular region is found again in the flattened basal hollow of the concave disc and constitutes the adhesive organ of the primary hydropolyps. The chitinous sleeve of the actinula elongates with the aboral part, which undergoes a considerable extension and which is ramified to form the colony; it forms the perisarc layer. The apical cnidoblastic proliferation is started again in all the coenosarc layers of the colony. Just as in the actinula, the perisarc is stopped, at the base of the aboral tentacles of the hydranths, by an annular groove limited by a pad of thickened ectoderm.

b). The other part, the endodermic later, delimits two superimposed cavities, dilated as ampullae. The lower vesicle, the more important, is joined to the upper vesicle by a cylindrical, narrow peduncular cavity.

In the adult tubulariid, the proximal gastrovascular cavity is found under the aboral crown of tentacles, while the peduncle unites with the considerably lengthened distal cavity in becoming the gastrovascular cavity above the primary polyp of the colony.

B. In the actinula the apical region surmounts a short, cylindrical middle section. That which supports the full, long aboral tentacles. The endoderm of the tentacles is prolonged into the gastrovascular layer as a sort of circular endodermic pad which narrows the cavity to a canal, the endodermic ring. At the level of the tentacles, the stratified bare ectoderm produces some reserves of cnidoblasts. These elements migrate towards their place of function on the tentacles.

In the adult tubulariid, this middle region is retained unchanged.

C. The inferior part of the actinula represents the buccal cone. Its gastric cavity is large and uniform; the cnidoblastic zone of the middle region becomes hollow and some short, full, oral tentacles arise.

In the adult tubulariid, the shape of this buccal cone is retained unchanged. But, at the level of the aboral tentacles, the wall of the buccal cone of the actinula begins to bud some blastostyles - producers of sporosacs.

2. Comparison of actinula and siphonula larvae.

The siphonula larva (fig. 4D-4E) represents the most primitive degree of development which exists in the siphonophores. Its diverse parts correspond exactly to those which constitute the actinula larva (fig. 8A).

a) The superior region of the siphonula is characterised by the float. This float is formed by a simple apical invagination. In the simplest case, the float is composed of two very distinct regions; an inverted cone, inferior, covered with bare stratified ectoderm; the funnel is surmounted by an ovoid cavity, the reservoir, in which the

simple ectoderm secretes a chitinous layer, the wall of the pneumatocyst. This pneumatocyst takes the shape of a bell with or without an apical pore, its edge stopped at the level of the annular constriction of the thickened ectoderm situated between the reservoir and the funnel.

One can easily imagine that, in the actinula, all the apical part comes to invaginate towards the mid region of the gastrovascular cavity of the larva. In this case the apical glandular zone becomes the surface of an internal cavity covered with ectoderm. This surface is limited by a groove which corresponds to the apical circular opening of the actinula; it does not produce chitin in the physophorids other than the chondrophorids. This surface is depressed and its invagination forms the funnel. The chitinous collar that surrounds the cylindrical apical region of the actinula has rotated toward the inside: it is the pneumatocyst limiting the reservoir. The inferior part, limited by the thickened ectodermic pad situated at the base of the aboral tentacles of the actinula, is found again around the orifice of the invagination of the pneumatocyst, the apical pore. The endodermic cavities of the actinula are mingled with each other in the siphonula, those which precede and surround the invagination of the float: they remain simple or better they are complicated as the organisms attain a certain size.

The beginning of this phenomenon of invagination which affects the apical part of the larva is actually seen in the planula larva of the hydropolyp *Eutina mira* (fig. 12) and the anthomedusan *Turritopsis nutricula* McGrady. Always, in the course of development of actual physophorids, one finds none that are distinct from this primitive formation. Instead of a hollow at the apical part of the planula, it develops an intense proliferation of primitive ectoderm, that which begins the formation of the secondary ectoderm. This button gives rise to the shape of the float; it becomes a cavity which, sometimes, pierces the layer of primitive ectoderm and appears on the outside (figs. 9, 10).

b) The inferior part of the siphonula comprises the primary gastrozooid provided with its tentacle and its cnidoblastic swelling.

It is easy to homologise this part of the siphonula with the distal extremity of the buccal cone in the actinula and to the hypostome in the tubulariids. The tentacle of the siphonula constitutes a vestige of the oral tentacle of the actinula and its nematoblastic swelling corresponds to the inferior part of the nematoblastic zone that covers the buccal cone of the actinulae.

c). The annular constriction, immediately below the float (fig. 4D) in the siphonula represents not only the mid region of the actinula, but also the zone of proliferation of the blastostyles which, in the adult tubulariid, are manifest on the hypostome underneath the aboral tentacles.

On the one hand, in the siphonula of the physophorids, the aboral tentacles have disappeared, but they reappear in the Ratarula of chondrophorids (fig. 1B). The mid region where they are formed in the actinula becomes the nectosome in the physophorids.

On the other hand, the budding zone of the blastostyles in the actinula is homologous with the zone of proliferation of the blastostyles in the Ratarula and with those of the cormidia, including the reproductive elements, in the siphonula. The nematoblastic zone of the buccal cone in the actinula remains diffuse in the adult tubulariid and in the siphonula, while, in the Ratarula, it actively proliferates towards the inferior in the internal endodermic mass, where it forms a nematoblastic mass.

In summary, in the actinula larva of the tubulariid hydropolyps, the growth it makes at the expense of the aboral part, the mid regions and the buccal part remain

unchanged, while the region below the crown of aboral tentacles becomes the seat of active proliferation. In contrast, in the siphonophores, the oral region remains unchanged and the aboral region is transformed into a float, while growth is made by proliferation in the mid region.
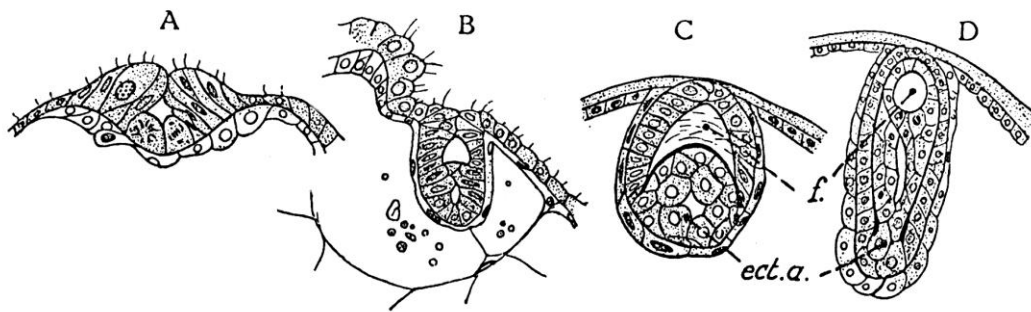
Figure 9. Successive stages in the development of the pneumatophore of
Agalma elegans (Sars, 1846) (after R. Woltereck, 1905).
ect.a. = aeriferous ectoderm. - f. = float.

D. Pelagic Tubulariids

In support of this hypothesis, one can still involve the ascertained facts in the pelagic adult form of this same family of tubulariids. One knows that certain species (*Margelopsis, Pelagohydra, Climacocodon*) attain maturity whilst leading a free life. They are liberated from the primitive sessile life (at least during a long period of their existence; because there exists no chronological observations permitting one to affirm with certainty that these organisms do not have a fixed hydropolyp stage).
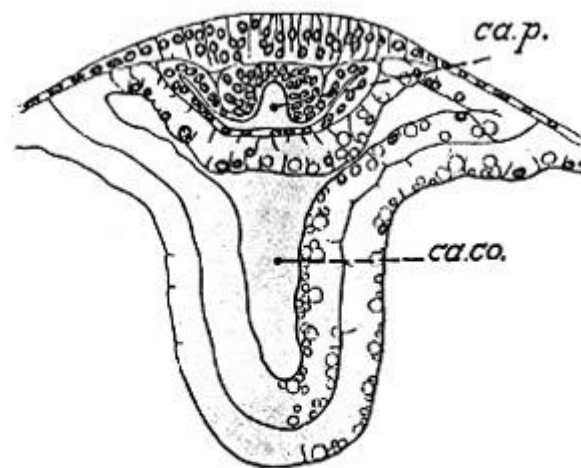
Figure 10. Median longitudinal section of a Conaria of Porpita
(after H.C. Delsman, 1923), aboral part.
Debut of the formation of the pneumatophore, ectodermic bud
ca.co. = cavity of cone. - ca.p. = cavity of pneumatophore.

In such hydropolyps are represented some tachygenic actinulae of which the evolutionary cycle can be imagined as follows: the actinulae borne on the manubrium of the free medusa are liberated and become some hydropolyps. At the beginning of their existence, the latter probably should be fixed and take up a sessile existence, but only precise observations can prove that the hydropolyps found floating do not undergo a period of fixation at the beginning of their ontogenesis. They are detached from their support, either normally or accidentally, after strong agitation in the water; they appear thereafter in the category of planktonic animals. They reproduce asexually by medusoid buds which are transformed into free medusae. On their manubrium the medusae give rise sexually to some planulae that develop into actinulae. The free hydropolyps swim with the buccal orifice directed towards the base; they progress thanks to the flexing movements or to the elevation and depression of their aboral tentacles.

In these species flotation is assumed in two different ways. On the one hand, in *Pelagohydra* (fig. 11A), the tissues in the aboral part of the hydranth are strongly developed and complicated: the superior part is swollen and becomes what A. Dendy (1903) calls the float. This veritable hydrostatic balloon carries the aboral tentacles dispersed and mixed with the gonozooids: it allows the animal to maintain itself at the surface.

On the other hand, in *Margelopsis* (fig. 11B) and in *Climacocodon* (Fig. 11C) the hydranth is slightly augmented in size; meanwhile it has modified slightly its general shape. The gonozooids appear between the two circles of tentacles. In *Margelopsis* the aboral part hollows out a capsule.

E. Origin of the Float.

In the first place it cannot be a question of the hypothesis of F. Moser (1925).

According to this author, in which the medusoid form is primitive and the fixed life secondary, one must ask how a free heteromedusa can be transformed into a colony of sessile hydropolyps. At the beginning of ontogenetic development, the planula affixes itself by the aboral ciliated layer before even the appearance of an apical organ. From this aboral plate emerges the basal plate or fixation disc of the heteropolyps which is transformed into the hydrorhiza, homologue of the bell in siphonophores. But it seems to me indisputable that the pelagic life is secondary and derived from the primitive fixed life.

In reality, the difficulties lie in imagining the manner by which a sessile polyp or a small colony of a hydroid can become free and adapt itself to a floating pelagic life. One should first consider that the primitive float was inert and that floats capable of contraction are acquired as secondary characters: in effect, this latter form of float is found especially in organisms of great size (Velellas, Auronectids, Physophorids) where the important muscular layers are developed.

Several hypotheses have been envisaged. For the supporters of the medusomorph theory, the float will only be medusoid, a modified swimming bell where the water is replaced by air organs.

R. Woltereck (1904(, while considering the pneumatophore as a homologue of a medusa, suggested the hypothesis that the pneumatophore and medusa can be derived from a particular organ which he explains as following the evolution in the disc of fixation of a "first Radiate (?)" polymorph colony that takes the form of a cylinder in the pelagic larva. This aboral vesicle executes some contractions which,

not only invest the larva with movement, but which can equally entrain the food in the interior of the vesicle (and later to eject the genital products). When the larva does not affix itself, as in the siphonophores, certain organs, vesicular, terminal, exclusively locomotory and sterile, can remain (pneumatophore, swimming bells), while the others (limited later by the secondary parts of the colony) to hold back the reproductive cells.
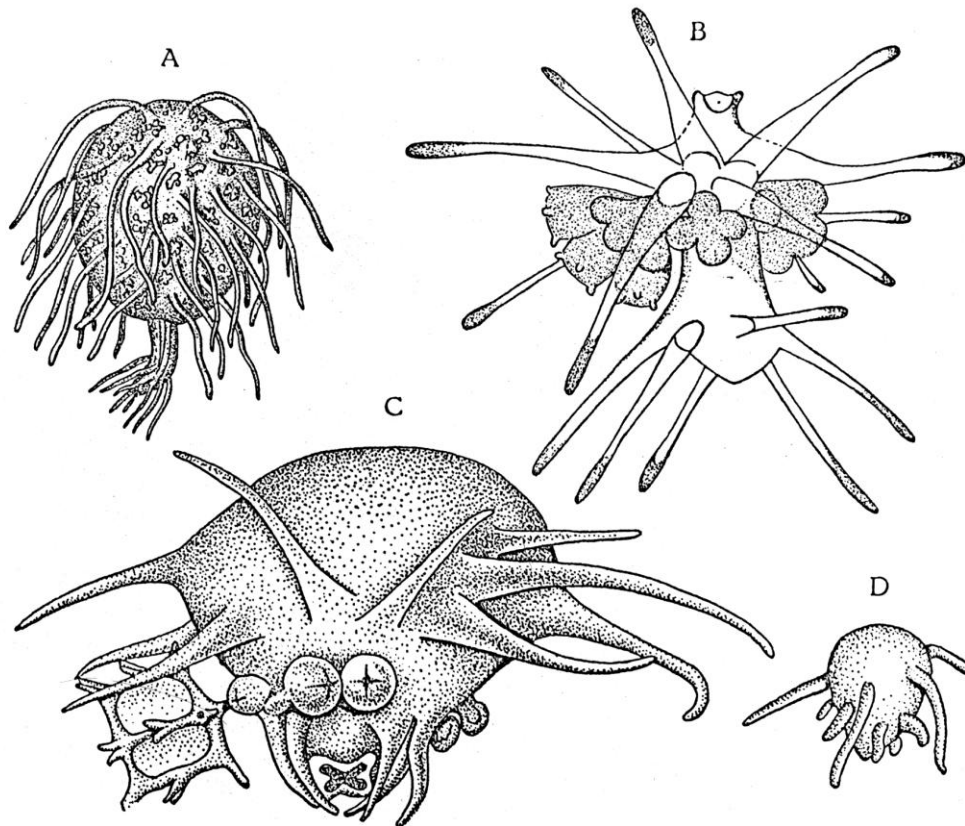
Figure 11. Pelagic Tubulariids.
A: Swimming hydropolyp of Pelagohydra mirabilis Dendy, 1903 (after A.Dendy, 1903).
B: Swimming hydropolyp of Margelopsis haeckeli Hartlaub, 1897 (after C. Hartlaub, 1897)
C: Swimming hydropolyp of Climacocod ikarii Uchida, 1924 (after T. Uchida, 1924).
D: Swimming hydropolyp from Friday Harbor (after M.L. Fraser, 1939).

In 1905, the same author defined that, of the fixation disc of the actinula, of is able to derive the aeriferous pocket of *Velella*, and from this the intermediary organ of the planula of *Eutima*.

R. Woltereck makes a difference between the float (air sac) of the chondrophores and the float with gas (gas sac) of other siphonophores.

In my opinion, only the concept of E. Korschelt and K. Heider (1890) merits further attention.

At the surface of the water, the superficial film serves to support mechanically a number of organisms (neuston) and the two faces of this film can behave to this effect. Under the inferior face, there exists the infraneuston can climb occasionally or during the whole of their life. According to E. Korschelt and K. Heider, a planula of a hydropolyp could, thanks to surface tension, affix itself to the surface of the water by its enlarged aboral plate and become an infraneustonic animal. The flatted basal disc

depresses itself into a boat-shaped concavity; this state exists normally in *Margelopsis* and, in addition, according to E. Korschelt and K. Heider, in the planulae of different cnidarians, the glandular apical region that will become the disc of fixation shows a more or less deepened concave depression. Finally, the depressed wall invaginates entirely and forms the pneumatophore. The inferior part of the invaginated ectoderm is transformed into a characteristic tissue with a strongly granulose structure of protoplasm. Following W.. Jacobs (1938) in the siphonulae and adult colonies of *Stephanomia*, these ectodermic cells secrete some minute gaseous vesicles that are expelled as they explode. Rapidly these bubbles enlarge, forcing a way between the cells that adhere slightly between them and come into the cavity of the float, which they finally dilate.
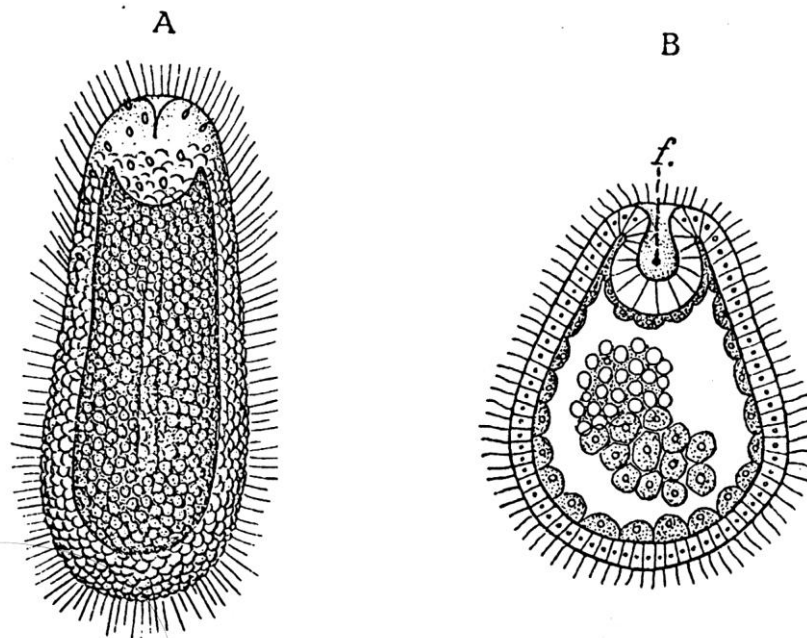
Figure 12. Two planulae of Eutina mira Mc Grady, 1875
(after W.T. Brooks, 1886) with the apical pole towards the top (f. = float).
A: Entire view. - B: optical section.

After having developed its hydrostatic apparatus, the siphonophore can either free itself from the surface, descend towards the depths and become a nektonic organism, pelagic (calycophorids, physophorids) or bathypelagic (rhizophysids), or, if the float acquires a sufficient volume, break through the surface and pass on to an adult life above the plankton (physaliids, chondrophorids).

W.K. Brooks (1886) has mentioned and figured a vesicular aboral invagination in the planula of the leptomedusan *Eutima mira* McGrady (fig. 12) and in the anthomedusan *Turritopsis nutricula* McGrady. This author considers the invagination as an ectodermal gland which serves to affix the planula on its support.

On this side, E.W. McBride (1914) supports the hypothesis of E. Korschelt and K. Heider. He writes "that this is a possible and even probable contingency will be sufficient for anyone who has watched young starfish walking upside down on the surface film, like flies on the ceiling of a room, or who has seen some members of a swarm of ascidian tadpoles thus affix themselves to the film. The surface film,

although able to sustain the weight of a larva, would soon bend under the growing weight of the hydroid colony which developed from it, and this would lead to a cupping of the base. If we suppose this base to secrete mucus and the entangled bubbles of air, the elements of a float would thus be presented.".

J. Hadzi (1918) thinks that the float of air of the chondrophorids does not constitute a derivation of a medusa (aeromedusa) like the gas float and the swimming bells of siphonanths. The air float constitutes a differentiation of the aboral end of the polyp; it is homologous to the organ of flotation in *Pelagohydra* or the concave and glandular disc of fixation in the actinula; its chitinous internal surface recalls sooner a cauline ectoderm than a subumbrella.

In support of these observations of E.W. McBride, H.C. Delsman (1923) has observed some planula larvae of Scyphomedusae hanging at the surface of the water by their aboral region.

In summary the pneumatophore of the physophorid siphonophores becomes hollowed by invagination of the aboral extremity in the actinuloid larva (actinula larva of sessile tubulariid hydropolyps, tachygenic actinulae or pelagic tubulariids like *Margelopsis*). Instead of developing a ramified surface for the formation of the hydrorhiza of the sessile hydropolyps, the aboral wall proliferates internally in the pelagic organism.

III. PHYLOGENY OF THE SIPHONOPHORES.

The embryology and comparative anatomy of the siphonophores forces one to recognise four subdivisions amongst these organisms so polymorphic: the Chondrophorids, the Cystonectids, the Physonectids and the Calycophorids. From the morphological point of view, the representatives of the first three groups possess a float and can be characterised by the name Physophorids without which, for this reason, it should be possible to state the direct relations between the three subdivisions.

These four great sub-groups have been recognised for a long time by researchers. Meanwhile, even with the present state of knowledge, it has proven impossible to retrace their evolution on the basis of embryological observations, comparative anatomy or by ethological studies on live material. In effect, presently, the intermediate forms are totally absent and one knows of none of the really primitive forms. As F. Moser (1925) mentions with just right "No absolute, or relatively primitive forms are preserved. The intermediaries between the large groups are missing etc...".

Also, for want of palaeontological observations, one is obliged to search for the phylogenetic relations of the four sub-groups in the single domain of embryology where the phenomena are very condensed, as well as in the morphological and ethological relations provided by the recent organisms themselves.

The hypothesis for a common origin, actinuloid larva, in which, primitively, the float and trunk each had the same importance, but which later had evolved in two opposite ways, that it to say toward the predominance of the siphosome in the Physophorids, and toward that of the nectosome in the Calycophorids, is logical and objective. Because all the siphonophores can be reduced to an initial form, derived from an actinuloid larva, the *siphonula*.

This latter is found in a characteristic form in the Physonectids. In consequence, it is incontestable that the physonectids made their appearance before

the Calycophorids, of which the *calyconula* larva, more evolved, can be derived from the siphonula larva.

On the other hand, it has been established earlier that the *Ratarula* larva of the Chondrophorids and the *Cystonula* larva of the cystonectids are easily united with the siphonula; more over, these two larval forms cannot arise one from another. In consequence, it will be necessary to consider separately the Chondrophorids, Cystonectids, the Physonectids and their derivatives the Calycophorids.

Certain authors Claus (1885), Delage and Heruard (1901) have established no relations between the four sub-groups.

In contrast, other authors have suggested some phylogenetic theories that tend to establish the diphyleticism of the siphonophores.

Haeckel (1888), Hadzi (1918) and Garstang (1946) separate the Siphonanths (Cystonectids, Physonectids, Calycophorids) from the Disconanths (Chondrophorids). The former arise from a planula by unilateral (ventral) budding, being bilaterally symmetrical; and the latter are derived from an actinuloid (*Conaria*) larva have radial symmetry.

Chun (1897), Moser (1925), Lameere (1929) and Leloup (1929) compare the calycophorids, without a float, with the three other sub-groups that possess one; Chun (1897) separates the Chondrophorids from the group of Cystonectids and physonectids, while Moser (1925) divides the physonectids from the group of cystonectids and chondrophorids, as did Lameere (1929), for whom the chondrophorids represented the last branch in the long evolution of the siphonophores.

On his side, Weill (1931), based on a study of the cnidome, hesitated between the two alternatives: 1. "to take unique account of the absence of one category of nematocysts". In this case one can isolate the calycophorids from the other three sub-groups; 2. "to take account of the valency of the cnidome and the presence or absence of the three categories". The author adopted the latter method of investigation. He admits a clear division between the siphonophores that possess a tetracnidome (Calycophorids and physonectids) and those that possess a bicnidome (Cystonectids and chondrophorids), because, from the point of view of the cnidome, this concept makes "calls upon the more numerous and more important characters".

The group of statements by Weill confirm our hypothesis. In effect, although the four sub-groups are all derived from the same ancestral larval type, the *siphonula*, one is not able to join together the chondrophorids and true cystonectids with the true physonectids and calycophorids.

On the phylogenetic tree, chondrophorids and cystonectids, without swimming bells, constitute lateral branches in the lower part of the siphonophore trunk. They are separated, at that time, by the disappearance of the primitive intermediate forms; always their mode of ontogenetic development recalls their ancient links. Their relations should be investigated further.

On the subject of the Physonectids and Calycophorids, certain authors [Lameere (1929, Moser (1925)] believe that the calycophorids are primitive, while others [Korschelt and Heider (1890, Totton (1932)] believe that the calycophorids descended from the physonectids; this latter concept has my preference. For Korschelt and Heider, the float is a primitive organ of locomotion gradually replaced by a secondary swimming trunk; the physophorids are the oldest and the calycophorids derived from them by loss of the float and by limitation and more accentuated differentiation of the swimming bells. These are not the longest forms, nor do they

possess the largest number of organs that show the greatest complexity; in contrast, the large forms show the simple and repeated structures from which one can easily derive the smaller forms, but with complicated structures.

The almost totality of the authors (except notably Korschelt and Heider, Totton) admit that the most primitive organisms only possessed a single bell and a primitive mode of development they gave rise to that of the calycophorid *Muggiaea kochi* Will.

But, in the course of evolutionary tendencies of the group one remarks that either the monophyism is due to tachygenesis or that it constitutes a very early evolved stage of the siphonophores which tend to acquire a superior speed by reducing the number of their organs.

A. Phylogeny of the Physophorids.

Under the name Physophorae Eschscholtz, 1829 one understands, like C. Chun (1897) and several other authors, all those siphonophores provided with a float, and in which the physiological summit corresponds to the morphological summit, at least during their young stages.

These siphonophores have some different forms that can be classified into three groups: Chondrophorids, Cystonectids and Physonectids. The adult animals of these three groups are very distinct. But during ontogenetic development they an identity such that one cannot strongly separate them. In addition, R. Weill (1934) mentions "It would be perhaps interesting to establish that, by the possession of stenoteles, the Cystonectids - Chondrophorids are more closely related to the Physophorids than to the Calycophorids, which could be considered, in transformation language, as an indicator of a closer parentage".

The Chondrophorids and Cystonectids have only a single zone of proliferation: the siphosome alone exists. In addition, as R. Weill (1934) showed "the stinging batteries (Cystonectid and Chondrophorid) resemble best to a commonplace type which is seen so often in all the groups, the cnidarian tentacles". One must consider Chondrophorids and Cystonectids as being very old and very primitive siphonophores, although there does not seem to be a direct relationship between the two groups.

The study of ontogenesis proves that the larva of the Chondrophorids, the *Ratarula*, possesses a more ancient organisation than the siphonula larva of the Cystonectids. The *Ratarula* presents a mixture of primitive and more evolved characters with regard to the actinula larva of certain present day hydropolyps.

A distant ancestor of the Physophorids that resemble a free actinula and has acquired a float by invagination of its aboral extremity ought to evolve in two directions. One group that preserves its aboral tentacles has elongated in the horizontal plane and acquired an internal mass of vacuolated tissue (central mass) which, by a decrease in its density, participates in the floatation of the organism, the *Ratarula* (Chondrophoridae); the adults living at the surface of the oceans.

Another group has lost its aboral tentacles, and is elongated in the vertical sense, the *Siphonula*; the adults have colonised the seas down to great depths.

The Chondrophorids, without bells and elongated in the horizontal plane, have an important pneumatophore, with complete walls, polythalamous and perforated, at least at the beginning of its development. The siphosome is short and consists of a central gastrozooid and a complicated gastrovascular cavity that is encircled by the

reproductive polyps borne on medusoid gonophores charged with genital products and which are detached to lead an independent life (Chrysomitras). The aboral tentacles, in the form of dactylozooids are found around the periphery.

Bathypelagic during their first ontogenetic stages, the Chondrophorids become planktonic and when their float is sufficiently voluminous they push through the water surface and pass on to live on the surface of the sea; floating there passively. Meanwhile their density can vary; some contractions in the muscles of the float expel gas and the heavier colony sinks as far until the fresh quantity of gas secreted again is sufficient to reduce the density to below that of water; then the chondrophore re-ascends to the surface.

The Chondrophorids are divided into:

Porpitidae - flattened, rounded, with permanent apical pore; with club-shaped tentacles provided with pedunculate cnidobands, and

Velellidae - elliptical, with a vertical sail secondarily covering the apical pore; with simple filiform tentacles.

I have shown earlier that the siphonophores are derived from a vertically elongated siphonula.

A middle zone of proliferation furnishes some assemblages of polymorphic appendages, accompanied by the reproductive organs, the cormidia (Cystonectidae) which remain constantly fixed to the stem of the siphosome.

The *Cystonectidae*, without nectophores, have a monothalamic float, a radiated structure with a permanent apical pore; a tubular, more or less extended, trunk, and some very simple cormidia without bracts. It floats passively.

The cystonectids comprise various forms with a monothalamic pneumatophore; bathypelagic:

Rhizophysidae - with cormidia growing along the length of a very elongate siphosome and controlled also.

Epibulidae - with shortened vesicular siphosome, with a row of palpons under the pneumatophore protecting the spirally arranged cormidia.

In the cystonectids, deprived of bracts and swimming bells, the float alone supports the colony. They can execute some limited movements of descent and ascent by muscular contractions that provoke either a change in the volume of the float, or a shortening or lengthening of the trunk.

The *Physalidae* have undergone, secondarily, a horizontal elongation; their major axis becoming horizontal and the physiological summit is perpendicular to the morphological summit. The adults possess a macrothalamic, vesicular, closed, very voluminous pneumatophore; which exists passively and constantly above the water; a vesicular siphosome, elongated horizontally is present beneath the pneumatophore and bears, on its inferior side, cormidia arranged in a longitudinal series.

In certain siphonulae, there is formed a second region of budding where modified medusae are developed; the swimming bells (nectosome).

The nectosome and siphosome, on which the elements are developed from the top downwards, can be arranged in two ways: a) the float persists; the nectosome forms, lying above the siphosome and its prolongation, it supports the apical float; siphonophores with slow movement, more or less passive (Physonectidae); b) the float is not developed; nectosome and siphosome originate at the same point but are directed in opposite directions; the cormidia are detached and live freely (eudoxids); siphonophores that swim more and more energetically (*Calyconula*).

The Physonectidae (or *Amphinectidae* according to W. Garstang (1946)) have a monothalamic pneumatophore of greater or lesser importance; a siphosome and well-developed nectosome; with more or less complicated cormidia with bracts. They free themselves from a passive life and progressively become swimming animals.

Amongst the physonectids, movement is effected by several methods. Thus, on the one hand, in *Stephanomia*, the float is provided with an apical pore alone carries the animal; the colony has few bracts and swimming bells. Descents and ascents are made possible by several means: a) by the strong muscles of the pneumatophore wall and of the siphosome contracting or relaxing, increasing or decreasing the density of the colony; b) by gas escaping from the float, the heavier colony descending; the gas gland secreting fresh gas, the pneumatocyst refills and the colony re-ascends; c) the swimming bells, by their inactivity or their contractions, permitting the colony to be stationary or to be displaced.

On the other hand, in *Agalma* and *Forskalia*, the float, deprived of a distal pore, supports only the upper part of the trunk with the young swimming bells; while the numerous mesogloeal bracts maintain the rest of the colony. In this case the displacement of the colony results from active swimming, by the combined action of the nectophores.

As primitive forms of these Physonectids, I consider them to be the siphonophores with little active movement. They have a small unpierced float, of little importance; an elongated nectosome, provided with numerous powerfully swimming bells and with a length less than that of the siphosome; an elongate siphosome endlessly producing well-developed cormidia with bracts (Siphonectes).

The *Forskaliidae* are the most primitive, with their swimming bells arranged multi-serially, longitudinally, and their complicated pedunculate cormidia, of multiform structure, with ramified tentacles.

The other Siphonects which are derived with the presence of only two rows of alternating nectophores.

The *Apolemiidae* have cormidia with uniform structure, non-pedunculate, separate by bare internodes, provided with numerous gastrozooids and dactylozooids, and non-ramified tentacles.

The *Agalmidae* possess complicated cormidia, of multiform structure with ramified tentacles.

In the other species, the siphosome is shortened while spreading out into a vesicle. The numerous and diverse elements are disposed in horizontal, very condensed whorls. The nectosome always shows some important, biserial swimming bells. The float acquires greater importance (Cryptophysonects).

Amongst these, at the base of the nectosome:

the *Nectaliidae* - a circle of very large, very rigid bracts, and

the *Physophoridae* - possess one or two whorls of much thickened, large dactylozooids.

Physophora has a float with a lateral pore, of secondary origin.

But in certain species the nectosome and siphosome are considerably reduced; they effect a passive life. The importance of the swimming bells is decreased as the value of the pneumatophore is increased. The float becomes very large and vesicular. The siphosome is very short, vesicular, with very numerous cormidia (Asiphonects).

In the *Anthophysidae*, instead of swimming bells, one sees several whorls of much thickened, tough bracts, that execute the very movement of a paddle (= greatly modified swimming bells). In *Anthophysa* the pneumatophore is piriform,

hemispherical, of medium size; in *Athorybia*, where C. Chun has recognised the presence of rudimentary bells, the float forms a huge vesicle.

In the *Rhodaliidae* a row of nectophores surmounts the bulbous stem. The very large, vesicular float possesses a lateral extension, the aurophore, which probable correlates with the enormous pressures that must support these bathypelagic organisms.

B. Phylogeny of the Calycophorids.

1. Authors concepts

The group Calycophoridae Leuckart, 1854 is considered by the majority of authors to comprise the monophyid, diphyid and polyphyid forms, according to whether the colonies normally have one adult non-replaceable bell, two or several constantly replaced bells. These authors have established the families Monophyidae, Diphyidae and Polyphyidae (Legendre, 1940).

Two tendencies divide these authors; the one believe that the Monophyids are primitive and that, by progressive complication, have given rise to all the group; while the others think, in contrast, that the polyphyids constitute the ancestors of the calycophorids.

Amongst those for the first hypothesis Chun (1897) and Moser (1925) believed that the polyphyids were derived from the diphyids, which in turn arose from the monophyids.

Chun (1897), within the diphyids, recognised the Oppositae (Prayomorphs) with opposed, rounded, smooth swimming bells; and the Superpositae (Diphyomorphs) with superimposed, pyramidal bells with sharp angles; he considered *Clausophyes* as an intermediate form.

Moser (1925) divided the calycophorids into *mononecta*, with a single upper bell, and into the *Polynecta* composed in addition with some inferior bells of varying number. The mononects include only a single family Monophyidae. The polyphyids, other than the families Polyphyidae - Stephanophyidae, also include the Diphyidae and the Dimophyidae (an artificial family composed of diphyids with a more or less degenerated posterior bell). For that author the monophyids, the oldest siphonophores, gave rise to the Galeolariids, which form the stem of the diphyids; these having given rise to the prayids, which are followed by the polyphyids and finally by the physophorids.

In contrast, Lameere (1929) mentions that "the fundamental type that we have described, that of the monophyids, does not appear to be absolutely primitive" and "in the monophyids there is only the dorsal bell which is found at the head of the colony; ventral bells are lacking, and we can imagine that they have disappeared". Always the author considers the Polyphyids as the superior form "because their cormidia only detach in the form of eudoxids and their medusae are transformed into sporosacs".

On the other hand Delage and Herouard (1901) have established a classification in consequence of the polyphyids. They borrowed their description of the type of calycophorids "as forms with multiple bells (polyphyines), although these forms are neither the most numerous nor the most perfect, because they are the simplest, from which the others are easily derived".

In contrast Schneider (1898) proposed to distinguish only two families. He did not mention the monophyids; he places *Sphaeronectes* in the family Prayidae and *Muggiaea* in the Diphyidae.

On his side Totton (1932) refused to recognise that the Monophyidae Chun or the Sphaeronectidae Bigelow form a single natural homogeneous and primitive group, because their species are only brought together by the possession of a single bell. "There is evidence that such a condition has been brought about along several converging lines of information". The author formulates the hypothesis that the physophorids with numerous rapidly pulsating bells gave rise to forms resembling the prayids with numerous reduced bells. These prayomorphs gave rise to some forms resembling the galeolariids and the diphyids, where the two bells are placed one behind the other, strengthening the effect of their pulsations and acting in conjunction; also that the diphyids, that are capable of protecting their contracted trunk, were able to augment their speed in escaping from their enemies.

2. Personal concepts

Under the name Calycophorae Leuckart, 1854 I include all the forms deprived of a float and in which the nectosome and siphosome, arising from a common point, develop in opposite directions.

One is able to derive them from a common ancestor, one of the physophorids close to the larval *siphonula*. Only in the calycophorids does the first bell developed very rapidly acquire a sufficient strength to carry along the colony in a more or less accelerated progress.

The most primitive calycophorids are, undoubtedly, those that possess the most elements but the simplest structure, the Hippopodiidae. In effect, amongst the siphonophores where the adult element remains in limited numbers, the very complicated organisation shows an advanced evolutionary stage.

Ethology enlightens all the phylogeny of the group and demonstrates its evolution; the siphonophores free themselves from an actively slow life (prayomorphs) and pass on to an actively rapid life (Diphyomorphs) with then a return to the primitive life (sphaeronectids).

The colonies tend to become smaller and this reduction affects the two zones of proliferation. On the one hand, in the nectosome, the adult colonies no longer show numerous definitive nectophores but these become more and more limited; at first numerous; they are reduced to two and eventually to monophyism. The adult bells fall off, young bells replace them, but in such a way that there are no more than two adult bells present at the same time. Sometimes only a single adult definitive bell is formed, without a replacement bell; sometimes this monophyism has a tachygenetic origin.

On the other hand, on the siphosome, the cormidia are detached from the colony before the maturity of their sexual elements and lead a free life (eudoxids). This separation lightens the colony and allows it a greater speed. Thus appears the alternating generations.

Without any doubt, the regular replacement of the adult bells by some reserve bells occurs in relation to the sessileness of the cormidia. In the colonies where the trunk is long and carries numerous cormidia (Hippopodiids), the reserve swimming bells are numerous and replace the older ones. In contrast, in the siphonophores where the trunk is shortened by the accelerated liberation of eudoxids, the reserve bells become very few in number and even disappear completely (monophyids).

Moreover the shape of the swimming bells changes, previously rounded, in the siphonophores with slow movement, to tapered in the colonies with rapid movement (Diphyids).

In others the respective positions of the swimming bells are modified, and this change in position, which primitively is opposite (prayids) results in one moving back more and more (diphyids) and eventually to become situated behind the other (abylines), considerably favouring the movement faculties.

Synchronously, with this tendency toward a constant increase in motion; is effected a more and more efficient protection for the essential parts of the stem, that is the proliferation zones of the nectosome and siphosome. Accordingly, as the calycophorids acquire greater motility, the hydroecium is displaced and transformed in the anterior bell. At first lateral, in reality a gutter, it occupies the whole length of the bell (hippopodiids, prayids) in the calycophorids with slow movement and opposite bells. As the bells become more superimposed, then the hydroecium diminishes in height. By the fusing of the two wings, it becomes a lateral cavity, parallel with the nectosac, surmounted by the somatocyst, and whose orifice is found in the same posterior plain as that of the nectosac (diphyids). In the distinctly superimposed forms (ceratocymbids, abylines), the hydroecium becomes a hollow at the centre of the posterior face; with the nectosac and somatocyst on either side of it. In the posterior bells the hydroecium persists in the primitive gutter-like state, but the lateral wings are more complicated.

All the calycophorids swim in an active fashion by co-ordinated contractions of their swimming bells. In nature, they advance quite rapidly (hippopodiids, prayids) or very rapidly (diphyids). Their nectosome is less dense than water, because when detached they float up towards the surface. But in the siphosome there are organs that are heavier than water (palpons, tentacles, sexual bells) as well has less dense ones (mesogloeal bracts). In its entirety the colony has a specific gravity almost equal to that of water; it can vary this by contractions of its trunk.

In the passive state the polyphyids or prayids float with the nectosome usually uppermost. The diphyids have uppermost either the anterior bell (*Chelophyes appendiculata*) or the inferior one(*Sulculeolaria quadrivalvis*), according to which bell is the most important or more primitive.

The Polyphyidae have numerous adult swimming bells, rounded and smooth (*Hippopodius*) or pentagonal with tubercles (*Vogtia*), with a long, open, simple hydroecium; without eudoxids; cormidia without bracts or special nectophores, with simple gonophores in bundles.

The Desmophyidae which have superior bells dispersed in two vertical rows, cormidia with special swimming bells and bract, have a poorly defined systematic position.

The Stephanophyidae have four adult bells arranged along a tightly twisted helix.

The polyphyids have a quite rapid movement are followed by the

Prayidae with only two adult swimming bells, which are rounded, equal in size, sub-opposed, caducous with more or less complex gastrovascular canals; with a long hydroecium which has a simple opening; with detachable cormidia, eudoxids, that establish the alternation of generations.

From the prayids are evolved, on the one hand, neotenous monophyid forms, or to degenerated diphyid or monophyid forms and, on the other hand, some forms with more and more rapid movement where the bells tend to become superimposed.

In the Sphaeronectidae the larval bell is retained. There is no nectosome, thus no replacement bells; the siphosome produces numerous eudoxids. The rounded swimming bell is helmet-shaped or hemispherical, and the bracts rounded and

smooth. Somatocyst and phyllocyst are simple. There are two genera *Monophyes* and *Sphaeronectes*. The genus *Monophyes* is more primitive; with a hydroecium made up by an open, simple gutter delimited by two wing-like and parallel projections; while in the genus *Sphaeronectes* it forms a caecum hollowed into the mesogloea.

The degenerated prayids comprise some diphyids (*Amphicaryon*, *Mitrophyes*) and some monophyids (*Nectopyramis*).

The Amphicaryonidae are diphyids with a rounded superior bell, and an inferior one transformed into a pseudo-bract, with a closed sub-umbrella and a rudimentary hydroecium; without replacement bells.

The Mitrophyidae are diphyids with a cylindrical superior bell, a small inferior one, in the form of a bract, without sub-umbrella or hydroecium, with rudimentary gastrovascular canals; without replacement bells.

The Nectopyramidae are monophyids with pyramidal bells, with rounded edges, or cylindrical; with highly ramified somatocyst and phyllocyst; a rounded smooth bract with a large hydroecium.

On the other hand the prayids with opposed bells have evolved toward those siphonophores with two adult bells that are partially opposed and partially superimposed; each possessing a somatocyst. In these colonies, the morphological summit no longer corresponds to the physiological one; these summits being found on two parallel axes.

In the Clausophyidae the two swimming bells are conical and more or less identical; in the superior bell the hydroecium extends up to mid length; in the inferior bell it is long and open. Eudoxids?

The genus *Clausophyes* appears to have given rise to the genus *Conophyes* [? Sphaeronectes] which is monophyid and neotenous (?) with a cup-like hydroecium.

These clausophyids are followed by those siphonophores in which the two adult bells are of different structure and are more and more superimposed, the Diphyidae. The anterior (superior) bell persists throughout life; its hydroecium is shortened and finally disappears; the other, the posterior (inferior) one is replaceable; with a long open and complicated hydroecium. According to how the bells are superimposed, the open hydroecium of the anterior bell is displaced from being dorsal to become posterior; surmounted by the somatocyst; finally becoming situated in the plane of the buccal orifice where it is transformed into a deep cup hollowed out parallel to the nectosac. The colonies give rise to eudoxids. The anterior bell is the more important propulsive organ.

The swimming bells of the diphyids can keep their rounded, smooth and conical shape (Galettinae) or acquire angular contours and become pyramidal (Chuniphyinae, Diphyinae).

In the Galettinae, with rounded bells, a somatocyst is absent from the posterior bell.

In the genus *Dimophyes*, which appears primitive, the small anterior bell, with its tapered but rounded summit, has a hydroecium in the shape of an inverted cornet. The small, degenerated, cylindrical posterior bell has a feeble hydroecium in the form of a gutter. Replacement bells are rare. The eudoxids have a helmet-shaped bract, extended below by a wing-like extension.

The genera *Galetta*, without buccal teeth, and *Sulculeolaria*, with buccal teeth, appear quite evolved; in effect the hydroecium of the superior bell is insignificant or absent.

In diphyids with pyramidal bells, the lateral wings of the hydroecium of the anterior bell are terminated by a buccal plate. Those of the posterior bell are complicated. The most primitive possess a somatocyst in both bells.

In the Chuniphyinae the hydroecium of the anterior bell stretches up to the mid height of the bell. The anterior bell has four ridges apically and eight inferiorly; the posterior bell has three ridges apically and 6 inferiorly.

The other diphyids have a posterior bell deprived of a somatocyst.

The anterior bells of the Diphyinae possess 4 or 5 ridges.

The bells with 4 ridges are found in the genus *Chelophyes*, where the anterior bell is pointed at its apex and has a short and narrow hydroecium. Small simple eudoxids.

Amongst the pentagonal bells, one finds:

The genus *Lensia* with anterior bell with a very shallow hydroecium; with an apically truncated posterior bell which is very fragile; with eudoxids without a special nectophore composed of a large, rounded bract with smooth posterior side, and gonophores truncated anteriorly.

The genus *Eudoxoides* with pointed anterior bell, with shallow hydroecium truncated at its summit; with asymmetric helmet-shaped bract and elongated gonophores with four sides (*E. spiralis* is monophyid).

The genus *Diphyes* with pointed summit, deep elongated hydroecium; with large, well developed eudoxids; with or without a special swimming bell (*D. chamissonis* is monophyid).

The diphyids with pentagonal anterior bells have evolved toward monophyism.

The genus *Muggiaea* is close to the preceding genus, has a short hydroecium; eudoxids with conical bracts and quadrangular genital bells.

Amongst the other diphyids, of monophyid form, certain ones show the somatocyst above the nectosac, a very primitive character that is found in the sphaeronectids and in the larval bells of diphyids.

The genus *Heteropyramis* has a hydroecium open the length of the bell, with pigment spots, a swollen somatocyst, bracts with the shape of pentagonal pyramids with pigment spots; and some genital bells of similar shape.

The genus *Thallasophyes* has a hydroecium open to the mid height of the bell and a vesicular somatocyst.

Other monophyid forms have their somatocyst displaced laterally.

The genus *Crystallophyes* has a hydroecium as long as the bell and a cylindrical somatocyst swollen in its mid region.

Certain diphyids, the Abylinae, show a progressive reduction in the anterior bell and a corresponding enlargement of the pyramidal posterior bell. The anterior bell shows a tendency to develop asymmetrically and to increase or diminish its number of facets. The posterior bell is typically diphyid and generally has five ridges. The deep hydroecium of the anterior bell is placed centrally on the posterior face; the somatocyst and nectosac are pushed apart to lie on either side. The physiological summit is found superimposed on the morphological one and both are on the same axis.

In *Ceratocymba* the longitudinal axis of the two bells is found on the same line. The anterior bell remain pyramidal, very pointed with an ovoid somatocyst. The eudoxids have a prismatic bract and asymmetric genital bells.

The species described recently by Sears (1953) in the genus *Ceratocymba* constitute the elements of a series illustrating the progressive reduction in the anterior bell; they mark the transition from one species (*sagittata*) with a well developed apical extension toward the species (*leuckarti*) that is deprived of it.

In the other Abylinae, the anterior bell becomes prismatic and very small. The asymmetric posterior bell has a very complicated hydroecium, and is the more important organ of locomotion.

The genus *Abyla* has the longitudinal axis of the two bells on the same line. The somatocyst of the anterior bell is spherical, wither apical extension; the hydroecium is not extended. The eudoxids have a prismatic, flattened bract and asymmetric genital bells.

In contrast in the other two genera, *Abylopsis* and *Bassia*, the longitudinal axis of the two bells forms an angle. This shows an anterior bell with hydroecium extended by a posterior wing and with eudoxids with the same shape and with more ore less symmetrical, polygonal sexual bells.

The genus *Abylopsis* has a rounded somatocyst with a small apical extension. A reduction in the posterior bell is seen in *A. eschscholtzi*.

The genus *Bassia* has a rounded somatocyst without apical extension.

The abylines with prismatic anterior bells and bracts, and with reduced posterior bell, have given rise to the monophyid genus *Enneagonum*. It has a pyramidal anterior bell, with four sides superiorly and four triangular facets inferiorly. The posterior, central and deep hydroecium is surmounted by the somatocyst.

IV RÉSUMÉ

The siphonophores have derived from littoral gymnoblastic hydropolyps which are joined to the family Tubulariidae; descended from actinuloid tachygenic larvae, they are freed from a benthic sessile life.

The siphonophores show the evolution of a planktonic group which tends progressively to abandon a passive life, by the acquisition of an active life and a passage toward an alternating generation.

CLASSIFICATION BASED ON ETHOLOGY

ACTINULA
of Tubulariimorph
Pelagic life, float, siphosome

Vertical elongation

Horizontal elongation
Passive planktonic life
Float exaggerated
CHONDROPHORIDAE

Pelagic passive life
Passage to active life
Nectosome
PHYSONECTIDAE

Bathypelagic passive life
CYSTONECTIDAE

Planktonic Life.
Horizontal elongation. Float exaggerated
PHYSALIIDAE

Planktonic passive. Loss of float
CALYCOPHORIDAE

PHYLOGENY OF SIPHONOPHORES BASED ON MORPHOLOGY AND EMBRYOLOGY

Ancestral Type - Tubulariidomorph pelagic
ACTINULA of tubulariidomorph hydropolyp

Aboral invagination = float
Physiological summit = Morphological summit

Vertical   -   Primary elongation   -   Horizontal
Mono-micro-thalamic   Polythalamic
Aboral tentacles disappear   Aboral tentacles present
SIPHONULA   RATARULA

CHONDROPHORIIDAE

2 proliferation zones   1 proliferation zone
Nectosome developed   Nectosome not developed
CYSTONECTIDAE

Float disappears   Float present
Siphosome & nectosome   Nectosome in the
CALYCONULA   extension of siphosome   Siphosome elongated
                                          PHYSONECTIDAE   RHIZOPHYSIDAE

CALYCOPHORAE   Siphosome elongated   Shortening of siphosome
(see below)   Float small   EPIBULIIDAE
                                          Nectophores multiserial
                                          FORSKALIIDAE

                                                                                    Secondary horizontal
                                          Nectophores biserial   elongation. Macrothalamic
                                          AGALMIDAE - APOLEMIIDAE   Physiological summit not
                                                                                    = morphological summit
                                                                                    PHYSALIIDAE

                                          Shortening of siphosome
                                          Float more important
                                          NECTALIIDAE - PHYSOPHORIDAE

                                          Secondary horizontal elongation
                                          Macrothalamic

With nectophores   With rudimentary nectophores or bracts

RHODALIIDAE   ANTHOPHYSIDAE
                          CALYCOPHORIDAE
                          without float

                          |
                          ↓

              Physiological summit = morphological summit
          Nectophores numerous, with somatocyst, constantly renewed
                          Simple cormidia
                          HIPPOPODIIDAE

                                        DESMOPHYIDAE (?)
                                        STEPHANOPHYIDAE
                                        Nectosome very short
          2 opposed, identical, rounded definitive   4 adult bells
                 nectophores with somatocysts.
                          PRAYIDAE

Larval bell permanent   Inferior bell degenerates
SPAERONECTIDAE   AMPHICARYONIDAE
                                              - MITROPHYIDAE

              Physiological summit not = Morphological summit
                 2 almost identical bells, with somatocyst,
                      semi-superimposed, rounded
                          CLAUSOPHYINAE

                                        Monophyism (?)
                                        CONOPHYES

                 2 different bells, with axes on
                      two parallel planes
                          DIPHYIDAE

Rounded contours   Pyramidal bells
Without somatocyst in pn
GALETTINAE

                          With somatocyst in pn
                          CHUNIPHYINAE

              Without somatocyst in posterior bell
                          DIPHYINAE

                                              Monophyism

with 4 facets   with 5 facets   Somatocyst lateral
CHELOPHYES   LENSIA, DIPHYES   MUGGIAEA   Somatocyst above
                     EUDOXOIDES   CRYSTALLOPHYES   nectosac
                                                            HETEROPYRAMIS
                                                            THALASSOPHYES

Reduction of anterior bell with central hydroecium.
Longitudinal axis of two bells on same line
CERATOCYMBINAE

Anterior bell prismatic
ABYLINAE

Longitudinal axis of 2 bells
forms an angle
ABYLOPSIS, BASSIA

Longitudinal axis of 2 bells
on same line
ABYLA

Monophyism
ENNEAGONUM