Siphonophores of the seas of the USSR
and the Northern Pacific

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## ORIGIN AND EVOLUTION OF SIPHONOPHORES

There is hardly any doubt now that siphonophores are colonial creatures in their origin. Moreover even amongst the historical views on the nature of siphonophores there are very few examples of these creatures being explained as separate individuals. Discounting the ideas of Huxley (1859) and Eschscholtz (1829) who saw each siphonophore as a single medusa and its multiple features as organs, the majority of researchers have more or less confined themselves to the view that siphonophores represent colonies from the stem of which a large number of zooids are budded.

Differing opinions on the nature of siphonophores basically amount to which of the generations of hydrozoan ancestors of siphonophores would have given rise to colonies of siphonophores - the medusoid or the polypoid.

Adherents of the so-called "medusomorph" theory - Müller (1871), Metschnikoff (1871, 1874), Fewkes (1880b), Haeckel (1869, 1888b), Moser (1925) and others regard colonies of siphonophores as having originated as a result of budding of polypoid and medusoid specimens from the manubrium of a primary medusa; but the mode of its formation from a bell and the explanation of the manubrium of the primary medusa as a stolon of the colony is treated by various adherents of the medusomorph theory somewhat differently (Beklemishev, 1944; Leloup, 1954).

Adherents of the other theory - the "polypoid" or the "hydroid-polymorph" theory - Lesueur (1813), Milne-Edwards (1840), Vogt (1854), Leuckart, 1854, Claus, 1878, A. Agassiz, 1865, Schneider (1896a,b) and others derive siphonophores from colonies of hydroid polyps that have changed to a pelagic life style.

Finally, recently there has been wide acceptance of the view that siphonophores as a whole are neotenic creatures that originated as a result of the early development of a free-swimming hydroid larva (actinula) that began to bud off polypoid and medusoid individuals. This view, evinced earlier by Perrier (1881), Chun (1897a) and Hadzi (1918), was most recently supported by Leloup (1954), Garstang (1946), Totton (1954, 1960) and others.

Thus, however much the various theories on the origin of siphonophores do differ in principle from one another[1] they are unanimous in recognising the colonial nature of these creatures.

V.N. Beklemishev (1944, 1950, 1952, 1964) has further developed the coloniality theory of siphonophores. In his view siphonophores are an example of the highest development of colonial individuality, since as numerous individuals comprise a colony of these free-swimming hydrozoans they are most fully and organically governed by the integrating role of the colonial entity, and yet not one of the individuals is dominant in the colony. This super-growth of the colony, almost to the level of an individual, by the path of integration, is produced by the free-swimming life style of siphonophores. This phenomenon knows no equal in all the animal kingdom and is only comparable with the body of Metazoa where specialised

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[1] See section on "Ancestors of siphonophores" for an evaluation of the different theories of the origin of siphonophores.

cells involved in the composition of a multi-cellular organism lose their individuality and are exclusively devoted to the integrating role of the whole organism.

## *I. INTEGRATION IN COLONIES OF SIPHONANTHAE.*

As already mentioned, the high development of colonial individuality in Siphonanthae arose as a result of a change to a free-swimming, pelagic life style.

The structure today of contemporary Siphonanthae, linked with their high specialisation, differs greatly from that of ancestral forms and is a result of the protracted evolutionary path of development taken by siphonophores. Thus the morphology of different Siphonanthae cannot give a graphic picture of the gradual complication of the structure of the colonies and of the heightened colonial integration in this group of creatures (as opposed to distinct morphological series, as observable in Leptolida).

Nonetheless an attempt is made below, using data on the morphology, physiology, individual development and ecology of siphonanth colonies as one of the leading factors in the evolution of this group.

### 1. POLYMORPHISM IN COLONIES OF SIPHONANTHAE.

One of the inescapable consequences of the free-swimming life style of siphonophores is the suppression of the individuality of each zooid comprising the colony. Being subject to the co-ordinating role of the whole colony, the various zooids have in the course of evolution come to fulfil specific functions, gradually also changing even morphologically.

As is evident from the morphological description six basic groups of individuals comprise a colony of contemporary siphonophores: a pneumatophore, nectophores, bracts, gonophores, gastrozooids with tentacles, and palpons with palpacles. The function of each of the listed groups is completely distinct. In contemporary siphonophores (with rare exceptions) it is impossible to find such zooids sufficiently self-sufficient and independent of the other individuals in the colony. Almost all individuals of colonies of siphonophores evidence the protracted evolution of their structure that diverged towards functions fulfilled by these individuals.

Just as there is no single view on the nature of all colonies of siphonophores, there are also varying opinions on the path of origin of the separate individuals. In contrast to the widely held view that some individuals of colonies of siphonophores originate from polyps, and others from medusae, there is another view (Metschnikoff, 1870; Haeckel, 1888b) that affirms the exclusively medusoid origin of all individuals of siphonophore colonies.

Apart from the fact that in the majority of cases there are no immediate data to form the nature of one or other individual, nonetheless specific features of their morphology and individual development help to clarify the origin of all the components of colonies listed above.

There is hardly any need to dwell in detail on the origin of pneumatophores, nectophores and gonophores since their medusoid nature is accepted by the majority of researchers. Even less unchallenged is the polypoid nature of gastrozooids and palpons. There is the view (Haeckel, 1888b; V.N. Beklemishev, 1944, 1952, 1964)

that integration of organelles in colonies of siphonophores has reached such limits that medusoid individuals budding on the colonies and having completely lost their individuality, have become subject to breaking away, the consequence of which is the appearance of gastrozooids and palpons as manubria of past medusae, and bracts appear on the stolon of the larva as self-sufficient individuals, each originating from its own bud. In this respect the young larvae of all three suborders of Siphonanthae are very representative, each of them having a typical polypoidal individual at the oral end – a primary gastrozooid inside which gradually develops a gastric chamber through the differentiation of endodermal cells. Nonetheless if we consider the gastrozooids as the manubrium of the medusa whose umbrella has turned into a corresponding bract, then it follows that we consider the hydroecial chamber of the latter as the chamber of the subumbrella. In fact in any of the medusoid individuals of siphonophores the subumbrella and hydroecial chambers are independent formations. In the case of the bracts this is confirmed by the presence of a subumbrella chamber in larval bracts of *Agalma elegans*.

Consequently, a bract also appears in a colony of siphonophores as a self-sufficient individual. In form, and in the majority of cases, in its substantial mesogloeal layer, the bract is a highly modified medusoid that has lost its subumbrella chamber and manubrium. This view of the nature of the bract is significantly supported not only by the structure of the larval bract of *Agalma elegans*, but also by the budding of a hat-shaped larval bract in the larva of the self-same species (see p. 45), which is highly reminiscent (in its nature) of the budding of the larval nectophore in *Hippopodius hippopus* (figs 39, 44).

It is here appropriate to examine the question of the origin of the tentacle and the palpacle. In the present work the tentacle and palpacle are seen as tentacles, the first belonging to a gastrozooid, the second to a palpon. But there is another view (V.N. Beklemishev, 1944, 1952, 1964) whose adherents consider the tentacles and palpacles as specimens of polypoid origin or explain each of them as homologues of the manubrium of a medusa, which has in the course of evolution lost its umbrella.

The following speak in favour of the tentacular nature of these formations;

1. The budding of the tentacle in the larvae of all three suborders of siphonophores originates either simultaneously with the gastrozooid or is slightly delayed after the gastrozooid.

2. Both gastrozooid and tentacle (just like the palpon and palpacle) always bud next to one another. There is not formation of buds between them. This link is always retained in the definitive colonies in which the tentacle is always to be found on the gastrozooid (either on its pedicle or on is basigaster).

3. There is a concentration on the surface of the tentacle and palpacle of nematocysts, the presence of a large number of which is also characteristic of tentacles of hydroid polyps.

Along with this there are features that throw doubt on the view of the tentacle and palpacle as well as on tentacles of polyps.

1. There is an unusual distribution of both of these in the proximal portion of corresponding polyps. It is well known that in the majority of hydrozoans tentacles are spread out in the distal part and yet he place where the tentacles attach forms the boundary of the mouth cone or the hypostome of the polyp.

2. There is a gastrovascular canal inside the tentacles and palpacles. In most of the hydropolyps the endodermal layer form as a solid rod inside the tentacle - the endodermal axis of the tentacle.

3. There are branches with stinging batteries along one of the sides of most of the tentacles. Branching of tentacles is a very rare phenomenon among hydrozoans - it is well known in polyps of *Cladocoryne* and is found in medusae of *Cladonema* type.

4. There is  a batch of tentacles in the form of self-sufficient buds on the stolon of larvae.

The first three positions can be rejected - there are sufficiently convincing objections to them. Amongst hydroid polyps the well-known ones are those whose tentacles have a more or less irregular disposition on the body of the polyp (*Myriothela, Pelagohydra*) or form basal crowns (Pennariidae). If we assume a reduction in all tentacles of a polyp, with the exception of a single basal one, then the origin of the tentacle and palpacle becomes clear.

Among the hydroids there is a well known fairly small number of polyps that have hollow tentacle (for instance, the primary tentacles of Myriothelidae). We can assume from one point of view the homology of tentacles and palpacles as similar to the hollow tentacles of hydroids. From another point of view the appearance of tentacles and palpacles is feasible as secondary buddings of the polyp's body. Pointing to this possible path is the presence of secondary definitive tentacles (hollow body outgrowths) in polyps of the same Myriothelidae.

Finally, branching of tentacles which from one point of view can be compared with the branching of tentacles in polyps of *Cladocoryne* can reasonably be seen from another point of view as an adaptive facility produced secondarily as a result of the oligomerisation in the number of tentacles down to one, which has been the reason for the branching of this single remaining tentacle.

As regards the way tentacles are built up, the solution of this question demands further embryological research.

Thus a variety of individuals making up colonies of siphonophores has arisen as a result of colonial integration.

Each colony of siphonophore consists of groups of individuals of medusoid and polypoid origin, fulfilling narrow specialised functions and correspondingly different from one another morphologically.

Tentacles of gastrozooids and palpacles of palpons must be seen not as separate individuals of a colony but as tentacles of polyps whose number has diminished as a result of oligomerisation down to one in each polyp.

### 2. OLIGOMERISATION OF HOMOLOGOUS ELEMENTS AS ONE OF THE FEATURES OF INTEGRATION IN COLONIES OF SIPHONANTHAE.

The law of oligomerisation of homologous elements as one of the basic paths in the evolution of the animal kingdom as discovered by Dougall (1963, 1954) has most recently been confirmed by the work of a series of researchers (V.N. Beklemishev, 1944, 1950, 1952, 1964; Zenkevich, 1949; Zakhvatkin, 1949). As shown by Naumov (1957, 1960) the laws of the oligomerisation process have been fully accepted as an explanation of the development path of colonial Hydrozoa, in which during evolution there has been oligomerisation not only of the number of organs but also the number of actual individuals.

Oligomerisation plays no less an important part during the evolution of colonies of Siphonanthae, being "one of the paths and features of integration of an organic individual" (V.N. Beklemishev, 1964: 427).

Involving as it does a decrease in the number of homologous elements of a colony (be they organs or individuals) oligomerisation is achieved by reduction, an amalgamation or change in functions of a part of them (Stepanjants, 1965).

Amalgamations of organs or individuals in colonies of siphonophores just as in colonies of *Leptolida* is not observed. Thus other means of oligomerisation are quite clearly manifested.

The oligomerisation of organs belonging to different zooids in colonies is achieved during evolution by partial or complete reduction of their number. Morphological material gained by study of contemporary siphonophores yields almost no evidence of the course of oligomerisation of one or other organ. Colonies of all contemporary siphonophores exhibit an already completed process of reduction in the number of organs without intermediate stages. Thus all individuals of medusoid origin are devoid of sensory organs and marginal tentacles (an exception are the "special nectophores" of *Desmophyes annectens* Haeckel[2], which carry fine tentacles along the edge of the subumbrella). Polypoid individuals of colonies each have either a tentacle (a tentacle in the gastrozooid, a palpacle on the palpon) or are completely devoid of them (cystozooids of some Physophorae). Oligomerisation of the number of radial canals in certain situations has led to a reduction in their number from 4 to 2 (the larval nectophore of *Vogtia glabra* Bigelow)[3] [actually *Hippopodius hippopus*].

There is a more distinct picture of oligomerisation of the number of individuals in colonies of different Siphonanthae through a change in function or a reduction of part of them. Apart from this there is yet another path of oligomerisation of homologous individuals in siphonophores: the reduction of the number of zooids as a result of the neotenic development of colonies.

As seen in the previous section the appearance of polymorphism is in itself a result of oligomerisation produced by a change in functions of a part of the medusoids and polypoids of a colony.

Another method of oligomerisation of the number of individuals in a colony is their partial or complete reduction.

The pneumatophore, a single one of which is found in all Physophorae and in Cystonectae, is finally completely reduced and is absent in the suborder of Calycophorae. The proposition that a single pneumatophore is the result of oligomerisation and that in ancient siphonophores there was possibly a greater number of pneumatophores in each colony is supported by Metschnikoff's observations. In Metschnikoff's (1974) description he found larvae of *Physophora hydrostatica* (Forskål) in which sometimes there were simultaneously incorporated not one but two rudiments of future pneumatophores.

Oligomerisation of the number of nectophores can be traced very accurately in different Siphonanthae. In the suborder Physophorae the primitive family Forskaliidae possesses the largest number of nectophores (300-400 in a colony), and the latter are

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[2] *Desmophyes annectens* - a doubtful species described by Haeckel (1888b) from the Indian Ocean and not observed recently, it belongs to the family Desmophyidae suborder Calycophorae.
[3] In representatives of the genus *Praya* (Polynectoidea, Calycophorae) the subumbrella of the nectophores has numerous branching radial canals. It is possible that this is a secondary increase in the number of canals produced by their subdivision.

distributed multiserially down the stem of the colony (fig. 6b). In the family Agalmidae the number of nectophores does not exceed 40-50 inns its biserial distribution while representatives of the majority of other families of Physophorae have no more than 4-6 pairs (fig. 6A).

Amongst the Calycophorae only representatives of the family Hippopodiidae, which is the closest of all to the ancient calycophores (as is also the afore-mentioned family of Desmophyidae), have up to 7 pairs of nectophores (fig. 6Г). Remaining families of Calycophorae are characterised by no more than two definitive nectophores in a colony (fig. 6 Δ, E) and in some genera (*Muggiaea, Enneagonum*) there number is reduced to one per colony (fig. 126, 127). It is interesting that among Calycophorae there are genera with partial reduction of one of the two nectophores present - *Maresearsia, Amphicaryon, Dimophyes*  (fig. 49).

Finally, in the suborder Cystonectae, total reduction of nectophores is observed.
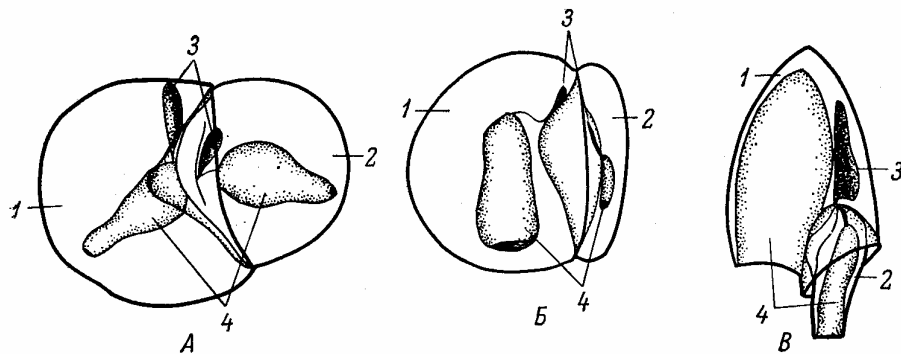


Fig. 49. Colonies of different representatives of Calycophorae with a different stage of reduction of one of the nectophores.
A. *Maresearsia*; Б *Amphicaryon*, B. *Dimophyes*.
1. Normally developed nectophore. 2. Nectophore subject to partial reduction; 3. Somatocyst. 4. Subumbrella cavity.

The number of bracts is also subject to reduction. Thus in the order Physophorae, amongst the representatives of the families Forskaliidae, Apolemiidae and Agalmidae, the number of bracts reaches 100-1000. At the same time in representatives of the Forskaliidae and Agalmidae bracts can be found not only in cormidia (up to 20-40 per cormidium) but also between them. In other families of this suborder the number of bracts in a colony is reduced and may not even exceed 8 (family Nectaliidae). In representatives of the families Physophoridae and Rhodaliidae bracts in colonies are totally absent.

In the suborder Calycophorae the number of bracts corresponds to the number of cormidia in the colony (and in each cormidium there is no more than one bract).

The suborder Cystonectae is characterised by the total reduction of bracts.

Oligomerisation of the numbers of gastrozooids and palpons is clearly visible especially in the suborder Physophorae. Forskaliidae have 30-50 and sometimes 100-500 gastrozooids per colony, and 60-100, and even more than 500 palpons, whilst colonies from the family Agalmidae have no more than 20-50 gastrozooids but somewhat more palpons. Here it must be pointed out that the number of these zooids in each cormidium of colonies of different Physophorae is not the same.

In the suborder Calycophorae palpons are completely absent. The number of gastrozooids, always corresponding to the number of cormidia in the colony, varies from more than 100 (*Rosacea, Sulculeolaria*) to between 90 and 30 (*Amphicaryon, Diphyes, Abyla, Abylopsis*) and even 20-10 (*Eudoxoides, Enneagonum*).

Oligomerisation of homologous zooids as a result of neoteny is widespread amongst siphonophores and involves the sexual maturity of the colony taking place before one or other group of individuals has time to bud, since some individuals only bud partially. Thus colonies of Athorybiidae (suborder Physophorae) that have arisen as neotenic larvae of Agalmidae, have one nectophore each (*Melophysa*) or are completely devoid of the latter (*Athorybia*). The absence of bracts in its colonies can be explained by the neotenic nature of *Physophora hydrostatica* (family Physophoridae).

The end result of oligomerisation, beyond a reduction in the number of homologous elements, is their spatial attachment and an increase in the dimensions of organs or individuals: this is linked with an intensification of their functions (Dougall, 1936, 1954; Naumov, 1957, 1961).

As an example of the strict fixation of the position of organs in different zooids of siphonanths we can cite the position of the single tentacle in the gastrozooid (or the single palpacle in the palpon). A reduction in the number of tentacles down to one has led to an intensification of the functions of each such organ. Obviously for this reason the size of each tentacle as a rule exceeds the length of the tentacles of hydroid polyps.

The spatial attachment of individuals as a consequence of their oligomerisation can also be well traced in different colonies of siphonophores. The stem of colonies of all extant Siphonanthae is divided into the part that buds only a pneumatophore and nectophores (the nectosome)[4], and a part bearing all remaining individuals of the colony (the siphosome). In contemporary siphonophores there are no forms in which the positions of the pneumatophore and nectophores within the nectosome are not strictly fixed. But the distribution of zooids on the siphosome is still not yet sufficiently distinct for all siphonophores. Thus some representatives of Forskaliidae or Agalmidae (Physophorae) as yet do not have distinctly formed cormidial complexes. There is no strict order even in the distribution of zooids on the siphosome of most representatives of Hippopodiidae (Calycophorae).

In the remaining families of Physophorae, just as in most of the Calycophorae and Cystonectae, the positions where zooids are distributed on the siphosome are strictly fixed and restricted by the bounds of the cormidia.

The provenance of cormidial groupings in colonies of siphonophores is due to oligomerisation of the number of homologous zooids due to the integrating role of the colonial individual.

In siphonophores there is an increase in the dimension of individuals in the colony produced by the heightened functional burden on each of the individuals remaining after oligomerisation. For instance, the size of each nectophore in diphyid colonies of Calycophorae often exceeds 2-3 times the size of the nectophore of physophorids.

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[4] An exception is *Forskaliopsis* (a doubtful genus of which, since Haeckel described it in 1888, there has been no mention in the literature) of the family Forskaliidae and the family Apolemiidae whose representatives carry cystozooids and palpons on the nectosome in addition to a pneumatophore and nectophores.

It must be noted that sometimes  intensification of functions of specific zoids and a corresponding increase in their dimensions occurs because of the complete disappearance of other zooids that, though not homologous to them, nonetheless fulfil similar functions. Thus the disappearance of nectophores in *Physalia physalis* (Cystonectae) has meant the functions of the pneumatophore as an organ of passive movement have been significantly strengthened. It is precisely for this reason that the length of the pneumatophore oh *P. physalis* is about 30 cm while pneumatophores of other siphonophores have a length of no more than 2-20 mm.

Finally, an increase in the dimensions of specific individuals of siphonophores also takes place occasionally, and this is because apart from an intensification of their own functions some individuals of the colony begin to fulfil functions of the disappearing zooids, i.e. the functional load on each such individuals would seem to double.

Thus amongst contemporary siphonophores there are examples of a different stage of oligomerisation of homologous elements.

As regards the majority of organs this process is close to completion. In other words a reduction in the number of organs leading sometimes to the complete disappearance of parts that are vitally important to the individuals has contributed to the loss of individuality of individuals and a corresponding increase in the role of the colony as a whole.

In relation to oligomerisation of the number of individuals this has led to a decline in the number of some zooids down to a single one in the colony or to their complete reduction. In the latter case functions of disappearing individuals have been taken on by zooids of other origin, which also testifies to the co-ordinating role of a superior colonial entity.

All the above evidence points to the fact that in the course of siphonophore evolution oligomerisation of the number of homologous elements of a colony played a not unimportant part, since it was one of the basic paths of integration and of building up the colony on an individual level.

### 3. CHANGE IN FUNCTIONS AMONGST SPECIFIC GROUPS OF INDIVIDUALS IN COLONIES OF SIPHONOPHORES.

As is obvious from the previous section, during oligomerisation of the number of homologous zooids in colonies of some siphonophores there can be a total reduction of specific groups of individuals. Then, influenced by the integrating role of the colony, other groups can fulfil the functions of the disappearing zooids.

Sometimes such an exchange is complete, i.e. zooids are completely switched to new functions. An example of this phenomenon is the appearance of "special nectophores" in *Ersae* of Calycophorae or in gonodendra of *Physalia physalis*. As mentioned earlier "special nectophores" are sterile gonophores that have been modified to fulfil exclusively locomotive functions.

In most cases the change in functions takes place only partially. In other words, zooids that have replaced disappearing specimens also continue to fulfil their own functions. Thus bracts in representatives of the family Athorybiidae (Physophorae) which function as the locomotory apparati of the colony instead of the absent nectophores also fulfil their general functions of protecting the colony and act as flotation devices. In the family Physophoridae (Physophorae) the defensive role is

played by palpons (instead of absent bracts) that lie like a corona immediately below the nectosome of the colony. At the same time these zooids also fulfil their own basic functions, being unique organs of sensation to the colony. Just as interesting is the example of partial exchange of functions amongst gonophores in eudoxids of Calycophorae. Those zooids, which have sexual functions at the same time, serve as locomotory apparati. Gastrozooids of Calycophorae colonies, apart from fulfilling a feeding function, also play a part as excretory and probably sensory apparati in place of the palpons and cystozooids absent in this suborder.

Thus the capacity of other groups of individuals of siphonophores functionally to replace other disappearing groups of zooids, i.e. to switch to fulfilling other functions not generally their own, also testifies to the integrating influence of the colonial entity.

## 4. The physiological aspect of the question of colonial integration in siphonophores.

The appearance of polymorphism as a result of the division of functions between individuals of a colony and the oligomerisation of single-type elements in a colony is a morphological aspect of the question of colonial integration in siphonophores.

The ability of many zooids to switch to fulfilling other functions not characteristic of a given group of individuals is evidence that physiological processes occurring in siphonophores, including the distribution of functions among zooids, and a change in functions are under the control of the whole colony. In other words, a siphonophore is not only morphologically but also in a functional and physiological sense a unique entity on the borders of a colony's transition to the level of a higher order.

The functional dependence of individual zooid on the whole colony has in siphonophore been expressed in the formation of cormidia - complexes of dissimilar individuals linked by a common functional task. Thus within the chief morpho-physiological entity - the colony - there are other smaller, morpho-physiological entities subordinate to it - the cormidia - whose functions of individual components are strictly defined. The highest expression of this dependence is found in the ability of cormidia among most of the Calycophorae to exist freely in the form of eudoxids and *Ersae*. These formations break off at a given period in the life of the colony and, leading to a free-swimming life style, bring about sexual reproduction and dispersal of sexual products.

As is well known (Naumov, 1960) the life time of individual zooids of Hydrozoa in comparison with the life of the whole colony is not great. The integrating role of the colony as a whole is borne out by the fact that there is regular replacement of dead individuals with new. Such an exchange is also characteristic of siphonophores. Thus a constant number of nectophores is subject to continuous budding of young swimming bells in the nectosomal budding zone. Young zooids and cormidia budding off on the siphosome repeatedly replace the dying old zooids of the siphosome or, in the Calycophorae, the mature cormidia that are breaking off. It is characteristic that eudoxids and *Ersae* also have on themselves a budding zone, producing new gonophores that replace the dying old ones. Interestingly, individuals present singly in a colony (a pneumatophore or definitive nectophore of a monophyid Calycophorae) are retained throughout the life of the colony and are not subject to

replacement. Apparently this is explained by the fact that in the absence of each of these individuals the existence of the colony would be impossible even at the moment of exchanging the old individual for the new. Here also there is evidence of the integrating role of the colony as a whole, safeguarding the irreplaceability and constant existence of vitally important individuals.

In colonies of siphonophores at the height of the development of organelle integration overall regulatory activity is quite well evidenced and exists with the help of conductive systems. The nervous system of siphonophores is somewhat different from that of hydroids and although it cannot be called more complete it nevertheless, in a certain sense, is at a higher stage than that in the Hydroidea, since it is subject to the co-ordinating role of the colonial whole. Basically this is shown in the presence of ganglion cells in the ectoderm of the stem walls of a colony of siphonophores (Schaeppi, 1897; Mackie, 1964) while in the coenosarc of Hydroidea no nerve elements have been discovered (Naumov, 1960). Because of the presence of a layer of nerve cell in the stem walls and also a nerve network in zooids of a colony linked to nerve elements in the stem, the stimulation of any part of the specimen produces a momentary response reaction in the whole colony. As this happens the colony either contracts strongly or (as often happens) releases several zooids and sometimes even the whole falls into pieces[5]. Such protective "self-amputation" (autotomy) can be explained in the following way. During stimulation of a siphonophore the nervous and muscular systems come into action. Having received a nerve impulse both the circular and longitudinal muscles of the stem contract simultaneously while the volume of the gastrovascular canal of the stem is reduced and the fluid within, unable to take compression, "detonates" some other parts of the colony, seeking an outlet. As a result, parts are shed or there is total disintegration of the colony into pieces (Schaeppi, 1897).

The morphology and peculiarities of the individual development of siphonophores are significant evidence for the establishment of a colony of siphonophores on an individual level, also testifying to the fact that from the point of view of morphology of specific zooids and on the basis of the individual development of the latter siphonophores still remain polymorphic colonies. The majority of individuals (nectophores, gonophores, gastrozooids and to a certain extent both pneumatophores and palpons) have retained an undeniable morphological similarity with medusae or polyps. The way all the above-named zooids are built up during a colony's ontogenesis is also the typical means of budding polyps and medusae in colonies of Hydroidea. Thus from the morphological and developmental standpoint the above elements are undeniable individuals and, consequently, the siphonophore - a colony.

As regards the physiological aspect of the question the functional specificity of separate zooids puts them on the level of organs, while the functional peculiarities of the colony as a whole not only underlines the high level of colonial integration in siphonophores but also leads to the belief that siphonophores have already crossed the boundary of coloniality and converted from polymorphic colonies into self-sufficient organisms.

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[5] Because of this peculiarity, colonies of siphonophores rarely fall into the hands of researchers complete.

Thus the dual nature of siphonophores is obvious. On the one hand they are polymorphic colonies though also at the height of colonial integration (evidenced by their morphology and development); on the other hand they have already crossed the boundary of coloniality and reached the level of self-sufficient organisms (which is convincingly demonstrated by their physiology).

### 5. SOME PECULIARITIES OF THE LIFE CYCLE AND DEVELOPMENT OF SIPHONOPHORES.

The planktonic environment has caused the aberrancy of siphonophores and the growth of colonial integration could not fail to find expression in the life cycle and nature of the development of Siphonanthae. Thus it is not surprising that the life cycle of siphonophores has a range of peculiarities.

Having most bearing on these peculiarities is the suppression of the sexual medusoid generation in all siphonophores and a complete absence of free-swimming medusae from the life cycle of most Siphonanthae.

Having arisen as a result of colonial integration masked metagenesis has become, for some groups of siphonophores, an obstacle in the dispersal of their sexual products. And then again as a result of colonial integration in the life cycle of Calycophorae true alternation of colonial generations has arisen during which free-swimming eudoxids and *Ersae* have taken on the function of sexual reproduction and dispersal of sexual products in the absence of free-swimming medusae.

The influence of the colonial entity has also spread to the early stages of larval development.

It is noteworthy that in the earliest ontogenesis of a colony the larva of siphonophores is still not evident as an individual (until the start of budding only a planula can be attributed to this); it appears as a unique stolon on both ends of which there appear successive buds of zooids of the future colony. Such an amalgamation of the state of coloniality at early larval stages is very typical of the ontogenesis of siphonophores.

And finally, the early larva of siphonophores is not simply a rudiment of a colony, but a rudiment of a polymorphic colony since its development results in the stage that is characterised by the presence of a polypoid generation only. The first medusoid individual appears on the larval stolon at the same time as the first polypoid one. Consequently polymorphism as a sign of the colonial integration of the colony also is widespread.

### II. THE INFLUENCE OF HABITAT ON THE NATURE OF THE EVOLUTION OF ZOOIDS IN COLONIES OF SIPHONOPHORES.

The basic tendency in the evolution of siphonophores is the growth of the role of colonial integration. As is well known this evolutionary feature was basically produced by conditions in siphonophore habitat.

Above all it was the transfer to life in the pelagic zone that led to the appearance of a range of specific adaptations in siphonophores. If the suppression of the medusoid generation and the influence of colonial integration facilitated the appearance of polymorphism and oligomerisation of mono-type elements of a colony produced the regulation of their distribution, then habitat has proved to have an

immediate effect upon the nature of polymorphism and peculiarities of distribution of the individuals on the stem of a colony.

A planktonic mode of life has provoked the appearance of one or other groups of individuals and different environments in the plankton (at the surface, in the water column or at great depths) have had an influence on their functional features and morphology.

The need to move about in water led to the appearance of special individuals. All these individuals are distributed in the upper part of the colony, forming a complete locomotive complex, permitting different means of travel for the colony in both a horizontal and vertical direction.

Thanks to its ability to generate the pneumatophore mostly acts as the hydrostatic apparatus of the colony. Muscle walls of the pneumatophore can increase or decrease the volume of the chamber containing the gas, and the latter, also increasing or decreasing in volume, ensures the vertical migration of the colony at different levels. In most Physophorae that live in the surface layers of water and vertically migrate within the boundaries of 0-300 m, 0-400 m, the pneumatophore is not large (from 2-10 mm) while Rhizophysidae (Cystonectae) and Rhodaliidae (Physophorae) that live at great depths (up to 2000 m) need a significant increase in the volume of their gas reserve in order to migrate to upper layers of water. Thus in representatives of the above families a pneumatophore sometimes reaches a length of 20 mm or more.

In the family Physaliidae (Cystonectae) the evolution of the pneumatophore has taken a different direction. As is well known the development of the earliest stages of *Physalia physalis* occurs at depth, and only with the growth of the larva do they rise to upper levels. Adult forms of *P. physalis* live exclusively at the surface of the water. Correspondingly changes have been undergone by the pneumatophore of this species. In the larva, the pneumatophore is relatively small and, regulating the volume of gas in its chamber, it enables the floatation and sinking of the young colony. In the adult *Physalia* a huge pneumatophore (up to 30 cm) filled with gas serves as a float keeping the colony at the surface and acts as a sail, enabling its passive movement by wind action. In addition, on the surface of the pneumatophore of *Physalia* there is a special longitudinal crest. This crest, as well as the pneumatophore itself, is always placed in such a way that the longitudinal axis of the pneumatophore forms an angle of about 45° in relation to the direction of the wind. Finally, in *Physalia* there is a characteristic formation of so-called "right" and "left" forms, i.e. forms in which the asymmetrical pneumatophore has either right-hand or left-hand curvature. All the above features allow the colonies of *P. physalis* to drift at the ocean surface like a sailing ship, moving on a left or right tack[6].

It is perfectly apparent that, given the previously listed functional peculiarities of the pneumatophore, its positioning at the most apical part of the colony is the most rational.

Nectophores comprise the basic part of the locomotive complex of a colony of siphonophores. As is well known, the walls of the subumbrella of a nectophore have a powerful musculature that if relaxed or contracted enable the drawing in and consequent ejection of water from the chamber of the nectosac. Thus with the aid of nectophores the colony moves by the principle of jet propulsion - in the direction

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[6] Tack - the course of a vessel (and in this case the course of the colony) relative to the wind.

directly opposite to that of the water ejected by the nectophores. It is natural that there is the most rationally compact disposition of all nectophores in the upper part of the colony (immediately below the pneumatophore, or if the latter is absent, then at the top of the colony).

In most Physophorae each colony has a large number of nectophores that are densely packed and which, with the pneumatophore and subsequent stem parts, give the colony its streamlined form, enabling the creature to move around in different directions.

In the Calycophorae nectophores also have evolved towards enabling greater and greater speeds of movement for a colony. Thus representatives of the families Hippopodiidae and Prayidae, well-known as mediocre swimmers, have circular nectophores positioned one against another, while nectophores of the speedy Diphyidae, which have an arrow-like movement, are conical or pyramidal in shape and arranged one above the other.

Calycophorae, which have no pneumatophore, also carry out vertical migrations with the help of their nectophores; in other words, the latter in some way facilitate a reduction or increase in the specific gravity of the colony. It is quite possible that the hydrostatic apparatus involved in this is the somatocysts of upper nectophore. In fact it is well known that the somatocysts of upper (and sometimes lower) nectophores of Calycophorae are somewhat better developed than in physophorids.

A complex of zooids facilitating the feeding of the colony (the siphosome) is always distributed in its lower part and always found under water even if the nectosome with its pneumatophore and swimming bells is found at the surface. The reason for this phenomenon lies in the density of the siphosome that, on account of its gastrozooids, tentacles, palpons and gonophores is heavier than water, the point being that any siphonophore, irrespective of its place of habitat (whether this is at the surface of the water or at different depths), finds its food in the water column. Safeguarding maximum fishing of the surrounding area is above all achieved along the stem of the colony, and also by the fact that the stem is twisted into a spiral. Consequently, gastrozooids, which in fact bud only on one side of the stem, prove to be turned in different directions from it, which also increases their fishing possibilities. Finally, the intensity of fishing is facilitated by tentacles that reach several metres in length. It is interesting to note that in *Physalia* the length of the tentacles sometimes exceeds 10 m, thanks to which this siphonophore can, at the surface of the sea, fish quite large parts of the water column.

Of all the zooids of the siphosome, bracts and gonophores in their evolution are notably subject to the influence of the environment.

Bracts, originating from medusoids, protect other individuals of the siphosome, which are without a skeleton and consist only of soft parts, from possible damage. In the physophorids the many bracts of each cormidium lie densely packed next to one another and form what resembles a protective shield for the remaining zooids, while the single bract of each cormidium of calycophorids covers the latter in the form of a hood. It is interesting to note that bracts of Calycophorae have a very well developed phyllocyst. The latter, resembling the somatocyst of the nectophore, is possibly a hydrostatic adaptation and also, because of the fat globules accumulating in it, is involved in the change in density of the colony, associated with its vertical migrations. On the other hand, the phyllocyst of bracts of Physophorae, just like the

somatocyst of their nectophores, is poorly developed and the pneumatophore fully copes with the functions of the hydrostatic apparatus found in these siphonophores.
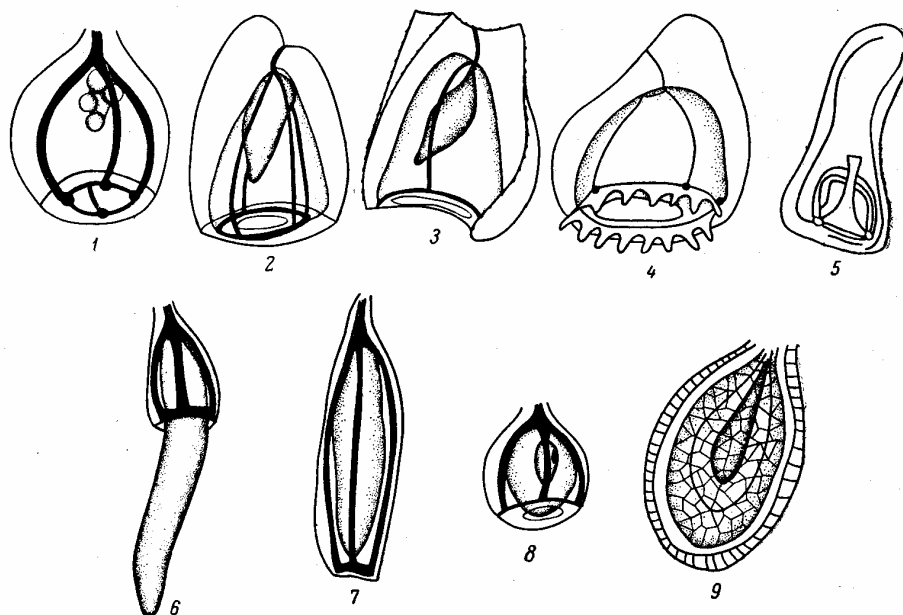


Fig. 50. Gonophores of different representatives of Siphonanthae.
Top row: gonophores participating in the movement of the colony;
Bottom row: gonophores exclusively fulfilling sexual functions,
1-3: gonophores of *Amphicaryon*, *Rosacea* and *Muggiaea*;
4-5: special nectophores of *Desmophyes* and *Physalia*;
6-8: gonophores of *Vogtia* and *Agalma*; 9: sporosac of *Anthemodes*.

As already mentioned in the previous section, gonophores of Calycophorae that participate in the movement of eudoxids are very reminiscent of free-swimming medusae (Fig. 50, 1-3). They have a quite spacious subumbrella cavity whose wall musculature is excellently developed. The rim of the subumbrella of these gonophores is equipped with a velum. Moreover in some calycophorids, and also in *Physalia physalis*, some of the gonophores fulfil only locomotive functions, having completely lost the ability for sexual reproduction (Fig. 50, 4, 5).

Gonophores of Physophorae and Hippopodiidae have evolved differently. In this group of siphonophores gonophores take no part in the movement of the colony. Fulfilling only sexual functions they have very well developed manubria, and minimal development of umbrella bells (Fig. 50, 6-8). Finally in some physophorids sexual medusoid specimens have been reduced to the state of sporosacs (Fig. 50, 9).

## III. NEOTENY AS ONE OF THE EVOLUTIONARY PATHS OF SIPHONOPHORES

The term neoteny (Greek – young, Greek – to preserve, prolong) implies a shift in the moment of reaching maturity to one of the earlier stages of development (Kazas, 1936). This phenomenon, well known since the time of Agassiz and called

"neoteny" by Kollman (1884) as applied to the axolotl, is characteristic of many groups of creatures.

Classic examples of neoteny are the premature sexual maturity of tadpoles observed in some tailless amphibians (*Pelobates* and *Alytes*) and tritons (Molgae), or the early development of sexual organs in the larvae of *Amblystoma tigrinum* (axolotls). This phenomenon can be provoked naturally and arises as a reaction of the organism to a change in its customary environment. Such situations, when the creature can become neotenic or develop normally depending on external conditions, are called by Kazas (1936) facultative neoteny.

Facultative neoteny is also well known in termites (Escherich, 1910), pantopods (Shimkevich, 1909) and certain insects (Heymons, 1896).

Besides facultative neoteny there is neoteny in which a creature has finally lost the capacity to reach full development, corresponding to the definitive stage of its ancestors. This manifestation of neoteny Kazas calls fixed neoteny.

There are examples of fixed neoteny in very different groups of animals, invertebrates included. The neotenic nature of these forms is indicated by their remarkable similarity to larvae of certain other creatures. Among these are Ctenophora (Tretyakov, 1936)[7]; Acoela (Turbellaria) (Graff, 1905; Zakhvatkin, 1949; Dougall, 1959); Amphilina (Cestoidea) (Janicki, 1928; Fuhrmann, 1930); Dinophylidae and Histriobdellidae (Polychaeta) (Livanov, 1940; Jagersten, 1947; Lang, 1950) and certain others. To date, the question of the neotenicity of Rotifera and Appendicularia has been resolved in the negative.

Cases of neoteny are also found in Coelenterata. Hamann (1883) considers, for example, that the family of Ephyropsidae (Ephyridae) from the coronate Scyphomedusae is neotenic since individuals of the medusoid generation of this family are morphologically very similar to Ephyrae of other Scyphomedusae. Remane (1927) described a new family if trachilids, the Halamnohydridae, which he views as neotenic.

Kazas regards the basic factor giving rise to neoteny as a change in the organism's environment. Besides this the reason for neoteny may simply be a tendency to reduce developmental periods and to speed up the onset of sexual reproduction. The transfer from a fixed to a free-moving life style could in some coelenterates speed up periods of sexual maturation. On the other hand, accelerated maturation as one of the adaptive facilities is more characteristic among free-moving than stationary creatures (Schmalghausen, 1946). Thus the tendency to reduce development periods in pelagic Coelenterata is also perfectly understandable.

Neoteny may also be characteristic of Siphonanthae that are exclusively pelagic creatures. Thus the similarity between definitive nectophores of siphonophores and larval colonies of other species allows interpretation of these definitive colonies as neotenic in origin.

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[7] Beside the neotenic origin of the whole group of Ctenophora the particular manifestation of facultative neoteny is characteristic of specific genera of Ctenophora. Larvae of Ctenophora from the genera *Bolina* and *Euctiaria* become sexually mature at an early stage in their development, setting by fertilised eggs, after which their testicles and ovaries degenerate. Later there follows a prolonged sterile period when, due to metamorphosis, adult stages with new gonads appear. This form of neoteny was called dissogony by Chun (1880). Thus besides fixed neoteny in some Ctenophora there is, as it were, a second wave of neoteny in the form of dissogony.

If the neoteny is characteristic of some Scyphozoa and Ctenophora (just as it is of other neotenic animals) involving early development of sexual products in single individuals (the larvae of medusae or ctenophores) then among siphonophores neoteny is unique in that it arises not among individuals but colonies. In relation to the whole colony it is involved in the early budding of medusoids whilst in relation to each medusoid (the gonophore) as an individual it consist in the early reduction of periods of sexual maturation. Taking a colony of siphonophores as a unique physiological individual (see above) it is possible to speak of the neoteny of Siphonanthae as a whole, involving premature budding on the stem of the larval colony of medusoids capable of producing sexual products during reduced periods. Contrary to the neoteny of single individuals, that in colonial animals can be termed "cormo-neoteny".

Facultative neoteny in siphonophores is unknown. Its presence among Siphonanthae is extremely difficult to establish in natural conditions. An attempt to evoke facultative neoteny in some species of Siphonanthae so far has not been carried out.

Thus in the case of siphonophores there can only be discussion of fixed neoteny, i.e. of forms of siphonophores neotenic in origin.

As already stated, to date it is primarily the theory of the neotenic nature of all groups of Siphonanthae that has been widespread. In Totton's (1960) view contemporary siphonophores (just like contemporary Chondrophora, Myriothelidae, *Corymorpha, Margellopsis* and *Pelagohydra*) should be seen as actinula-like larvae capable of reproducing individuals that generate sexual products. An assessment of this view is given in the section on ancestors of siphonophores.

Apart from fixed neoteny as one of the possible paths in which the whole group of Siphonanthae came into existence, neoteny is probably linked with the origin of specific species, genera and also sub-families of siphonophores. In order to be completely certain of the neotenic nature of any of the Siphonanthae it is not enough to have only one morphological comparison of their colonies with larval stages of close forms. It demands other experimental confirmation. Despite the fact that as a rule this is not available the morphology and development of indicated representatives of three suborders point to their neotenic nature.

Thus in all probability the Athorybiidae family is neotenic. Definitive colonies of both genera belong to this family (*Athorybia* and *Melophysa*) \re structurally on a level with larvae of Physophorae. Definitive stages of *Athorybia*[8] are very similar to the early larvae of *Agalma elegans*, when in the latter there is still no nectosome and consequently no nectophores, and the siphosomal zone is extremely poorly developed. Meanwhile bracts of adult *Athorybia* are homologous to the larval bracts of the second order of larvae of *A. elegans*. Thus it is possible to assume that colonies of the genus *Athorybia* have developed along the path of neoteny from larvae of some Agalmidae or other, reminiscent of larvae of *A. elegans*. The obvious similarity of *Athorybia rosacea* (Forskål) and *Agalma elegans* (Fig. 51, a, б, b) speaks in favour of this view.

In Totton's (1954) view adult forms of *Athorybia* are homologous to the early larvae of S*tephanomia bijuga* (delle Chiaje) when sexually mature. This link is

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[8] Genus *Athorybia* is characterised by an absence of a nectosome and nectophores, a very short siphosome and the fact that bracts are positioned like a corona, around the pneumatophore.

obviously less probable since as far as the development of *S. bijuga* (see description of life cycle and development of siphonophores) is known, its larva is devoid of larval bracts that otherwise would have formed the bracts of the adult colonies of *Athorybia* and judging from the descriptions of Haeckel (1869) and Schneider (1896a, 1896b) are present on larvae of *Athorybia rosacea*.

*Melophysa* in Totton's view can be considered a sexually mature larva of Agalmidae at the stage when it manifests an already distinct nectosomal zone and buds the first nectophore (Fig. 51, b). The only nectophore in the colony of *Melophysa melo* Quoy and Gaimard is in form and relative position on the axis very reminiscent of young nectophores of other Agalmidae. Totton (1954, p. 37) suggests that the nectophore of *Melophysa* is an early stage of these zooids.

Many researchers consider Physophoridae with a single genus and species, *Physophora hydrostatica* Forskål, as another neotenic family in the suborder Physophorae. This specialised species, possessing a range of secondary features (basal pore of pneumatophore and corona of large protective palpons), has probably come from an even later larval stage of physophores in which there are buds of up to 4 pairs of nectophores, while the siphosome, also sufficiently developed, has not yet assumed a vertical position and is twisted spirally in a horizontal plane, and has the appearance of a disk (Fig. 51, $b_2$). The absence of bracts in representatives of *P. hydrostatica* can be explained in different ways. On the one hand, as a loss of larval bracts with different stages of ancestors of this species (as testified by larvae of *P. hydrostatica*, Fig. 51, $б_2$, devoid of bracts of the second order), and at the same time by the fact that definitive nectophores have as yet not started to bud. On the other hand, bracts can be intermittently lost by this species in the course of its specialisation.
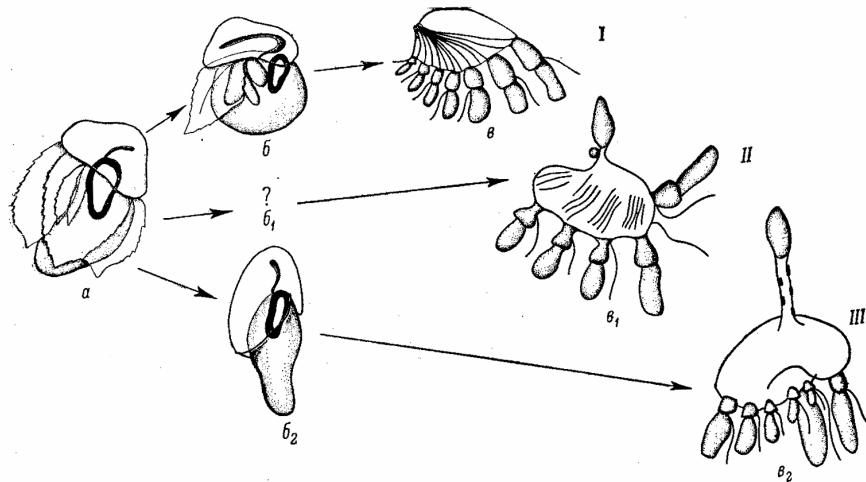


Fig. 51. Diagram of neotenic path of origin of *Athorybia rosacea* (I), *Melophysa melo* (II), and *Physophora hydrostatica* (III).
a – larva of Agalmidae (*Agalma elegans* type): б – larva of *Athorybia rosacea*; $б_1$ – unknown larva; $б_2$ – larva of *Physophora hydrostatica*; Б – adult form of *Athorybia rosacea*; $Б_1$ – adult form of *Melophysa melo*; $Б_2$ – adult form of *Physophora hydrostatica*.

In the order Calycophorae neotenic forms are also represented. They belong principally to the family Sphaeronectidae. A colony of *Sphaeronectes* (the only genus of this family) is very similar to the larvae of two other contemporary families of the suborder Calycophorae – Hippopodiidae and Prayidae (Fig. 52). Considering the aberrancy of the Hippopodiidae it will be more correct to seek the origins of *Sphaeronectes* amongst ancestors of Prayidae, i.e. to derive *Sphaeronectes* from larvae of ancestral types of Prayidae.

Probably also neotenic in origin is the genus *Nectopyramis* of the subfamily Nectopyramidinae, belonging to the family Prayidae. In Totton's (9154) view *Nectopyramis* developed from later larval stages of Prayidae ancestors.

Finally, the genus *Monophyes*, attributed earlier to the family Sphaeronectidae and by many authors even compared synonymously to the genus *Sphaeronectes* (Bigelow, 1911b) must apparently be considered as a neotenic form close to the larvae of Diphyidae (of *Muggiaea kochi* Will or *Sulculeolaria quadridentata* type) (Fig. 53). Like sphaeronectids, representatives of *Monophyes* (subfamily Monophyinae, family Diphyidae) each have one unchanging nectophore of larval type.
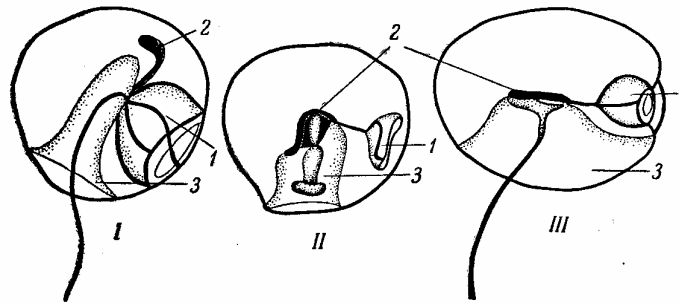


Fig. 52. Comparison of nectophore of definitive colony of *Sphaeronectes* (I) with larval nectophores of *Rosacea* (II) and *Hippopodius* (III). 1. – chamber of subumbrella; 2. – somatocyst; 3. – hydroecium.
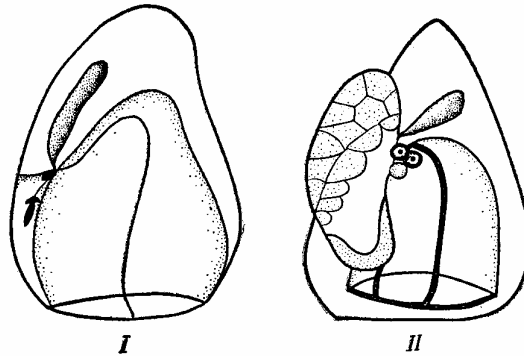


Fig. 53. A comparison of a nectophore of the definitive colony 0f *Monophyes irregularis* (I) with a larval nectophore of *Sulculeolaria quadridentata* (II).

Totton (1960) also considers *Physalia physalis* (Cystonectae, Physaliidae) a neotenic form. In fact this siphonophore what possesses an extremely shortened stem is very reminiscent of a larva, through also having a series of specialised features because of the peculiarities of its habitat. This similarity is also supported by the fact that the early stage of *Physalia* has much in common with the larvae of certain

Physophorae (for instance S*tephanomia bijuga*, fig. 54). Unfortunately, the larval stages of Rhizophysidae (Cystonectae with a long stem), from which *P. physalis* is tentatively derived are as yet unknown. But the definitive stage of *Salacella uvaria* (=*Salacia polygastrica* Haeckel, 1888b) is, in Haeckel's description, attributable to the Rhizophysidae family, i.e. possesses a long stem and in many ways resemble *P. physalis* (in structure of gastrozooids and tentacles, and in the arrangement of the gonodendra) (Totton, 1960: 346). If the presence of this species is confirmed (since Haeckel's time no researcher has succeeded in finding it) then it is possible to assume that *P. physalis* originated from forms that are close to larvae of *Salacella uvaria*.

Thus the morphology and development of some representatives of Siphonanthae testifies to the presence in siphonophores of fixed neoteny.

The uniqueness of neoteny in Siphonanthae lies in the fact that it extends not only to specific individuals of the colony but alto to the colony as a whole (cormo-neoteny).

It is possible to speak of cormo-neoteny associated with a high level of colonial integration in Siphonanthae. When we speak of the sexual maturity of a colony (or larva) of siphonophores we mean the sexual maturation of its gonophores, not only as morphological individuals but also as physiological organs of a single colonial individual.

In all three suborders of siphonophores there are forms that have arisen neotenically. Among these there may be both whole families (or subfamilies) and specific genera.

The relatively large number of neotenic forms in the order Siphonanthae is evidence that neoteny is one of the evolutionary paths of Siphonanthae.
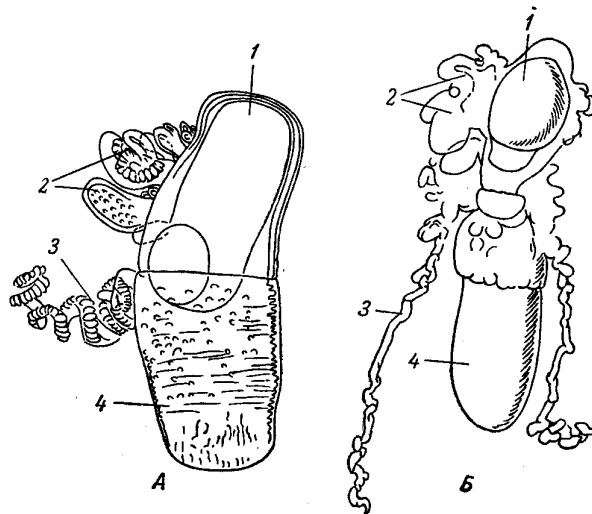


Fig. 54. A comparison of early larval stages of *Physalia physalis* (Cystonectae) (A) and S*tephanomia bijuga* (Physophorae) (Б) (according to Totton). 1. – bud of pneumatophore; 2. – budding zone of secondary gastrozooids; 3. – tentacles; 4. – primary gastrozooid.

*IV. THE ORIGIN OF SIPHONOPHORES AND THE GENERIC INTERRELATIONSHIPS BETWEEN CONTEMPORARY SIPHONANTHAE*

As became clear in the study of the life cycle and development of Siphonanthae, the individual development of each siphonophore as a single organisms ends at the stage of a planula, and at the appearance of the first medusoid nodule and first gastrozooid as a single organisms ends at the stage of a planula, and at the appearance of the first medusoid nodule and first gastrozooid with a tentacle the larva shows as a budding stolon. In other words, the ontogenesis of colonies of siphonophores has so changed that it is impossible to derive from it any facts about their closest prototype. Nonetheless, an attempt is made below, using data obtained by studying the morphology, features of life cycle and development of siphonophores, to present a general picture of their origin and evolution, and to establish what link there is between present day groups of Siphonanthae.

## 1. ANCESTORS OF SIPHONOPHORES

As stated above, metagenesis, which is the basis of the life cycle of siphonophores, is masked in most cases. But taking into account that all the forms (e.g. *Agalma elegans*) have been retained in which there is a facultative break in the medusoid generation, it is possible to assume that in the life cycle of the ancestors of siphonophores there did exist a free-swimming medusoid generation. On this basis the possibility arises that ancestors of siphonophores were some sort of colonial hydrozooids also having free-swimming medusae in their own life cycle. In other words siphonophores were produced from common metagenetic Leptolida (and not from Leptolida with masked metagenesis), i.e. the masked metagenesis of the Siphonanthae has arisen independently and irrespective of that of the Leptolida (Stepanjants, 1966).

Ancestors of Siphonanthae should evidently be south amongst Athecata since it is precisely among representatives of this subgroup of Leptolids that medusae, just like the gonophores of Siphonanthae, carry gonads on the oral proboscis only. Besides this most of the representatives of Athecata possess true alternation of polypoidal and free-swimming medusoid generations.

As stated above, a series of researchers (Hadzi, 1918; Garstang, 1946; Leloup, 1954) confirm the view that the provenance of Siphonanthae, just like that of *Pelagohydra* and Chondrophora from the Hydroidea, is associated with the early sexual maturation of a free-swimming larval phase (of the actinula type) of hydroids of the *Margellopsis, Myriothela* or *Corymorpha* type. Totton (1960) takes the theory further, suggesting that all previously mentioned hydroids (*Myriothela, Corymorpha, Margellopsis, Pelagohydra* and Chondrophora) just like the Siphonanthae appear to have arisen as a relatively recent new type of organisation of animals – the paedophore 0 a tentacle-bearing actinula larva in which early budding, just like in the early sexuality of gonophores budding on it, is an adaptation associated with a pelagic life style.

An attempt to firmly establish which of the contemporary Athecata are related to the closest ancestors of siphonophores is hardly opportune yet. There is no basis in fully rejecting the paedophore theory since there is no evidence opposing the positions of Hadzi, Garstang and Totton. At the same time their conclusions, constructed on a purely external similarity and hypothetical homologies, demand additional confirmation. It is quite possible that *Margellopsis* or the Myriothelidae themselves are relatives of ancestors of Siphonanthae. It may be in fact that the

neotenic larvae of some ancient representatives of thee families have been predecessors of siphonophores, but it may be that these have turned out already to be adult colonies of the *Margellopsis* type.

The least possible course of origin of siphonophores is from a medusoid generation of Athecata ancestors. To recognise the medusoid origin of siphonophores it would be necessary to consider the bell of the primary medusa as having given rise to a pneumatophore whose oral end would, in this case, lie at its base. But the morphology of the pneumatophore shows the reverse – the oral end of the pneumatophore is found at its apex. So an explanation of the pneumatophore as a medusa with a bell bent outwards by the subumbrella is a strained interpretation.

On the other hand, in support of the "polypoid" theory it seems logical to sup[pose that the predecessors of the siphonophores were some hitherto unknown colonial Athecata. Colonies of these hydroids, devoid of a skeleton (a fact supported by the complete absence of skeletal formations in siphonophores[9]) had budded on their hydrorhiza numerous medusoids and polypoids. It is difficult to say what such colonies looked like, but if we assume that they were trailing, with a slightly branched hydrorhiza, budding polyps and medusae upwards only, i.e. on one of their sides, then it is possibly to assume the homology of this side of the hydrorhiza of trailing Athecata with the so-called ventral side of the stem of colonies of siphonophores. The polypoidal generation of these Athecata possessed either irregularly positioned tentacles or a basal crown of tentacles, and medusae as they broke off had a free-swimming life style.

At the decisive moment in the evolution of ancient siphonophores, Archisiphonanthae came the transition of their hydroid predecessors to plankton.

What is the reason for so sharp a change in ecological conditions by these organisms?

On the one hand, according to the paedophore theory neoteny could be the reason. In this case the appearance of planktonic colonies of siphonophores went in parallel with the development of pelagic colonies of *Margellopsis* and *Pelagohydra* out of a free-swimming actinula-like larva of ancestral Athecata, which began to bud sexually mature specimens before it settled and took root on the bottom. Siphonophores were possibly produced from already definitive pelagic colonies of the *Margellopsis* and *Pelagohydra* type, which in turn also became planktonic in the course of neoteny.

On the other hand, the reason for the appearance of the free-swimming colonies could turn out to be the accidental break away of hydroids attached to the bottom. It is possible to suppose that some colony of the Athecata, weakly attached to the bottom, broke away as a result of wave action and was carried off by the current. Initially it swam passively and possibly part of the little medusae, which had not yet separated off from the hydrorhiza enabled it to be supported in the water and perhaps to move about, thereby not allowing this organism, unadapted to the new element, to die. Thus, having broken off initially by chance and survived in a new medium, colonies of this species of hydroids could later again break away, if not regularly, nonetheless still already quite naturally (among contemporary Hydrozoa there are well-known cases – *Obelia gracilis* (M. Sars), where at times planktonic colonies of polyps are formed that are morphologically almost indistinguishable from the bottom

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[9] The chitinous layer of the pneumatophore is a secondary formation.

dwellers). Gradually such colonies come to develop adaptations. Thus some of the medusoids came to fulfil the functions of colony locomotion initially along with sexual ones, later as a whole losing the latter (see below).

Then in the process of subsequent evolution a similar breaking away of colonies became an intrinsic step in the life cycle of these Hydrozoa, i.e. part of their life was conducted in a fixed state while another part of their life took place in the plankton[10]. Evidently in this case special locomotive individuals became necessary to the colony much earlier than when they budded in the creature's process of ontogenesis as sexual medusoids. The moment when locomotive medusoids appeared in a colony shifted amongst the Archisiphonanthae to earlier stages of ontogenesis by comparison with hydroid ancestors. This in the ontogenesis of contemporary siphonophores the budding of a pneumatophore and nectophores occurs almost at the same time as the budding of the first feeding individuals, while the moment when sexual medusoid budding begins much later.

The concluding transition of colonies of Archisiphonanthae to plankton began much later. From the moment of the development of the siphonophore had a general tendency to suppress the medusoid generation. In colonies that led a free-swimming life style the need for free-swimming medusae disappeared. This led to masked metagenesis.

The transition of a colony to a free-swimming life style and, to a certain extent associated with this, the strengthening of colonial individuality have brought with them a gradual suppression of the individuality of each zooid. A division of functions amongst individuals of a colony began to occur. Amongst the polypoid zooids there appeared feeding, excretory and protective individuals and a part of the medusoids had the function of colony propulsion. Most probable of all, this led to the appearance of the Archiphysophorae – a group most resembling the most primitive contemporary siphonanths, the Physophorae. Archiphysophorae already had floating bells (some of which correspond to the pneumatophore of *Physophora* and were possibly featured more than once per colony, others corresponded to nectophores, and had other specimens with still significant anarchy in their arrangement and number. Although each of the specimens of these ancient siphonophores gad adequate self-sufficiency it nonetheless already fulfilled some sort of defined function.

During the evolution of free-swimming Archiphysophorae the distribution of zooids on the stem turned out to be natural, so that individuals involved in movement were concentrated in the upper part of the colony, forming the locomotive complex (so giving rise to the nectosome), while the feeding individuals were found in the lower part of the colony, comprising the basis of the tropic complex (the siphosome). Individuals comprising the nectosome were fully reduced on the siphosome and conversely siphosomal zooids (with rare exceptions) were not featured on the nectosome, which is associated with an absence of need for them on these small parts of the colony.

The most recent development associated with the continuing growth of the colony integration took place in siphonophores along the lines of oligomerisation of the number of zooids and the regulation of their disposition on the stem of the colony (Dougall, 1936, 1954; Naumov, 1957, 1960; Beklemishev, 1964).

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[10]  The possibility of a similar change in ecological conditions throughout the life of a colony is confirmed by the presence among Athecata of forms, for instance *Moerisia pallasi* (Derzh.), whose colonies may alternate a fixed and planktonic life style.

2. ORIGIN OF SUBORDERS OF SIPHONOPHORES

Having appeared from a common root the Siphonanthae very quickly diverged, separating into groups, each of which assumed its own very specific characters. Because of a general tendency to accelerated development largely characteristic of free-swimming forms (Schmalghausen, 1946) the divergence of contemporary siphonophores has proceeded so far, and contemporary groups of Siphonanthae are so different from one another (as a rule there are no intermediate forms), that at times the link between them is difficult to establish (Stepanjants, 1966).

However it may be suggested that the most primitive of all the contemporary siphonanths are those closest to their ancestral forms are the Physophorae. In the first place, it is only amongst the Physophorae that forms are preserved with common unmasked metagenesis. Secondly, representatives of Physophorae contain the greatest number of individuals per colony as compared with other Siphonanthae, a fact that is also confirmed in the ontogenesis of this group, since in the larvae of some representatives of Physophorae (family Agalmidae) there is budding of a significant number of provisional zooids. Thirdly, some Physophorae (part of the Forskaliidae and part of the Agalmidae) have still retained a noticeable irregularity in the disposition of some individuals whose number is not always fixed in each cormidium of a colony. Fourthly and finally, colonial integration in Physophorae has still not reached the level where alternation of colonial generations has become possible.

Being most primitive, Physophorae at the same time carry certain specialisations features that significantly distance them from the Archiphysophorae. The singular pneumatophore and the strict division of the colony into locomotive and trophic sections testify to a prolonged course of evolution, and the strong reduction of gonophores (sometimes to the stage of a sporosac) during contemporaneous hypertrophy of the manubria are evidence of the narrow functional trend of these zooids.

Cystonectae are apparently another branch also derived from Archiphysophorae. That the evolution of Cystonectae is little understood is basically due to the fact that this group is the least studies (as already stated, of all the Cystonectae there is sufficiently detailed evidence only for *Physalia physalis*). Nonetheless on the evidence that an early larva of *P. physalis* is very similar to that of certain Physophorae (fig. 54), it is possible to speak of the closeness of these two suborders. But even here the divergence has led to a series of specific attributes. A complete loss of nectophores and corresponding contraction of the nectosome to minimal dimensions (its is here restricted by the part that buds a pneumatophore) and an absence of bracts distinguish this suborder from the Physophorae. And the capacity of some Cystonectae (*P. physalis*) to produce free-swimming gonodendra testifies to a higher level of colonial integration in Cystonectae as compared with Physophorae. Thus Cystonectae, being close to the Physophorae, are a step higher on the evolutionary ladder than siphonanths.

Calycophorae show the highest level of development of siphonanths. Representatives of this suborder show the highest degree of difference from Archiphysophorae. Oligomerisation of the number of single-type zooids is the basis of the evolution of Calycophorae. Colonies of them are completely devoid of a pneumatophore. Evidently in ancestors of Calycophorae there was not only a reduction in the pneumatophore itself but also a degeneration of that part of the stolon budding it. The overwhelming majority of Calycophorae possess two (or one) nectophores and the number of zooids in each cormidium among them is reduced to a minimum. Finally, in this suborder the integration role of the colony reached such limits that the formation of a secondary free-swimming colonial generation became possible, which as distinct from the gonodendra of *Physalia physalis,* is capable of a prolonged self-sufficient existence (see description of life cycle of Calycophorae).

Thus the evolutionary links between the suborders of contemporary Siphonanthae can be expressed in the following diagram:

Calycophorae

Cystonectae

Physophorae

Archiphysophorae

Archisiphonanthae
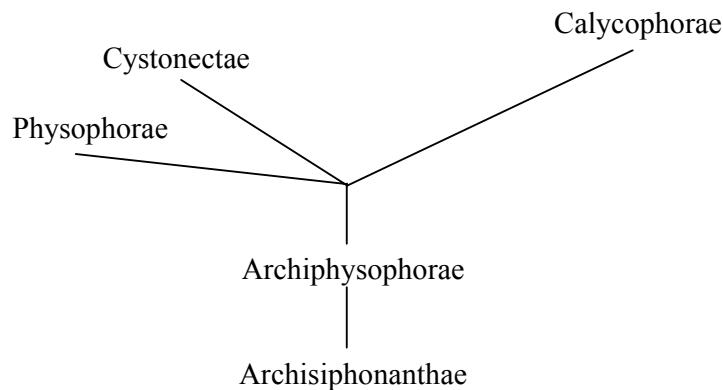
Before approaching the question of the origin of specific families of these suborders we must first address the question of the place of the Chondrophora group in the Coelenterate system, which has earlier been attributed to the subclass of siphonophores.

3. THE SYSTEMATIC POSITION OF CHONDROPHORA
(Chamisso et Eysenhardt, 1821)

Since Haeckel's time it has been customary to consider Chondrophora (synonym Disconanthae), like Siphonanthae, as a group belonging to the subclass (or class) Siphonophora. Some authors (Haeckel, 1888b) gave Chondrophora the rank of subclass but the majority of researchers (Chun, 1987a; Schneider, 1898; Bigelow, 1911b; Moser, 1925, etc) included this group of two families (Porpitidae and Velellidae) in the Siphonanthae as one of its suborders.

In recent times it has been claimed that Chondrophora are not generally related to Siphonophora. In V.N. Beklemishevs's view "siphonophores are not a true group: grouped under the same heading there are two separate orders of free-swimming colonial Hydrozoa: Siphonanthae and Disconanthae" (1964, p. 89). Totton (1954) considers Chondrophora and Siphonophora to be two, completely independent orders of Hydrozoa.

A comparison of Siphonophora and Chondrophora will show the obvious principal differences between them. This difference is primarily seen in the morphology of each. If colonies of Siphonophora have bilateral symmetry and are characterised by a high level of polymorphism, the symmetry of Chondrophora is typically radial and the polymorphism of their colonies is reduced to a minimum. The pneumatophore of the Chondrophora is not an individual but an organ that has arisen as an ectodermal outgrowth of the aboral terminal of the larva (V.N. Beklemishev, 1964) and is, therefore, not homologous to the pneumatophore of Siphonophora. Other elements of colonies of Chondrophora are featured by all of two groups of specimens – a single gastrozooid (main polyp) and sexual medusoids (fig. 55). Since there are in each colony dactylozooids that are not homologous to those of Siphonanthae (see morphological sketch) and in Metschnikoff's view (1870) and Mackie's (1959) they should be treated as organs not individuals as they are positioned like a crown around the main polyp, they are very reminiscent of hydroid polyps (fig. 55) that lie around the hypostome of the tentacle. In Naumov's (1961) view the same applies to blastostyles of Chondrophora, which bud medusae. If the blastostyles of hydroids are homologous to the gonostyles of siphonophores and are individuals of polypoidal origin developing exclusively on the coenosarc or stem of the colony, the blastozooids of Chondrophora, on the other hand, are not homologous to them, since they form on the very body of the main polyp and so must apparently be seen as its outgrowths, i.e. organs and not individuals. Naumov compares blastozooids of Chondrophora with gonodendra of hydropolyps of *Tubularia* and *Corymorpha*. Consequently all variation in individuals of Chondrophora is comparable with the single main polyp and sexual medusae. It must be noted that these individuals are not grouped into cormidia in contrast to siphonophores.
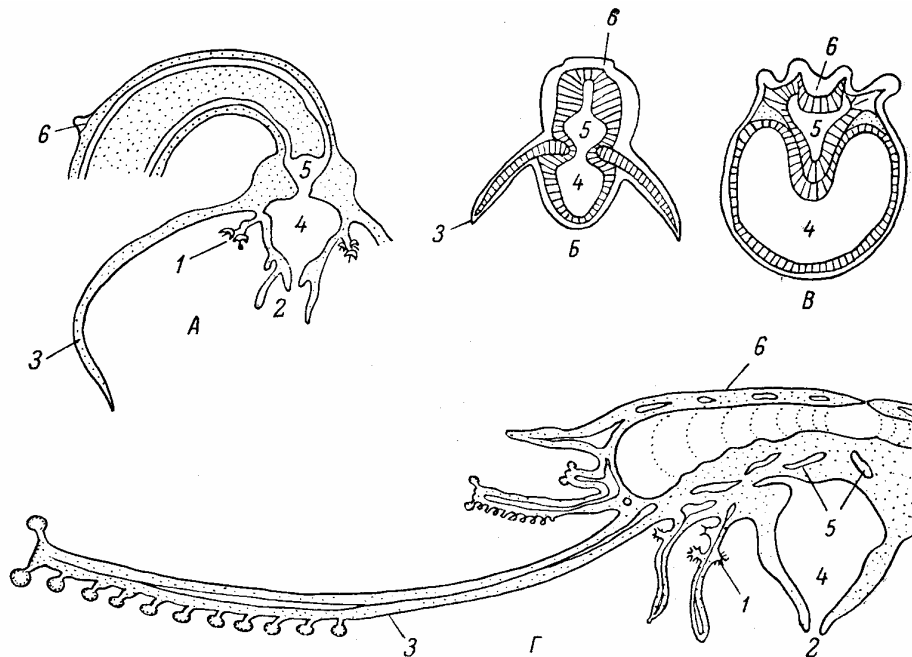


Fig. 55. Homology of structure in Chondrophora and tubulariids in cross-sections (according to Mackie).

A – hydranth of *Corymorpha*; Б – larva of *Corymorpha*, actinula;  - larva of *Porpita*, conaria; Г – *Porpita*.
1.  medusoid buds; 2 – oral aperture; 3. – aboral tentacles; 4. – oral part of gastric chamber; 5. – aboral part of gastric chamber; 6. – ectodermal chitinous formations.

Information on the development of Chondrophora testifies to the difference in structure of their larvae (conariae) (fig. 55) and the larvae of Siphonophora.

If there is customary masked metagenesis in the life cycle of Siphonanthae and free-swimming medusae are formed only as exceptions in some representatives, the life cycle of Chondrophora is characterised by a typical alternation of polypoid and medusoid generations in which the latter. Just like the former, leads a free – swimming life style. A medusa of Chondrophora – Velellidae (Chrysomitra) (fig. 56) has a well-developed bell, four radial and one ring-shaped gastric canals, and four (or two) untwisted tentacles with terminal pneumatocystic shields (Brinkmann, 1964). Gonads of Chryosmitra appear on the conical manubrium, finally maturing only after the mouth breaks through on the proboscis. A medusa of Chondrophora is radically different from the underdeveloped free-swimming medusa of *Agalma elegans* belonging to the s belonging to the siphonophores.
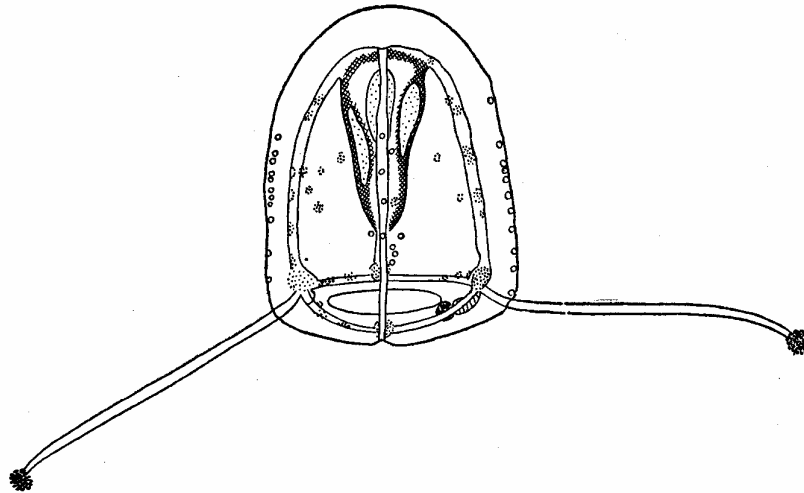


Fig. 56. Adult medusa of *Velella* (according to Brinckmann).

Consequently, data on the morphology, development and ontogenesis of colonies of Siphonophora and Chondrophora testify to the radical differences between these two groups.

Researchers, mainly united in their belief that the differences between the Siphonophora and Chondrophora are very great, have to date disagreed on the taxonomical classification of Chondrophora, their place in the Coelenterata system and their phylogenetic links with other Hydrozoa.

In this regard, most widespread is the so-called "anthomedusal" concept according to which Chondrophora are very loosely related to Anthomedusae[11]. On the other hand, Rees (1957) considers Chondrophora as a specialised group outside the Anthomedusae although close to them. On the other hand, most of the adherents of the anthomedusal theory (Garstang, 1946; Leloup, 1954; Totton, 1954; Mackie, 1959; Brinckmann, 1964) when comparing Chondrophora with Athecata (Anthomedusae) link *Porpita* and *Velella* with the hydroids of the Tubularia and Corymorpha type. Mackie, for instance, when comparing general structural plans of a hydranth of Corymorpha with a Porpita and a larva of Corymorpha with a larva of Porpita (fig. 55) establishes their homology. As a result, a colony of Porpita is regarded as a colony of Athecata in which one polyp has undergone maximum development and there is budding on its little head of sexual medusoids (of Tubulariidae type). This polyp, transferring to a planktonic life style, has turned its oral end downward and its base correspondingly towards the surface film of the water.

On the basis of all that has been stated we can conclude that Siphonophora and Chondrophora are related to one another, in so far as both are related to contemporary Athecata, but each of these groups undoubtedly arose independently.

Chondrophora should apparently be seen as one of the orders of Hydroidea originating from Leptolida (Athecata), colonies of which as a whole transferred to life in the plankton.

Certain additions can be made to Naumov's (1960) plan that illustrates the generic interrelationships between order and suborders:



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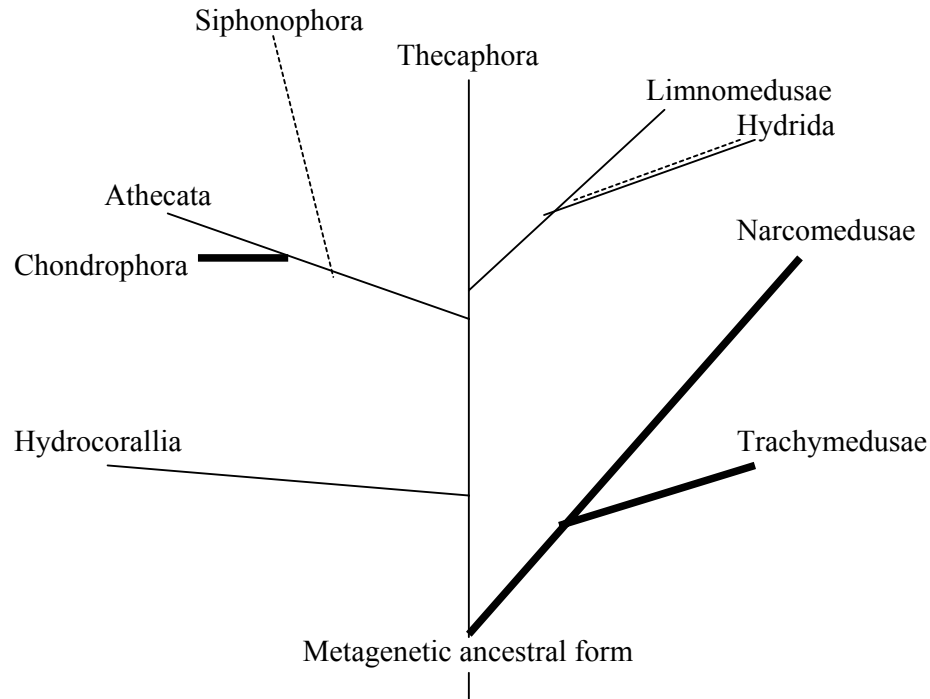
[11]  Anthomedusae – the name for medusae (according to the old system) that in Naumov's (1960) system along with the corresponding polyps entered the suborder of Athecata from the Leptolida order.

Homogenetic ancestral form

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Planular ancestral form
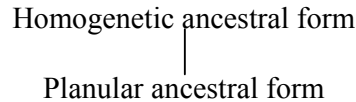
#### 4. THE ORIGIN OF SEPARATE FAMILIES AND GENERA OF SIPHONOPHORES

The origin of each of the families and genera of siphonophores, just as with the generic interrelationships between them, have not yet been established. Nonetheless, the level of development of one or other groups within each of the suborders and the approximate level of relationship between tem can now be indicated.

It is clear from all that has been said that in each of the suborders of siphonophores evolution took place on the lines of oligomerisation of the number of homologous zooids, right up until the complete disappearance of one or other groups of individuals.

In the suborder Physophorae the greatest number of different individuals is possessed by colonies from the family Forskaliidae, which on this basis can rightly be considered the most primitive. Moreover, it is characteristic that the nectophores in representatives of forskaliids are distributed along the stem multi-serially. Amongst the Forskaliidae the genus *Forskaliopsis* would appear to be the more primitive that *Forskalia* since its representatives possess a relatively disorganised distribution of individuals on the siphosome and have palpons in the nectosomal part of the colony (Haeckel, 1888b).

Another branch of physophores that have nectophores distributed bi-serially is formed by a group of families in which the Agalmidae should apparently be considered the most primitive. The presence of free-swimming medusae in the life cycle of its representatives (*Agalma*) is evidence of the primitiveness of this family that also possesses a large number of varied zooids per colony.

The position of the Apolemiidae is not completely clear. On the one hand, is seems feasible that this family is close to Forskaliidae through the genus *Forskaliopsis*) since palpons (or cystozooids) bud on the nectosome of both of them. But on the other hand, the presence of a bi-serial distribution of nectophores brings the Apolemiidae close to the Agalmidae. In all events this family stands on a higher level that the previous ones since colonies of its representatives have distinct cormidia, each of which is separated from its neighbour by a significant distance and zooids of the cormidium are positioned around the stem in whorls.

As stated in the chapter on neoteny, two families – Athorybiidae and Physophoridae – are neotenic and correspond to larvae of Agalmidae, at different stages of their development. The Physophoridae (the only genus being phys brings the Apolemiidae close to the Agalmidae. In all events this family stands on a higher level that the previous ones since colonies of its representatives have distinct cormidia, each of which is separated from its neighbour by a significant distance and zooids of the cormidium are positioned around the stem in whorls.

As stated in the chapter on neoteny, two families – Athorybiidae and Physophoridae – are neotenic and correspond to larvae of Agalmidae, at different stages of their development. The Physophoridae (the only genus being *Physophora*) also enter the group of families with bi-serial distribution of

nectophores, while Athorybiidae form a special branch of physophores devoid of nectophores. Of the 2 genera of this family *Athorybia* above all corresponds to the early larva of *Agalma*, and *Melophysa* is extremely reminiscent of the later larval stage of the same genus (see p. 70).

Apparently also originating from the Agalmidae are the Nectaliidae in which the nectophores are also positioned bi-serially. This family is characterised by a bank of zooids, very much reduced in number, and by a foreshortened siphosome. The specialisation of these representatives (a monotypic (and single) genus *Nectalia*) is manifest in the very large bracts, one for each cormidium. We can also assume that the neotenic nature of Nectaliidae is reminiscent, as with the Physophoridae, of late larvae of Agalmidae at the stage of their development when they begin to bud definitive bracts. But until embryological material is available the neotenic origin of Nectaliidae remains a supposition.

Best understood is the position of the Rhodaliidae in the genealogical tree of Physophorae. These siphonophores form an independent branch since the nectophores of representatives of the Rhodaliidae are distributed on a foreshortened nectosome in the form of a corona around the pneumatophore. Besides this, a special form of pneumatophore, the absence of bracts and a very unique bulbous form of the siphosome set this family most apart from the remaining Physophorae and testify to the greatest specialisation of its representatives. Possibly Rhodaliidae represent a group that isolated itself early on from the other physophores and was a highly specialised group of siphonophores. Amongst the Rhodaliidae, the genera *Stephalia, Rhodalia* and *Angelopsis* were apparently the primary ones since the lower part of the pneumatophore (aurophore) has a smooth exterior wall: this is reminiscent of the lower part of the pneumatophore of other physophores. Conversely, the genera *Archangelopsis* and *Dromalia*, whose aurophore is equipped with papillae with apertures at the end of each papilla (secondary apertures like the basal pore of the pneumatophore of Physophorae) obviously have a later origin.

The diagram illustrates the generic links between contemporary families of Physophorae:
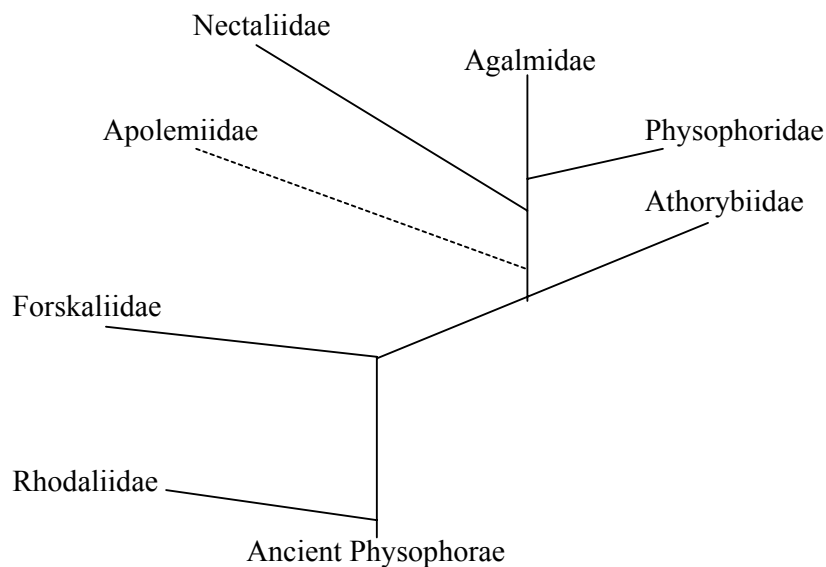
Of the two families that belong to the suborder Cystonectae, the Rhizophysidae have diverged from the common ancestor to the least extent. Colonies of representatives of this family, just like their ancestors, have a long stem and linear axial distribution of cormidial groups of individuals (Totton, 1960). Conversely, the Physaliidae, being a highly specialised family, has a series of features that are unique as much in the morphology of adult forms as in the ontogenesis of the colony. If the existence in nature of *Salacella uvaria* (Rhizophysidae) is confirmed, then probably the link between Physaliidae and Rhizophysidae through *Salacella* will become obvious.

Possible support will also be found for the neotenic origin of *Physalia physalis*.

Thus the link between contemporary families may be expressed in the following diagram.
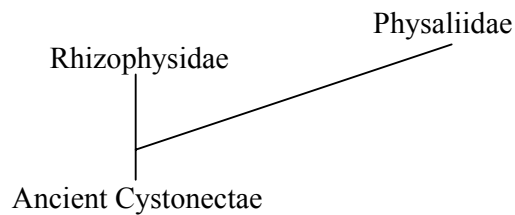


The evolution of siphonophores within the suborder Calycophorae presents the most complex picture. As is well known, in this group of Siphonanthae evolutionary complexity finds expression primarily in the oligomerisation of the number of nectophores. Thus calycophores that have more than two nectophores per colony can perfectly justifiably be considered as the most primitive. At present two families of Calycophorae, characterised by more than two nectophores per colony are well known. One of these is the Hippopodiidae. Representatives of this family do in fact possess a range of primitive features: apart from 8 pairs of nectophores, their colonies are devoid of distinct cormidia on the siphosome and they do not form either eudoxids or Ersae. At the dame time, the total reduction of bracts and the budding arrangement of gonophores in Hippopodiidae testifies to a certain complication of the morphology of this family in comparison with ancestral forms. Such a combination of primitive features along with signs of relatively high organisation allows Hippopodiidae to be considered as a family that, although close to the ancestral form of Calycophorae, nonetheless diverged from them as a result of specialisation. Of the two genera belonging to the family Hippopodiidae perhaps *Hippopodius* diverged to a lesser extent from ancestral forms (evidence of this is the oval shape of its nectophores, reminiscent of the shape of medusae) than did *Vogtia* (nectophores in colonies of this genus have a prismatic form and bear different notches and outgrowths).

Another family is the previously mentioned (p. 58) Desmophyidae. The presence of three or more pairs of nectophores per colony is evidence of the primitive nature of the Desmophyidae, while the presence of cormidia and the capacity to form Ersae point to the relative complexity of this group. Desmophyids can be considered as a family that arose as a result of direct development from ancient Calycophorae and subsequently produced the family

Prayidae. In fact, the form of the nectophores and bracts, and the composition and structure of the cormidia in colonies of Prayidae are very similar to those in Desmophyidae. But colonies of Desmophyidae are characterised by a significant reduction in gonophores (Haeckel, 1888b) (which is apparently linked with the presence of special nectophores that free gonophores from participating in movement of the Ersae. On the other hand, representatives of Prayidae are characterised by the normal development of sexual medusoids. Thus the origin of the Prayidae is immediately excluded from the Desmophyidae and the latter should be considered, just like the Hippopodiidae, as a branch that separated from the main stem of Calycophorae.

The family Prayidae referred to earlier seems to have arisen from certain other now unknown calycophores that have more than two nectophores in a colony with normally developed gonophores. Prayidae are a group of Calycophorae in which oligomerisation has led to a reduction in the number of nectophores down to two. Moreover in each pair both of the definitive nectophores lie one opposite the other. Very characteristic of Prayidae is the tendency to subsequent oligomerisation of the number of nectophores. This, along with genera characterised by a pair of identical nectophores per colony, is shown in the existence of genera (subfamily Amphicaryoninae) among whose representatives there is a gradual reduction of one of the nectophores. Whereas in the genus *Maresearsia* this reduction is hardly noticeable, in colonies of the genus *Amphicaryon* the second nectophore appears as a disk-like bract with a scarcely noticeable chamber of the subumbrella (Fig. 49, Б, 2). At present there are no known forms of Prayidae in which this reduction might have been achieved by the disappearance of the second nectophore. However, monophyism, though characteristic of some Prayidae, does not occur as the result of reduction bur as a consequence of neoteny. The subfamily Nectopyramidinae (genus *Nectopyramis*) is an example of this.

Another branch is found in the group of families also characterised by no more than two nectophores per colony, but lying one beneath the other. On one side it is related to the Diphyidae, whose nectophores are approximately of the same size in each colony. It is difficult to say which genera of this family are more primitive. It is possible to assume that it is *Sulculeolaria* and *Galetta* (which combine in the subfamily Galettinae), since they are not known to have free-swimming monogastric colonies, and besides this the listed genera are characterised by normal development of both nectophores. In representatives of the genus *Dimophyes* (subfamily Dimophyinae) there is a partial reduction of the second nectophore. In the subfamily Diphyinae there are genera (*Eudoxoides*) some of whose forms have two nectophores, while it is common for others only to have one nectophore per colony. Finally, in the genus *Muggiaea* complete reduction of the second nectophore has taken place. The other monophyid genus of the Diphyidae family is *Monophyes*. But here the reduction in the number of nectophores down to one per colony is a consequence of neoteny.

Thus monophyism (the presence of a single nectophore per colony) is seen in each of the well-known families of Calycophorae. It must be noted that colonies with one nectophore caught in samples are not always attributable to monophyids and can have one nectophore each as a result of a given specimen losing the second swimming bell. Apart from the absence in them of a second nectophore,

truly monophyid colonies are also defined by the fact that in the nectosomal budding zone of a colony there is an absence even of the buds of the larval nectophore. In this case the upper definitive nectophore develops in place of the larval nectophore while the lower definitive nectophore, having been subject to reduction in the course of evolution, does not generally bud.

It is not always possible to decide by which of the above described paths monophyism of one form or another took place. Thus for the genera *Heteropyramis*, *Thalassophyes* (subfamily Chuniphyinae) and *Enneagonum* (family Abylidae) (see below) the true nature of monophyism has not yet been established.

The subfamily Chuniphyinae includes the diphyid genera (*Chuniphyes*, *Clausophyes* and *Crystallophyes*) and those genera characterised by monophyism (*Heteropyramis*, *Thalassophyes*). The somewhat primitive nature of this subfamily is indicated by the presence, in the lower nectophores of its diphyid representatives, of a somatocyst (a feature not generally characteristic of lower nectophores of remaining Diphyidae representatives). It is possible that this subfamily, which sprung from ancestors of Diphyidae earlier than other representatives of this family, is highly deviant due to specialisation. In Totton's (1954) view Chuniphyinae should be considered as forms in transition toward the family Abylidae (protoabylids) because of the morphological similarity of nectophores of these two groups (fig. 57).
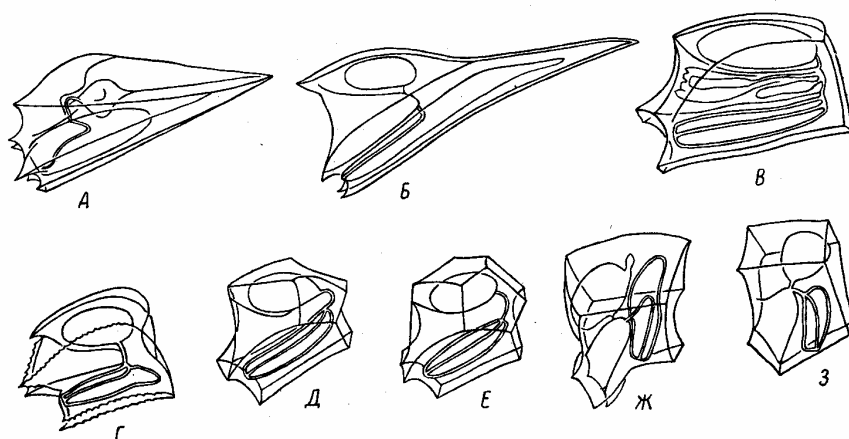


Fig. 57. Evolution of upper nectophore in colonies of different Abylidae (according to Totton).
А. *Chuniphyes multidentata*; Б. *Ceratocymba sagittata*; В. *C. leuckarti*; Г. *C. dentata*; Д. *Abyla trigona*; Е. *A. haeckeli*; Ж. *Abylopsis tetragonal*; З. *Bassia bassensis*.

In the family Abylidae two nectophores are also positioned one beneath the other but in each pair the upper nectophore is smaller than the lower one. Comparing the different genera of the Abylidae it is possible to trace the gradual reduction of the upper nectophore. Whereas relatively large upper nectophores of pyramidal form (fig. 57, Б) are still found in the genus *Ceratocymba*, the genera *Abyla*, *Abylopsis* and *Bassia* (fig. 57, Д-З) are characterised by small upper nectophores that are already prismatic in shape. The genus *Enneagonum* has a single

nectophore, upper in origin. It is difficult to say by what path this genus arriv3ed at monophyism. It is perfectly possible that representatives of *Enneagonum* arose as a result of neoteny, but also feasible is the possibility of a reduction within its colonies of the lower nectophore.

Finally, the family Sphaeronectidae characterised by absolute monophyism must be seen (see above) to have arisen from the larvae of some primitive Calycophorae as the result of neoteny.

A diagram is given showing the generic interrelationships between families of the suborder of Calycophorae.

Abylidae

Diphyidae

Prayidae

Sphaeronectidae

Desmophyidae

Hippopodiidae

Ancient Calycophorae
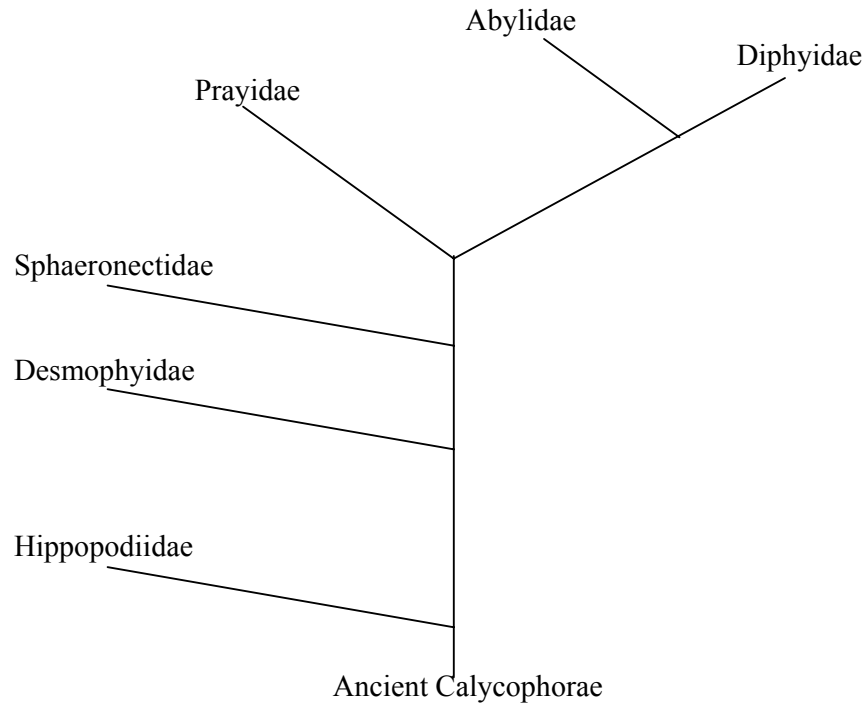
SYSTEMATICS OF SIPHONOPHORES

The first tentative attempts to establish the systematics of the siphonophores go back to the end of the eighteenth and beginning of the nineteenth centuries. Some researchers, such as Linné (1758), Forskål (1775), Lamarck (1801), and Peron and Lesueur (1804), have described some different species and even genera of siphonophores, but they joined them side by side with some medusae, ctenophores, actinulids and corals, just as with the holothurians and salps, to worms and zoophytes. In 1829 Eschscholtz joined the siphonophores together in an independent order Siphonophorae of the class Acalephae.

The independence of the siphonophores in systematics of the coelenterates has been recognised, with reserve, by the majority of subsequent researches. But the taxonomic rank of the Siphonophora, just as with the classification of the groups belonging to the siphonophores, has been envisaged differently by the various authors. Actually one knows of more than ten different systematics for the Siphonophora, amongst which we number some authors such as Haeckel (1888b),

Chun (1897a), Schneider (1898) and Moser (1921, 1925). It is necessary to note that the systematic system of Haeckel appears, as a basis, the most natural, as, firstly, in it the Siphonanthae and Disconanthae (Chondrophora) are elevated to the rank of independent units and are isolated one from the other as subclasses[12]; secondly, Haeckel attributes the value of order to the group of Cystonectae. In contrast, Chun and Moser place the Cystonectae, together with the Physonectae and Chondrophorae, in the Physophorae. Meanwhile the defect in the systematic system of Haeckel resides in its supersaturation of artificial families, genera and species, which later on and to a large measure have been reduced to synonyms.

Amongst the most recent systematic systems, the most valuable as a basis have been made by Totton (1954) and Hyman (1940) who consider the Siphonophora as an order, divided into two sub-orders: Calycophorae and Physophoridae, including in the latter the groups Physonectae, Rhizophysaliidae and Chondrophora. Garstang (1946) envisaged the Disconanthae (Chondrophora) and Siphonantha as two orders of which the latter was made up of two groups, A. Physophorida and B. Calycophorida. In the group Physophorida, Garstang joined the Cystonectae and Amphynectae (=Physonectae). After the systematic system of Totton (1954), the Chondrophora and Siphonophora are independent orders. Siphonophora (=Siphonanthae, Totton, 1954) is composed of three sub-orders: Cystonectae (=Pnemuatophoridae Chun and Rhizophysaliidae Chun), Physonectae – a synonym of Physophorae Eschscholtz, and Calycophorae.

Naumov (1960) has proposed a new systematic system for the hydroids, and in his opinion the class Hydrozoa is composed of two sub-classes: Hydroidea and Siphonophora. "The siphonophores have the appearance of a polymorphic colony swimming freely, composed of several types of medusoid and polypoid individuals. The hydroids have the characters of medusae or else of isolated polyps or else of colonies in the latter case, always attached)." (Naumov, 1960, p. 19). In the systematics of the hydroids proposed by Naumov, it is necessary to add the Chondrophora in the form of an order.

Blow is proposed the systematics of the siphonophores that corresponds best with that of Totton (with some modifications and adjustments).

The sub-class Siphonophora (Eschscholtz, 1829) (Totton considers the siphonophores as a order) includes a unique order Siphonanthae Haeckel, 1888, characterised by the polymorphism of the colonies and the alternation of the polypoid and medusoid generations with a suppression of the latter in the life cycle of some representatives.

The order Siphonanthae is divided into three sub-orders: the structure and composition of the nectosome of the colony (in particular, the presence or absence on it of a pneumatophore and of nectophores) and the composition of the siphosome (in particular, the presence or absence on it of palpons). On can judge the appurtenance of one or other sub-order by the mutual disposition of the nectosomal and siphosomal zones of budding in the colony. In others, the majority of cases, the presence of complete absence of eudoxids or ersae can serve as a taxonomic criterion for the sub-orders.

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[12] Haeckel considered the siphonophores as an independent class.

The sub-order Physophorae (Eschscholtz, 1829) is characterised by the presence of a nectosome that buds a pneumatophore and several nectophores[13] and also by the presence of palpons on the cormidia of the siphosome. The nectosome and siphosome of the Physophorae represent two parts on the unique stem of the colony, and further the budding zones of one and the other are separated by the length of the nectosome. In the Physophorae there are neither eudoxids nor ersae.

The sub-order Calycophorae Leuckart, 1854 is characterised by the absence of a pneumatophore. The nectophores are budded on a "false nectosome" made up of the muscular peduncles of the nectophores. Palpons are absent. The budding zone of the nectosome lies immediately to the side of that of the siphosome. The life cycle of representative Calycophorae is characterised by the presence, in the majority of cases, of eudoxids or ersae.

As had already been said in the Preface, in the actual systematic system one uses the rank of "super-family". Super-families do not have general taxonomic criteria: in the sub-order Physophorae, as criteria for the super-family one takes the length of the siphosome of the colony, whereas in the sub-order Calycophorae, the super-families are characterised by the number of nectophores on the nectosome of the colony.

For the families that make up each sub-order, there exist the following taxonomic criteria: the length and shape of the nectosome and siphosome, the number and disposition of the nectophores on the nectosome, the structure and arrangement of the cormidia on the siphosome, the presence or total absence of tentilla on the s. In most cases, the presence or total absence on the nectosome of individuals of polypoid origin, the presence or total absence on the siphosome of protective bracts.

One can consider as taxonomic criteria of the sub-families the following characters: the ratio of size of the nectophores within the limits of each colony, the similarity and differences of the nectophores within the limits of the same colony[14], in certain cases – the presence or total absence of somatocysts in the anterior nectophores, the relation of size of the different elements of the nectophore.

Totton does not divide the family Prayidae into sub-families. In the present systematic system, the Prayidae is composed of three distinctive sub-families: Nectopyramidinae, Prayinae and Amphicaryoninae. Into the family Diphyidae a new sub-family is introduced, the Monophyinae. The genera *Sulculeolaria* and *Galetta* (the latter retaining a right to be independent) are united together in the sub-family Galettinae. The name given to the sub-family has to be conserved according to the rules of priority (Totton replaces it by a new name Sulculeolariinae). The genus *Dimophyes* is not joined with the sub-family Diphyinae (as Totton did). The unique

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[13] An exception is shown the family Athorybiidae, the representatives of which are without nectophores or the number of nectophores in the colony is reduced to one.

[14] The family Abylidae being similar to the Diphyidae in the length and shape of the nectosome, equal in quantity and arrangement of the nectophores in the colony, are differentiated from the latter by a difference in the size of the nectophores and by the difference in their shape within the limits of a colony. It will be necessary rather to consider this group as a sub-family of the family Diphyidae. But the clear differences in the shape of the nectophores of the Abylidae in comparison with the Diphyidae, and the important difference in the size of the two nectophores of the same colony in Abylidae (in the colonies of Diphyidae this difference, if it exists, is not so clearly expressed) indicates a precise singularity of these groups of siphonophores and allows the consideration of the Abylidae as an independent family.

species of this genus *D. arctica*, forms an independent sub-family, called by Moser (1925) the Dimophyinae.

The taxonomic criteria of the genera are: the shape of the nectophores, the sculpturing of the surface of the mesogloea of the nectophores – the presence or absence ridges (their number), of teeth or excrescences, the shape of the radial canals on the nectosac, the presence or absence of ramifications of them, the shape of the hydroecium, the structure of its walls, in certain cases the shape of the bracts and the structure of the tentilla.

The taxonomic criteria for the species are: the size and shape of the somatocyst and the nectosac, the relation in size of these formations within the limits of a single nectophore, the presence or absence of a pedicle to the somatocyst and the size of this pedicle, the presence or absence of anastomoses of the radial canals, the degree of development of ridges and mesogloeal teeth on the nectophores, the orientation of the ridges in relation to the surface of the nectophore and in relation to each other, the position of placement of the superficial teeth on the nectophores, the presence or absence of superficial ridges, the presence or absence of different valves, plates and excrescences beside and inside the cavity of the nectophore, their size and their shape, in certain cases the structure of the bracts, the shape of their phyllocyst, the structure and shape of the gonophores and of the gastrozooids, and also the number and structure of the nematocysts in the tentilla.

In certain cases, the relative scarcity of taxonomic criteria and their limitation by the limits of different zooids is explained by the scarcity of information about one or other siphonophore. It is convenient to join together these faults of the systematic system giving, and probably ultimately, a measure of the accumulation of new information, it will be necessary to re-examine these matters in the systematics of siphonophores.

In the present systematics, there is one new genus and three new species of siphonophore.

In the list cited below, all the species actually known in the World fauna of siphonophores are given, that is necessary for the convenience of the work that will follow on this group of animals[15].

<div align="center">

Subclass **SIPHONOPHORA** (Eschscholtz, 1829)
Order **SIPHONANTHAE** Haeckel, 1888

Suborder **PHYSOPHORAE** (Eschscholtz, 1829)

Super-family **Brachistelloidea** Stepanjants superfam. nov.

Family **Physophoridae** (Eschscholtz, 1829)
Genus *Physophora* Forskål, 1775
</div>

1. *Physophora hydrostatica* Forskål, 1775

<div align="center">

Family **Nectaliidae** Haeckel, 1888
Genus *Nectalia* Haeckel, 1888
</div>

2. *N. loligo* Haeckel, 1888

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[15]  Asterisks show the families, genera and species whose existence is doubtful.

Family **Athorybiidae**
Genus *Athorybia* Eschscholtz, 1829
3. *A. formosa* Fewkes, 1882
4. *A. rosacea* (Forskål, 1775)
Genus *Melophysa* Haeckel, 1888
5. *M. melo* (Quoy and Gaimard, 1827)


Family **Rhodaliidae**
Genus *Angelopsis* Fewkes, 1886
6. *A. dilata* Bigelow, 1911
7. *A. globosa* Fewkes, 1886
Genus *Rhodalia* Haeckel, 1888
8. *R. miranda* Haeckel, 1888
Genus *Stephalia* Haeckel, 1888
9. *S. corona* Haeckel, 1888
Genus Archangelopsis  Lens and van Riemsdijk, 1908
10. *A. typica* Lens and van Riemsdijk, 1908
Genus *Dromalia* Bigelow, 1911
11. *D. alexandri* Bigelow, 1911


Super-family **Macrostelloidea** Stepanjants, superfam. nov**.**


Family **Forskaliidae** Haeckel, 1888
Genus *Forskalia* Kölliker, 1853
12. *F. contorta* Milne-Edwards
13. *F. edwardsi* Kölliker, 1853
14. *F. Formosa* Keferstein and Ehlers, 1861
15. *F. hydrostatica* delle Chiaje, 1829*
16. *F. tholoides* Haeckel, 1888
Genus *Forskaliopsis* Haeckel, 1888*
18. *F. magnifica* Haeckel, 1888
19. *F. ofiura* delle Chiaje, 1829
Genus *Erenna*
20. *E. bedoti* Lens and van Riemsdijk, 1908
21. *E. richardi* Bedot, 1904


Family *Agalmidae* Brandt, 1835
Genus *Agalma* Eschscholtz, 1825
22. *A. clausi* Bedot, 1888
23. *A. elegans* (Sars, 1846)
24. *A. haeckeli* Bigelow, 1911
25. *A. okeni* Eschscholtz, 1825
Genus *Anthemodes* Haeckel, 1888*
26. *A. ordinata* Haeckel, 1888
Genus *Lychnagalma* Haeckel, 1888
27. *L. utricularia* (Claus, 1879)
Genus *Cordagalma* Totton, 1932

28. *C. cordiformis* Totton, 1932
<div align="center">Genus *Halistemma* Huxley, 1859</div>

29. *H. rubra* (Vogt, 1852)
<div align="center">Genus S*tephanomia* Peron & Lesueur, 1807</div>

30. *S. amphitridens* Peron & Lesueur, 1807
31. *S. bijuga* (delle Chiaje, 1842)
32. *S. convoluta* Moser, 1925*
<div align="center">Genus *Nanomia* A. Agassiz, 1865</div>

33. *N. cara* A. Agassiz, 1865
<div align="center">Genus *Pyrostephos* Moser, 1925*</div>

34. *P. vanhoeffeni* Moser, 1925
<div align="center">Genus *Marrus* Totton, 1954</div>

35. *M. antarcticus* Totton, 1954
36. *M. orthocanna* (Kramp, 1942)
37. *M. orthocannoides* Totton, 1954
<div align="center">Genus *Bargmannia* Totton, 1954</div>

38. *B. elongata* Totton, 1954

<div align="center">

Family **Apolemiidae** Huxley, 1859
Genus *Apolemia* Eschscholtz, 1829
</div>

39. *A. uvaria* (Lamarck, 1816)
<div align="center">Genus *Ramosia* Stepanjants gen. nov</div>

40. *R. vitiazi* Stepanjants sp. nov.

<div align="center">

Suborder **CYSTONECTAE** Haeckel, 1888


Family **Rhizophysidae** Brandt, 1835
Genus *Rhizophysa* Peron & Lesueur, 1807
</div>

41. *R. eysenhardti* Gegenbaur, 1860
42. *R. filiformis* (Forskål, 1775)
<div align="center">Genus *Epibulia* Haeckel, 1888</div>

43. *E. chamissonis* Eysenhardt, 1821*
44. *E. erythrophysa* Brandt, 1835*
45. *E. ritteriana* Haeckel, 1888
<div align="center">Genus *Bathyphysa* Studer, 1878</div>

46. *B. abyssorum* Studer, 1878
47. *B. sibogae* Lens and van Riemsdijk, 1908
<div align="center">Genus *Pterophysa* Fewkes, 1886</div>

48. *P. conifera* (Studer, 1878)*
49. *P. grandis* Fewkes, 1886
50. *P. grimaldi* (Bedot, 1893)
51. *P. studeri* Lens and van Riemsdijk, 1908
<div align="center">Genus *Salacella* Delage & Herouard, 1901*</div>

52. *S. uvaria* (Fewkes, 1886)

<div align="center">

Family **Physaliidae** Brandt, 1835
Genus *Physalia* Lamarck, 1801
</div>

53. *P. physalis* (Linné, 1758)

Suborder **CALYCOPHORAE** Leuckart, 1854

Super-family **Polynectoidea** Kölliker, 1853

Family **Hippopodiidae** Kölliker, 1853
Genus *Hippopodius* Quoy and Gaimard, 1827
54. *H. hippopus* (Forskål, 1776)
Genus *Vogtia* Kölliker, 1853
55. *V. cuspitata* Moser, 1925*
56. *V. glabra* Bigelow, 1918
57. *V. pentacantha* Kölliker, 1853
58. *V. serrata* (Moser, 1925)
59. *V. spinosa* Keferstein and Ehlers, 1861

Family **Desmophyidae** Haeckel, 1888*
Genus *Desmophyes* Haeckel, 1888
60. *D. annectens* Haeckel, 1888

Super-family **Dinectoidea** Stepanjants superfam. nov.

Family **Prayidae** Kölliker, 1853
Subfamily Nectopyramidinae Bigelow, 1911
Genus *Nectopyramis* Bigelow, 1911
61. *N. diomedeae* Bigelow, 1911
62. *N. natans* (Bigelow, 1911)
63. *N. spinosa* Sears, 1952
64. *N. thetis* Bigelow, 1911

Subfamily Prayinae, Haeckel, 1888
Genus *Rosacea* Quoy and Gaimard, 1827
65. *R. cymbiformis* delle Chiaje, 1827*
66. *R. plicata* Quoy and Gaimard, 1827
Genus *Lilyopsis* Chun, 1885
67. *L. rosea* Chun, 1885
Genus *Stephanophyes* Chun, 1891
68. *S. superba* Chun, 1891
Genus *Praya* Blainville, 1834
69. *P. dubia* (Quoy and Gaimard,1834)
70. *P. reticulata* (Bigelow, 1911)

Subfamily Amphicaryoninae Chun, 1897
Genus *Amphicaryon* (Chun, 1888)
71. *A. acaule* Chun, 1888
72. *A. ernesti* Totton, 1954
73. *A. peltifera* (Haeckel, 1888)
Genus *Maresearsia* Totton, 1954
74. *M. praeclara* Totton, 1954

75. *M. sphaera* Stepanjants sp. nov.


Family **Sphaeronectidae** Huxley, 1859
Genus *Sphaeronectes* Huxley, 1859
76. *S. köllikeri* Huxley, 1859


Family **Diphyidae** Quoy and Gaimard, 1827
Subfamily Monophyinae Stepanjants superfam. nov [!]
Genus *Monophyes* Claus, 1873
77. *M. irregularis* Claus, 1873
78. *M. japonica* Stepanjants sp. nov.


Subfamily Galettinae Stechow, 1921
Genus *Sulculeolaria* Blainville, 1830
79. *S. monoica* (Chun, 1888)
80. *S. quadridentata* Quoy and Gaimard, 1834
81. *S. quadrivalvis* Blainville, 1830
Genus *Galetta* Stechow, 1921
82. *G. angusta* Totton, 1954
83. *G. australis* Quoy and Gaimard, 1834
84. *G. biloba* (M. Sars, 1846)
85. *G. chuni* Lens and van Riemsdijk, 1908


Subfamily Diphyinae Moser, 1925
Genus *Diphyes* Cuvier, 1817
86. *D. antarctica* Moser, 1925
87. *D. bojani* (Eschscholtz, 1825)
88. *D. chamissonis* Huxley, 1859
89. *D. dispar* Chamisso & Eysenhardt, 1821
Genus *Lensia* Totton, 1932
90. *L. achilles* (Totton, 1954)
91. *L. ajax* Totton, 1941
92. *L. campanella* (Moser, 1925)
93. *L. challengeri* Totton, 1954
94. *L. conoidea* Keferstein and Ehlers, 1861
95. *L. cossack* Totton, 1941
96. *L. exeter* Totton, 1941
97. *L. fowleri* (Bigelow, 1911)
98. *L. hardy* Totton, 1941
99. *L. hotspur* Totton, 1941
100. *L. hunter* Totton, 1941
101. *L. Leloup* Totton, 1941
102. *L. lelouveteau* Totton, 1941
103. *L. meteori* (Leloup, 1934)
104. *L. multicristata* Moser, 1925
105. *L. reticulata* Totton, 1954
106. *L. subtilis* Chun, 1886
107. *L. subtiloides* Lens and van Riemsdijk, 1908

Genus *Muggiaea* Busch, 1851
108. *M. atlantica* Cunningham, 1892
109. *M. bargmannae* Totton, 1954
110. *M. delsmani* Totton, 1954
111. *M. havock* (Totton, 1941)
112. *M. kochi* Will, 1854
Genus *Eudoxoides* Huxley, 1859
113. *E. mitra* (Huxley, 1859)
114. *E. spiralis* Bigelow, 1911
Genus *Chelophyes* Totton, 1932
115. *C. appendiculata* Eschscholtz, 1829
116. *C. contorta* (Lens and van Riemsdijk, 1908)


Subfamily Dimophyinae Moser, 1925
Genus *Dimophyes* Moser, 1925
117. *D. arctica* (Chun, 1897)


Subfamily Chuniphyinae Moser, 1925
Genus *Chuniphyes* Lens and van Riemsdijk, 1908
118. *C. moserae* Totton, 1954
119. *C. multidentata* Lens and van Riemsdijk, 1908
Genus *Clausophyes* Lens and van Riemsdijk, 1908
120. *C. galeata* Lens and van Riemsdijk, 1908
121. *C. ovata* (Keferstein and Ehlers, 1861)
Genus *Crystallophyes* Moser, 1925
122. *C. amygdalina* Moser, 1925
Genus *Thalassophyes* Moser, 1925
123. *T. crystallina* Moser, 1925
Genus *Heteropyramis* Moser, 1925
124. *H. maculata* Moser, 1925


Family **Abylidae** Totton, 1932
Subfamily Abylinae L. Agassiz, 1861
Genus *Abyla* Quoy and Gaimard, 1827
125. *A. bicarinata* Moser, 1925
126. *A. brownia* Sears, 1953
127. *A. carina* Haeckel, 1888
128. *A. haeckeli* Lens and van Riemsdijk, 1908
129. *A. ingeborgae* Sears, 1953
130. *A. peruana* Sears, 1953
131. *A. schmidti* Sears, 1953
132. *A. tottoni Seats, 1953*
133. *A. trigona* Quoy and Gaimard, 1827
Genus *Ceratocymba* Chun, 1888
134. *C. dentata* Bigelow, 1918
135. *C. intermedia* Sears, 1953
136. *C. leuckarti* Huxley, 1859
137. *C. sagittata* Quoy and Gaimard, 1927

Subfamily Abylopsinae Totton, 1954
Genus *Abylopsis* Chun, 1888
138. *A. eschscholtzi*(Huxley, 1859)
139. *A. tetragona* (Otto, 1823)
Genus *Bassia* Quoy and Gaimard, 1827
140. *B. bassensis* (Quoy and Gaimard, 1827)
Genus *Enneagonum* Quoy and Gaimard, 1827
141. *E. hyalinum* Quoy and Gaimard, 1827

Thus the proposed system for siphonophores consists of 3 suborder, 16 families, 60 genera and 141 species. In general it is characteristic of siphonophores to have few species in each genus and it is even known that there are 29 genera containing a single species. However, for the suborder Calycophorae, which make up more than half of all the species, there are genera that contain 9 (*Abyla*) or even 17 (*Lensia*) species.

**p. 94**
*ZOOGEOGRAPHICAL CHARACTERISTICS OF THE SIPHONOPHORE FAUNA FROM RUSSIAN SEAS AND THE NORTHERN PART OF THE PACIFIC OCEAN*

Siphonophores are encountered almost all over the northern and throughout the eastern Seas of Russia. Their absence in the White, Baltic, Black, Azov, Caspian and Aral Seas is associated with the low salinities of these waters (siphonophores being able to live and reproduce only in normal oceanic waters with salinities between 33 and 35‰). That being so the apparent absence of siphonophores from the east Siberian Sea could be explained by the low salinities there, but also by the fact that the area has been little studies.

In the present study, siphonophores have been studied not only from Russian Seas, but also from the Soviet sector of the Arctic Basin and the northern part of the Pacific Ocean.

**Need to verify translation as it is mine and, therefore, quite poor!!**

**P. 117**

SYSTEMATIC PART

Subclass **SIPHONOPHORA**

Order **SIPHONANTHAE**

Table of

**Stepanjants, 1967** pp. 130-133.

### III. Family **APOLEMIDAE** Huxley, 1859

*Physophorae* with small oval-shaped pneumatophore, devoid of an apical pore. Nectosome well developed and bearing 2 longitudinal rows of nectophores. Between nectophores on nectosome are attached tentacleless cystozooids. Long siphosome bearing cormidia, arranged with a significant spacing between each. Bracts present and covered in nematocysts. Tentacles not branched.

In the study area only a single genus -*Ramosia* gen. nov. - was discovered.

### 1. Genus *Ramosia* Stepanyants gen. nov.

*Apolemiidae*, in which the cormidia are arranged in small bunches growing from the siphosome.

The described species is very closely related to the genus *Apolemia*, which also belongs to the *Apolemiidae*. Examples of *Ramosia* and *Apolemia* have very similarly shaped nectophores, between which, in the nectosome, are arranged cystozooids. *Ramosia* is essentially distinguished from *Apolemia* firstly by the whole arrangement of the cormidial bunches. Beside that, the cystozooids in the nectosome of *Ramosia* are large, in contrast to those of *Apolemia*, and are arranged with only a single one between two successive nectophores in the series on the left side of the nectosome (in *Apolemia* cystozooids are arranged so that there are 2-4 between two nectophores).

Type species: *Ramosia vitiazi* Stepanyants sp. nov.
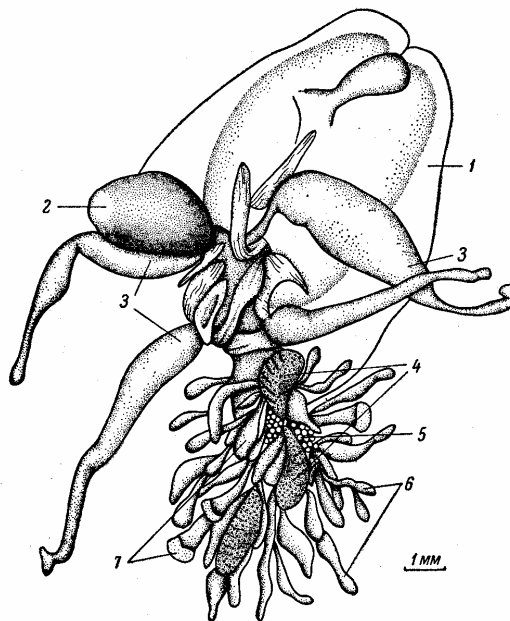


Fig. 74. General view of the arrangement of the colony. of *Ramosia vitiazi* Stepanyants.

1 – nectophore; 2. – pneumatophore; 3 – cystozooids; 4 – bract; 5. gonodendra; 6 – palpons; 7. – gastrozooids.

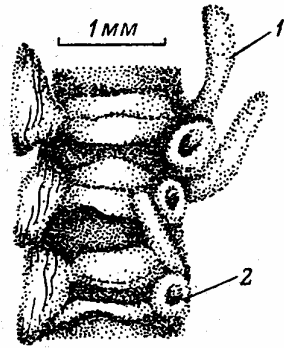1. *Ramosia vitiazi* Stepanyants sp. nov. (Figs. 74-78)



Fig. 75. Part of nectosome of *Ramosia vitiazi* Stepanyants.
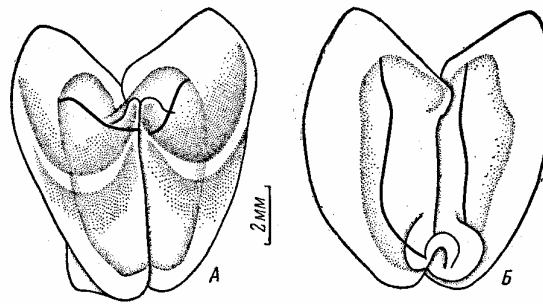1 – attachment point of nectophore; 2 – attachment point of cystozooid.

Fig. 76. Nectophore of *Ramosia vitiazi* Stepanyants.
A – ventral view; Б dorsal view.

Type specimen deposited in the collections of the ZIN AN SSSR. "Vitiaz" St. 917. The young colony (fig. 74), the total length of which is unknown due to the strong contraction of the stem, bears on oval-shaped pneumatophore (1-3 mm high). Pneumatophore devoid of an apical pore and coloured a brownish-red colour. Brownish-red nectosome (also contracted) bears the scars of 7 pairs of adult nectophores and 4-5 pairs of nectophore buds. Between two nectophores in the left-hand series is attached one cystozooid. The method of attachment of the cystozooids is such that at the base of each there is a scar, lying between the muscular lamellae connecting with the nectophores of the nectosome (fig. 75). Brownish-red nectophores (11-14 mm in height and 9-12 mm in width) having solid and thick mesogloea, with rounded contours and wings directed upwards (fig. 76). Ventral wall of nectophore concave, whereas dorsal, in contrast, convex. Nectosac occupying a greater part of the height of the nectophore and reflecting its shape. Lateral radial canals make very small
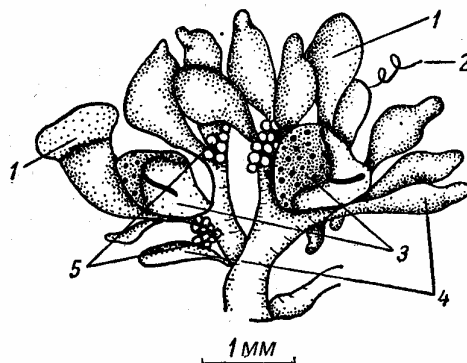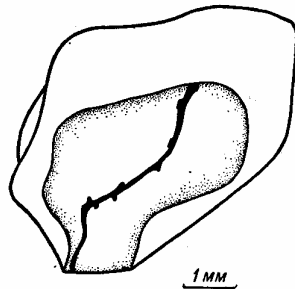
Fig. 77. Nectophore of *Ramosia vitiazi* Stepanyants. Lateral view

Fig. 78. Cormidia of *Ramosia vitiazi* Stepanyants. 1 – gastrozooid; 2 – tentacle; 3 – bract; 4 – palpon; 5 – gonophore.

bends and often have short side branches (fig. 77). Cormidia arranged in bunches (fig. 78): each bunch, provided with shoots of a secondary order, bearing gastrozooids (1) with unbranched tentacles (2); covering bracts (3) and palpons (4), close to the bases of which arise the gonophores (5). On account of the contraction of the stem it was impossible to assess the magnitude of the distance between successive cormidia.

Distribution. Okhotsk and Bering Seas; Pacific Ocean in coastal region of Kurile Islands.

Found in horizontal samples lying within the depth range 0 to 2000 m. In view of the capture of individual specimens at the surface in June it is possible to assume that in the summer months this species inhabits the upper horizons.

*R. vitiazi* resembles the single species of the genus *Apolemia -Apolemia uvaria* - in the shape and size of its nectophores and the shape of the covering bracts, but is distinguished by the colour of the colony (pneumatophore, nectophores and other zooids of *A. uvaria* colourless) and in particular the raised mesogloeal surface of the nectophore and the characteristic branching of the radial canals (in *A. uvaria* short branches arise from the apical part of the lateral canals, in that part where it makes a sweeping bend, whereas when the lateral canals on the nectophore of *R. vitiazi* have branches they are extensively distributed all along their descending parts).

Suborder *CALYCOPHORAE*

**P. 133**

Stepanjants, 1967, pp. 145-149 (From French translation!)

## Subfamily **PRAYINAE**

Prayidae with two definitive nectophores, being approximately the same size and identical in form.

## 2. Genus **ROSACEA** Quoy and Gaimard, 1827

Quoy and Gaimard, 1827: 176; delle Chiaje, 1841: 117 (*Physalia*); Vogt, 1841:144 (*Praya*); Leuckart, 1854: 38 (*Praya*); Gegenbaur, 1854b: 454 (*Praya*); Chun, 1885: 18 (*Praya, Lilyopsis*); 1897a: 12 (*Praya, Lilyopsis*); Haeckel, 1888b: 12, 15 (*Praya*); 145, 150 (*Lilyopsis*); Schneider, 1898: 78 (in part); Bigelow, 1911b: 200 (*Praya*), 201; 1913: 64; Moser, 1925: 373 (*Praya*); Bigelow & Sears, 1937: 10; Totton, 1954: 87, 88.

Two definitive nectophores (reaching 50 mm in length) in the shape of a bean or quite oval.. The somatocyst is simple. The radial canals on the nectosac are not ramified, there are always 4.

Type species: *Rosacea plicata* Quoy and Gaimard, 1827

## 1. **Rosacea plicata** Quoy and Gaimard, 1827 (figs. 91-93).

Quoy and Gaimard, 1827: 176, pl. 4b, figs. 2, 3: 177, pl. 4b (*ceutensis*); delle Chiaje, 1829; pl. 50, fig. 3 (? *Rhizophysa filiformis*); 1841: 135, pl. 149, fig. 3 (*R. filiformis*); Vogt, 1851: 140 (*Diphyes bragae*); 1854: 99. pl. 16, 17 (*Praya diphyes*); Kölliker, 1853: 33, pl. 9 (*P. diphyes*); Chun, 1885: 280 (*Lilyopsis diphyes*); Haeckel, 1888b: 150 (*Lilyopsis diphyes*); Bigelow, 1911a: 341-343; 1911b: 197-201, pl. 2, figs. 7-9; 1913: 64, 65, pl. 5, figs. 10, 11; Moser, 1925: 377 (*Praya diphyes*); Leloup, 1933a: 8; 1955: 6; Bigelow & Sears, 1937: 11, 76, figs. 9-14; Sears, 1950: 3; Totton, 1954: 89-92, figs. 32, 41-43; 1965: 116-118, text-figs. 65-67; Totton & Fraser, 1955d: 2, 3, figs. 10, 11.

Polygastric Stage. The larval nectophore (7-12 mm in diameter) has the shape of a sphere with a narrow opening to the hydroecium (fig. 91, Б). The somatocyst is short, comprised of ascending and descending canals, it departs from the "central organ" on the latter reaching also the pedicular canal to the nectosac.

The two bean-shaped definitive nectophores stuck one against the other by the ventral sides (fig. 92, A). One of them(which appears to be a little more apical than the second) is 7-30 mm in length and 4-17 mm in width, the other (distal) is 12-32 mm in length and 7-17 mm in width. The oval nectosac is not deep (2-4 mm in height) and has 4 subumbrella canal: two short (dorsal and ventral) and two long laterals curved into a sigma (sinuous). The subumbrella canals of the nectosac unite with a common pedicular canal, connecting with the somatocyst of the nectophore. The somatocyst is not ramified and is composed of two short stalks, ascending and descending (fig. 92, Б). The deep hydroecium is situated on the ventral side of the nectophore, occupying 2/3 to 1/3 of its surface. The slit-like opening oh the hydroecium leads to a quite large pocket where the origin of the stem of the colony is found (fig. 93, A). The gastrozooids are bottle-shaped, the tentilla filled with some anacrophores, the anisorhizas are homotrichous and the mastigophores are microbasic (fig. 93, Б).

Eudoxids. The protective bract (8-20 mm long and 6-15 mm in height) has the shape of a bonnet and is characterised by three lobes (two lateral and one ventral) (fig.

91, A). In the lobes run the canals of the phyllocyst originating from the "central organ": two lateral canals, unequal in length, a single ventral and a single dorsal diverging from the smaller lateral canal. The extremities of the canals of the phyllocyst are slightly swollen.

The gonophores (androphores and gynophores) possess apically two lobes of unequal size (fug. 91, B)

Distribution. Seas of Japan, Okhotsk, Bering, part of the north-east of the Pacific Ocean; eastern part of tropical Pacific; Atlantic Ocean (being found as far as 60°N; Mediterranean Sea; Indian Ocean

It is found at very different depths, from the surface to 3000 m. It forms a large number in the collections of the Zoological Institute, Academy of Sciences of the USSR.

*R. plicata* is undoubtedly close to the species *R. cymbiformis* delle Chiaje, and one can easily confuse one with the other. Table 4 gives evidence of the similarity of these two species.

In Table 4, one sees that the shape of the nectophores, the shape and the size of their nectosacs, the form of the somatocyst, the form of the tentilla just as the size and the shape of the bracts in *R. plicata* and *R. cymbiformis* almost cannot be differentiated.

One distinguishes the two species by the size of the nectophores, the shape of the hydroecium and its size in relation to that of the nectophore and also by the characters of the ramifications of the phyllocyst.
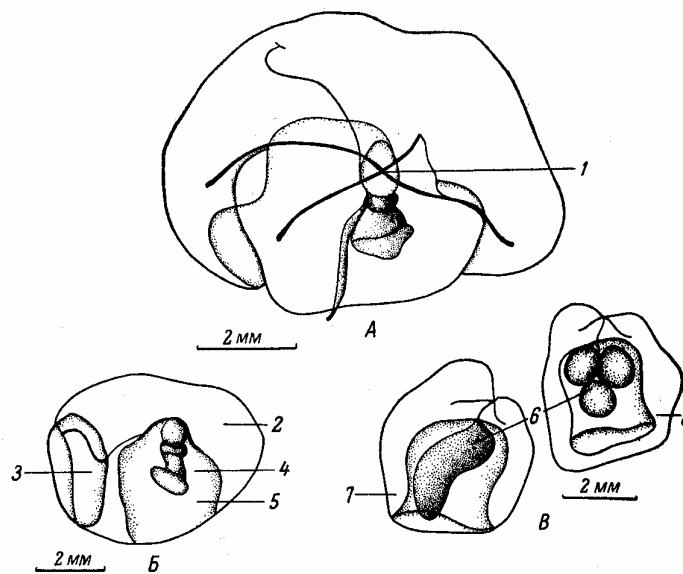


Fig. 91. *Rosacea plicata* Quoy and Gaimard.
A. Bract of the eudoxid; Б. larval colony; B. gonophores.
1. Phyllocyst; 2. Nectophore; 3. Nectosac of nectophore; 4. Gastrozooid; 5. Hydroecium; 6. Manubrium of gonophore; 7. Androphore; 8. Gynophore.
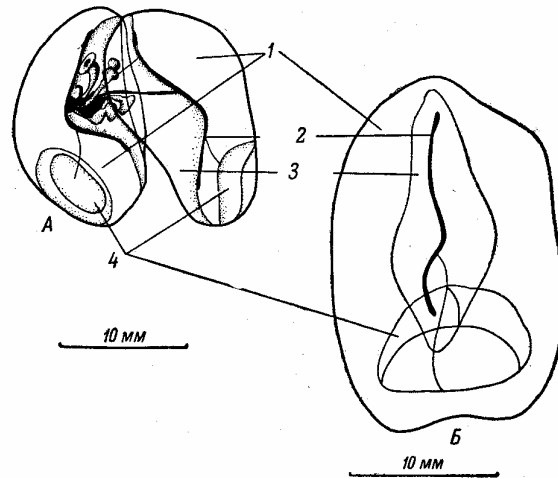
Fig. 92. *Rosacea plicata* Quoy and Gaimard.
A. Colony; Б. one of the nectophores of the colony showing its ventral side.
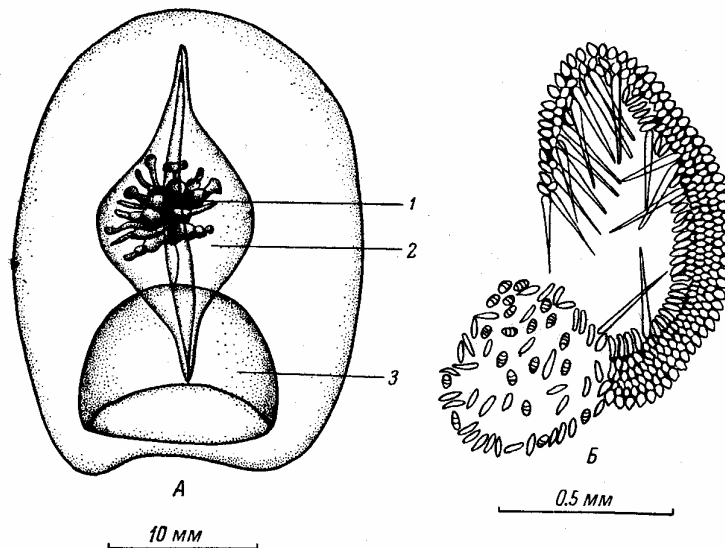1. Nectophores; 2. Somatocysts of nectophores; 3. Nectosacs.



Fig. 93. *Rosacea plicata* Quoy and Gaimard.
A. Ventral view of a nectophore of a colony; Б. Tentillum.
1. Contracted stem of the colony; 2. Hydroecium; 3. Nectosac.

Table 4.

Comparison of morphological characters of *Rosacea plicata* and *R. cymbiformis*.

| Character | *R. plicata* | *R. cymbiformis* |
|---|---|---|
| Shape and size of nectophore | Oval, bean-shaped; apically: 7-30 mm in length, 4-17 mm wide; distally: 12-32 mm long & 7-17 mm wide. | Bean-shaped or cylindrical; apically: 40 mm long & 25 mm wide; distally: 50 mm long & 35 mm wide. |
| Shape and size of nectosac | Oval, small, with sigmoid lateral radial canals. | Bell-shaped, oval, deeper, with sigmoid lateral radial canals. |
| Shape and size of hydroecium | Short and wide; occupying 2/3 to 1/3 length of ventral side of nectophore. | Long and narrow; occupying large part of ventral surface of nectophore. |
| Shape and size of somatocyst | Unbranched, short, with ascending and descending branches. Ends slightly swollen. | Unbranched, longer, with ascending and descending branch. Ends swollen or not. |
| Tentillum | Straight or slightly curved, containing anacrophores, rhabdomeres and microbasic mastigophores | Straight or bent, containing anacrophores, anisorhizas, rhabdomeres & microbasic mastigophores. |
| Shape and size of eudoxid bract | Cap-shaped, having 3 lobes, 8-20 mm long, 6-15 mm in height. | Cap-shaped, with 3 lobes; 10-12 mm long, 8-11 mm in height. |
| Branches of Phyllocyst | 4 canals, unpaired apical attached distally to branch of lateral canals. | 4 canals, unpaired apical attached proximal to branch of small lateral canal |
| Presence of special nectophore | ? | No |

3. Genus **PRAYA** Blainville, 1834

**p. 149**

Stepanjants, 1967, pp. 156-157.

## Subfamily **MONOPHYINAE** Stepanjants subfam. nov.

Diphyidae with single, permanent nectophore. Nectophore conical (rarely rounded) in shape. Surface of nectophore smooth. Hydroecium and somatocyst of nectophore lie on ventral side of nectosac.

Subfamily includes a single genus *Monophyes* Claus.

Most researchers have included *Monophyes* in the family Sphaeronectidae either as an independent genus, or as a synonym of the genus *Sphaeronectes*.

Whilst comparing colonies, belonging to the genera *Monophyes* and *Sphaeronectes*, under light [microscopy?], possible to detect certain differences. Apart from the shape of the nectophore, colonies of these genera can be discriminated from each other by the arrangement of the nectosac, hydroecium and somatocyst in the nectophore. In the nectophore of *Sphaeronectes* the hydroecium and somatocyst lie on the apical side of the nectosac (close to its summit), and as a result of this all 4 radial canals on the nectosac are of equal length, that is they in general merge with the pedicular canal also close to the summit of the nectosac. By this (and the shape of the nectophore) colonies of *Sphaeronectes* resemble closely the larval colonies of Hippopodiidae and Prayidae. In the nectophore of *Monophyes* the hydroecium and somatocyst lie on the ventral side of the nectosac. The four radial canals on the nectosac are of unequal length and, therefore, merge with the pedicular canal on the ventral side of the nectosac, where also occurs the junction of the pedicular canal with the somatocyst. Owing to this peculiarity, as well as the shape of the nectophore, the colonies of *Monophyes* resemble the larval colonies of other Diphyidae - *Muggiaea*, *Sulculeolaria*, *Diphyes*.

Taking this into account, the present findings suggest that the genus *Monophyes* should be excluded from the former family Sphaeronectidae, and that it should be ascribed to the family Diphyidae as an independent subfamily Monophyinae (on the basis of the similarity between its definitive colony and the larva of other Diphyidae). Within the Sphaeronectidae, as now thought, remains the single genus *Sphaeronectes*. This family appears to be phylogenetically distant from the Monophyinae, and most closely related to the Hippopodiidae and Prayidae, based on the evidence of the morphological similarity between the definitive colonies and the larval ones of those families.

## 1. Genus **MONOPHYES** Claus, 1873

Claus, 1873: 257 (part); 1874: 29 (part); Chun, 1885: 4; 1888: 761, 762; 1892: 10; 1897a: 9; Haeckel, 1888b: 128, 129: Schneider, 1898: 75, 78 (part, *Sphaeronectes*); Bigelow, 1911b: 182-184 (part, *Sphaeronectes*).

Individual, conical nectophore, rarely rounded in shape, 2-6 mm in height. Radial canals on nectosac of unequal length, lateral and ventral canals shorter than dorsal. Somatocyst bubble- or elongated oval shape, situated on ventral side of nectosac.

Type species: *Monophyes irregularis* Claus, 1873

1. **Monophyes japonica** Stepanyants sp. nov. (Fig. 99).

Type specimen deposited in the collections of the ZIN AN SSSR. "Vitiaz" St. 331.

Polygastric Stage. Single definitive nectophore 2.8-3.5 mm in height, conical in shape, transforming toward rounded. Deep cone-shaped subumbrella cavity (2-2.6 mm in height). Funnel-shaped hydroecium reaching to 1/2 height of nectosac. Bubble-shaped somatocyst (0.20-0.60 mm high) sitting on a stalk which runs almost perpendicularly to the hydroecium, but in some examples it is directed toward the subumbrella at a very slight angle.

Eudoxid. Unknown

Distribution. Colonies of this species were collected in the Japan Sea (39°21'N, 134°36'E) within the depth zones 100-0 and 200-100 m.

This newly described species can be distinguished from *M. irregularis* by the shape of the nectophore and the characteristic bend in the lateral radial canals on the nectosac.
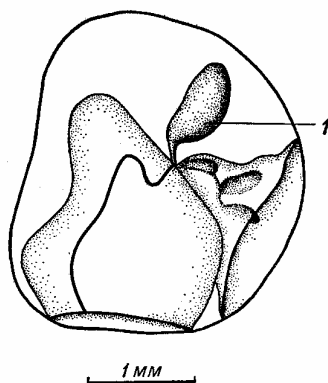


Fig. 99. Colony of *Monophyes japonica* Stepanyants sp. n.

Subfamily **GALETTINAE** Stechow, 1921.

Diphyidae with two definitive nectophores, the superior one being conical in shape, the inferior one approximately cylindrical, and also the two nectophores generally are laterally flattened. The nectophores are smooth, with or without teeth around the opening of the subumbrella. Each nectophore has at its base a particular kind of basal lamella – an extension of the ventral wall of the bell. The superior nectophore lacks a hydroecium; its somatocyst can be small, almost invisible, or slightly enlarged, or in the shape of a small, fine tube. The somatocyst of the inferior nectophore is reduced. The subumbrellas of the two nectophores have lateral canals curved in the shape of an arch, and in the superior nectophores they are connected to the ventral canal by commissures.

2. Genus **SULCULEOLARIA** Blainville, 1830

Blainville, 1830: 126 (*Galeolaria*); 1834: 138, 139 (*Galeolaria*); Quoy and Gaimard, 1833: 43 (*Galeolaria*); Chun, 1888: 765 (1157) (*Epibulia*); 1897a: 16, 7 (*Galeolaria*): Haeckel, 1888b: 150, 151 (*Galeolaria*); Vanhöffen, 1906: 15 *Galeolaria*); Bigelow, 1911b: 233-236 (*Galeolaria*); Moser,

1925: 135 (*Galeolaria*); Totton, 1932: 340; 1954: 100 (in part); Bigelow & Sears, 1937: 29; Leloup, 1955: 8.

The superior nectophore reaches 20 mm in height. The base of the nectophore is provided with 2-5 teeth and bears a lamella composed of two lobes stretching below the opening of the subumbrella. The somatocyst is either very small and oval, or elongated as a small, fine tube. The inferior nectophore (reaching 26 mm in height), like the superior one, bears at its base 2-4 teeth and a lamella. The latter can be entire or divided.

Type species: *Galeolaria quadrivalvis* Blainville, 1830.

### TABLE FOR THE IDENTIFICATION OFSPECIES OF THE GENUS SULCULEOLARIA BLAINVILLE

1. (2) The superior and inferior nectophores have 4 basal teeth (2 lateral and 2 dorsal), no mesogloeal outgrowths. Somatocyst of the superior nectophore represented by a small, fine tube occupying the lower third of the bell. Lamella of inferior nectophore consists of 2 lobes. **1. *S. quadridentata*** (Q. &. G)

2. (1) The superior and inferior nectophores with 3 basal teeth (all dorsal) and 2 small and blunt mesogloeal outgrowths. Somatocyst of superior nectophore is very small oval formation occupying approx. 1/20th of total length of nectophore. Basal lamella of inferior nectophore entire. **2. *S. chuni*** (Chun)

### 1. Sulculeolaria quadridentata (Quoy and Gaimard, 1833 (figs. 100-103)

Quoy and Gaimard, 1833: 45, pl. 5, figs. 32, 33 (*Galeolaria*); Keferstein and Ehlers, 1861: 18, pl. 5, fig. 26E (*Diphyes quadrivalvis*); Metschnikoff, 1874: 443-449, pl. XLIX-L (*Epibulia aurantica*); Lochmann, 1914: 262, pl. 7, figs. 1-3 (*Galeolaria aurantica*); Bigelow, 1918: 417, pl. 8, figs. 1, 2 (*Galeolaria*); 1931: 556, text-figs. 201-203 (*Galetta*); Moser, 1925: 139 (*Galeolaria quadrivalvis*, in part); Browne, 1926: 67 (*Galeolaria*); Totton, 1932: 340; 1954: 109 (*quadrivalvis* in part); Leloup, 1932: 4 (*Galeolaria quadrivalvis*, in part); 1933a: 20, (*quadrivalvis* in part); 1955: 9 quadrivalvis in part); Bigelow & Sears, 1937: 31; Totton, 1965: 143-145, pl. XXIX, fig. 4, pl. XXX, figs. 1-4; pl. XXXI, figs. 1-3; text-figs. 82 (in part).

Polygastric stage. The larval nectophore is conical and without superficial ridges. The radial canals on the nectosac are not of equal length. The pedicular canal joins the somatocyst on the ventral side of the nectophore (fig. 103, A). The superior definitive nectophore (6-20 mm in height) is conical in shape. The surface of the nectophore is smooth, without ridges. The base of the nectophore has 4 large triangular teeth (2 dorsal and 2 lateral) arranged parallel to the opening of the subumbrella (fig. 101). The lobes of the basal lamella are circular and divided. The nectosac occupies almost the entire height of the bell, with a slightly curved axis. The lateral canals form (for almost all the length of the nectosac) large curves, and are joined to the ventral canal by commissures arising from the ventral canal in the lower quarter of the nectophore (also, more often the left commissure arises a little below the right one rather than together with it). The somatocyst is a thin tube (sometimes enlarged by a swelling at its extremity), slightly curved towards the top and reaching to 1/3 the height of the nectosac, or a little higher. The pedicular canal is prolonged beyond the base of the somatocyst for approx. 1/3 of its length (fig. 100). The inferior nectophore (6026 mm in height) is approx. cylindrical in shape. Its base bears 4 large,

equally-sized teeth (2 lateral and 2 dorsal) and a basal lamella made up of 2 circular lobes, at the base of each of which is found a tooth-like outgrowth (fig. 102). The nectosac occupies almost the entire length of the nectophore, its lateral canals forming a double bend and join with the pedicular canal on the apical part of the nectosac. The lower bend usually has a short side branch.

The stolon, which is usually greatly shortened following fixation, carries several buds of reserve nectophores; these buds often having characters quite different from the bells (oral teeth, lateral canal bent in the shape of an arc, latero-ventral commissures). The bract is a sheath covering the portion of the stolon corresponding to a cormidium. It has a dentate edge and a deep groove on its right side (fig. 103 Б). The phyllocyst is represented by two ascending canals. The gonophores, until now having been known only to have an oval shape, are budded on the stalk of the gastrozooid. The latter is of the usual shape.

Distribution. Northern part of the Pacific Ocean (39-45°N and 160-170°E; Tropical Pacific, in the region of the Great Barrier Reef, Australia; Atlantic (Azores and Canary Islands, off Spain, Straits of Gibraltar; Mediterranean Sea; Indian Ocean.

Usually found in near-surface waters.

It has not been found in our waters. In the Russian collections, there a large number of superior and inferior nectophores of this species from the northern part of the Pacific Ocean.

Despite the great similarity in structure of the nectophores of *S. quadridentata* and *S. quadrivalvis*, it is necessary to recognise the independent existence of these species, because the nectophores of the former have 4 basal teeth, while those of the latter have only 2 basal teeth. From the fact that the small latero-basal outgrowths that are found on certain nectophores of *S. quadrivalvis*, these are different morphologically from the large latero-basal teeth of *S. quadridentata*.
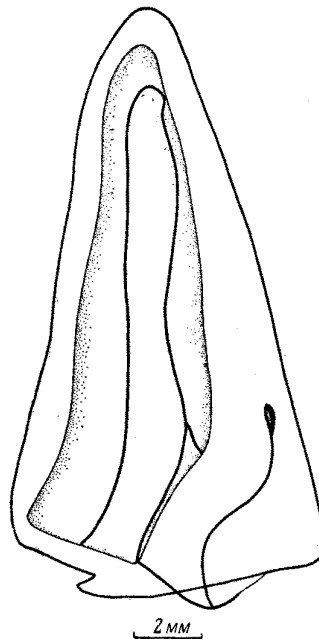


Fig. 100. Superior nectophore of *Sulculeolaria quadridentata* (Quoy and Gaimard)
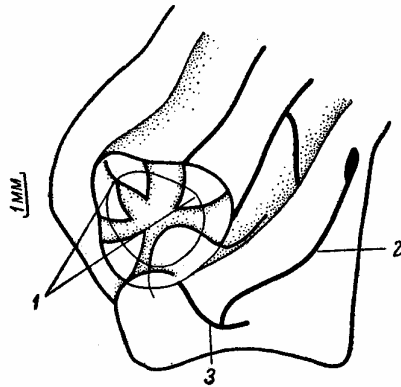
Fig. 101. Basal part of superior nectophore of *Sulculeolaria quadridentata* (Quoy and Gaimard (basal view). 1. basal teeth; 2. somatocyst; 3. pedicular canal.
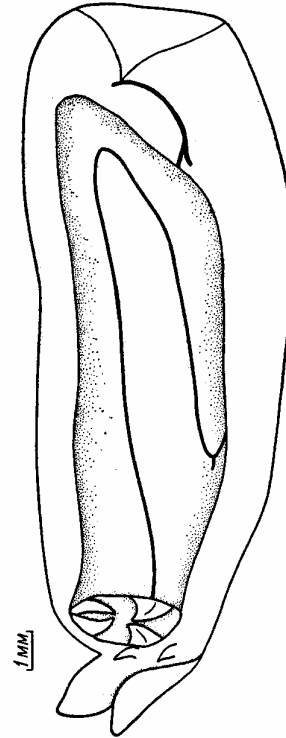
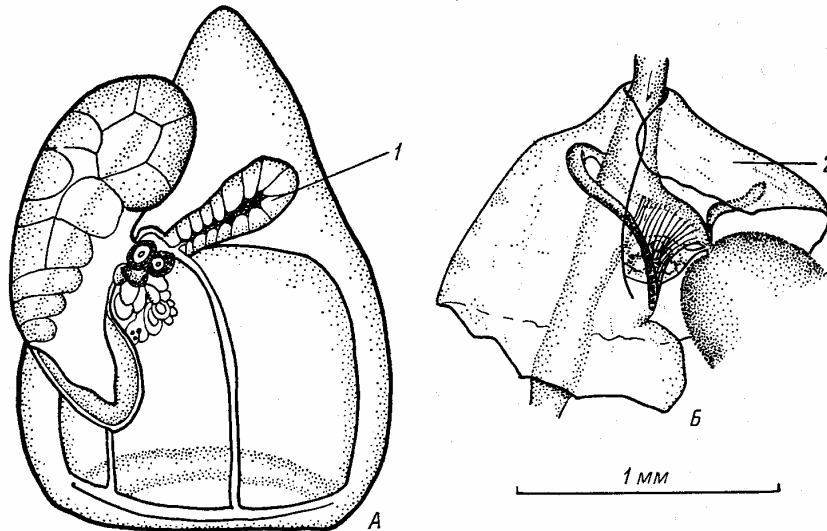Fig. 102. Inferior nectophore of *Sulculeolaria quadridentata* (Quoy and Gaimard)

Fig. 103. *Sulculeolaria quadridentata* (Quoy and Gaimard).
A. larval colony (after Metschnikoff); Б. portion of the colony with a bract (after Bigelow).
1. somatocyst; 2. bract.

## 2. **Sulculeolaria monoica** (Chun, 1888) (fig. 104)

Chun, 1888: 1157 (765) (*Epibulia*); 1897a: 17 (*Galeolaria*); Schneider, 1898: 86 (*Diphyes biloba*, in part); Lens and van Riemsdijk, 1908: 60, 61, pl. IX, figs. 76, 77 (*Galeolaria*); Bigelow, 1911b: 239, 240, pl. VI, figs. 4-6 (*Galeolaria*); 1913: 70 (*Galeolaria*); 1918: 418, 419 (*Galeolaria*); 1931: 558-559 (*Galetta*); Moser, 1925: 145 (*Galeolaria*); Browne, 1926: 69; Totton, 1932: 342; 1954: 16; 1965: 132, pl. XXXI, figs. 5-7, 10, 12; Leloup, 1933a: 25; 1937: 122; 1955:8, 9; Russell & Colman, 1935: 201; Moore, 1949: 22, fig. 50; Sears, 1950: 3.

Polygastric stage. Larval nectophore unknown. The superior definitive nectophore (6-20 mm in height) is conical in shape (fir. 104, A). The surface of the nectophore is smooth, without ridges or facets. The base of then has 3 basal teeth (dorsal), of which each is slightly divided toward its apex, and two lateral outgrowths. The lamella has to circular lobes of which the right slightly overlaps the left and the 2 mesogloeal outgrowths at the base of the lobes (fig. 104 Б). The longitudinal axis of the nectosac is lightly curved. The ascending branches of the lateral canals on the subumbrella in the shape of a loop, and arise from the ventral canal at the place where the pedicular canal separates from it. The lateral canals are reunited with the ventral canal by some commissures at one-third the height of the nectosac. Often these lateral canals are curved, sinuous and the loop of the commissures bears a short, apical branch. The somatocyst is very small (1/20 the height of the nectophore), oval. The pedicular canal is prolonged beyond the base of the somatocyst by 1/3 of its length. The inferior definitive nectophore (10-27 mm in height) has a shape not very different from that of
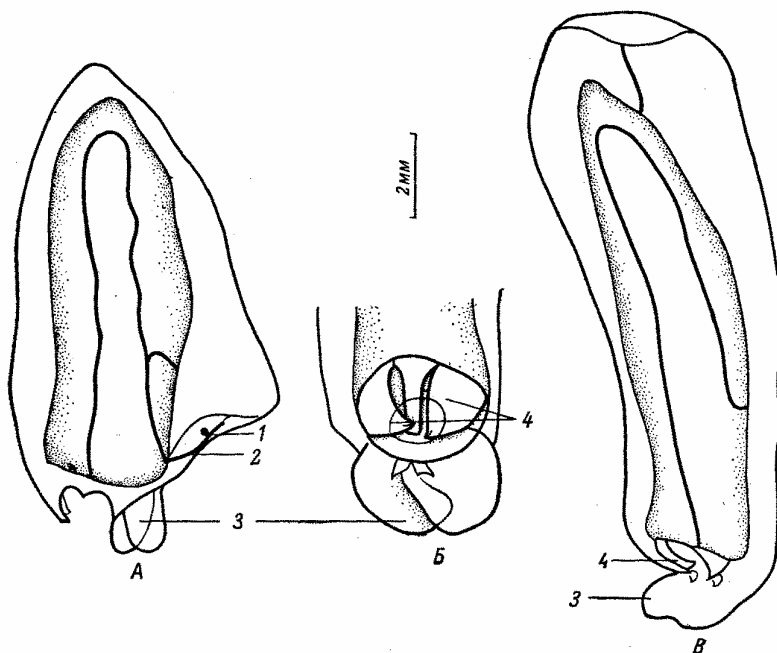


Fig. 104. *Sulculeolaria monoica* (Chun).
A. – Superior definitive nectophore; Б. – basal part of superior definitive nectophore
(basal view); B. – inferior definitive nectophore.
1. – somatocyst; 2. – pedicular canal; 3. – lamella; 4. – basal teeth.

*S. quadridentata*. The base of the nectophore has 3 teeth and lateral outgrowths. The lamella is entire (not having lobes) and bears almost at its base (close to the opening of the subumbrella) 2 outgrowths in the form of teeth (fig, 104, Б). The canal system of the subumbrella and the characters of the junction between them cannot be differentiated from that of *S. quadridentata*. Of the stolon and its appendages, there is nothing known. In our material the stolon is lacking.

Distribution. Northern part of the Pacific Ocean (eastern coast of Japan and between 30-35°N and 155-166°E; eastern part of the tropical Pacific; Atlantic Ocean (south of Bermuda as far as 10°N); south-east, southern and north-western parts of the Indian Ocean.

It has not been found in out waters. In the collections of the ZIN AN SSSR this species is represented by some superior and inferior nectophores from the northern part of the Pacific.

### 3. Genus **GALETTA** Stechow, 1921

Stechow, 1921: 261; Bigelow & Sears, 1937: 33; Leloup, 1955: 9.

The superior definitive nectophore not more than 17 mm in height (in the majority of cases, no more than 10-13 mm). By the shape and structure of its elements, it can almost not be distinguished from the genus *Sulculeolaria*. One can say the same thing about the inferior nectophores of *Galetta* that do not exceed 20 mm in height and mainly are not more than 15 mm.

The characteristic that differentiates *Galetta* from *Sulculeolaria* is the absence of basal teeth on the nectophores of the genus *Galetta*.

Totton (1954) considered the presence or complete absence of basal teeth in the nectophores of the subfamily Galettinae as an inconstant feature. In admitting that if the number of teeth on the nectophores can vary within the limits of a species (he reunites the species *Sulculeolaria quadrivalvis* with two basal teeth and *S. quadridentata* with 4 basal teeth as a single species – *S. quadrivalvis*), then within the limits of a genus, the teeth on the nectophore can be present or entirely absent. According to this factor Totton reunites the genus *Galetta* (without basal teeth on the nectophores) and *Sulculeolaria* (with basal teeth on the nectophores) as a single genus *Sulculeolaria*.

In order to be in accord with such affirmations, it is necessary to have at one's disposal a sufficiently large quantity of comparative material in which there will be representatives of the different intermediate forms; some nectophores with two teeth to the nectophores with 4 teeth; some nectophores totally deprived of teeth to some nectophores amongst which the teeth are well developed. In our material, these intermediate forms are absent. All our examples of *S. quadridentata* quite clearly have 4 basal teeth of which the dimensions are entirely constant and all the specimens are connected with the genus *Galetta* being totally deprived of teeth. That which Totton described for certain specimens of *G. biloba* are differentiated from true teeth by the fact that they are held on another surface (principally to the orifice of the subumbrella) and represent the fragile outgrowths of the mesogloeal wall of the nectophore not having precise shapes.

In the present work, *Galetta* and *Sulculeolaria* are seen as independent genera. Meanwhile in taking account of what has been said above, the independence of the

genus *Galetta* is recognised only under the condition as far as the obtainment of complementary material.

The species placed into the genus *Galetta*: *G. australis* (Q. &. G.), *G. biloba* (M. Sars), *G. chuni* Lens and van Riemsdijk and *G. angusta* Totton are very close to one another. The differences between them are so insignificant that it would be subsequently (with the possession of complementary material) to re-examine the right to independence of each of these.

In spite of this because in the region studied there has been found only one species – *G. biloba*, below is given a table for determining of the species and are based on the known comparative morphologies (with the figures) of all the species of the genus *Galetta* (table 5).

Type species: *Galeolaria australis* Q. & G. 1834.

### *TABLE FOR THE DETERMINATION OF THE SPECIES OF THE GENUS* GALETTA *STECHOW*

1. (2) Lamella of inferior nectophore entire, with a regular border. Somatocyst of superior nectophore has a height not more than $1/10^{th}$ total height of nectophore.

*G. australis* Q. & G.

2. (1) Lamella of inferior nectophore not entire. It has a concave basal border. Somatocyst of superior nectophore has a height of ½-1/11 total height of nectophore.

3. (4) Lamella of inferior nectophore has a trough-shaped hollow in the mid line on its dorsal side. *G. biloba* (M. Sars)

4. (3) Lamella of inferior nectophore is deprived of a trough-like hollow along the mid line of its dorsal side.

5. (6) Depression on side of the lamella of the inferior nectophore is arranged in such a way that it separates the inferior part of the lamella into two large, equal lobes. Somatocyst of superior nectophore is very small and constitutes approx. $1/14^{th}$ or a little less, the total height of the nectophore. *G. angusta* Totton

6. (5) Depression on border of lamella of inferior nectophore is arranged in such a way that it separates the inferior part of the lamella into two lobes of which the right is slightly larger than the left. Somatocyst of superior nectophore constitutes approx. ½ the total height of nectophore. *G. chuni* L. & van R.

Comparison of morphological characters of species of the genus *Galetta* (fir. 105, 106)

| Character | G. australis | G. chuni | G. angusta | G. biloba |
|---|---|---|---|---|
| Height of superior nectophore | 3-17 mm | 1.5-7 mm | 8 mm | 4.5-13 mm |
| Shape of somatocyst | Oval vesicle or small tube | Small sinuous tube | Oval | Oval vesicle |
| Size of somatocyst | 1/10th total height of nectophore | ½ total height of nectophore | 1/14th height of nectophore | 1/7th height of nectophore |
| Characters of junctions of commissural canals on lateral canals of nectosac | Commissures arise from lat. canals at level of ½-? height of nectophore, and join ventrals close to base of latter. | Commissures arise from lat. canals at level of lower 1/3rd of nectophore. The right joins above the left commissure. | ? | Commissures arise from lat. canals at ½ height of nectophore. Right commissure joins above left. |
| Height of inferior nectophore | 3-21 mm | 8 mm | 16 mm | 14 mm |
| Structure of lamella | Entire, with single border, no outgrowths on dorsal side. | Inferior border concave. A hollow separates the inferior part of the lamella into two lobes, of which the right is larger than the left. No outgrowths on the dorsal side | Concave inferior border. A hollow separates the inferior part of the lamella unto 2 lobes of equal size. There is 1 outgrowth on the dorsal side where the part of the lamella is thickened. | The lamella has a longitudinal furrow in the middle on its dorsal side. There are outgrowths on the dorsal side. |
| Size of lobes of the hydroecial furrow | The lobes are of equal size | The lobes are equal in length | ? | The left lobe is longer than the right. |
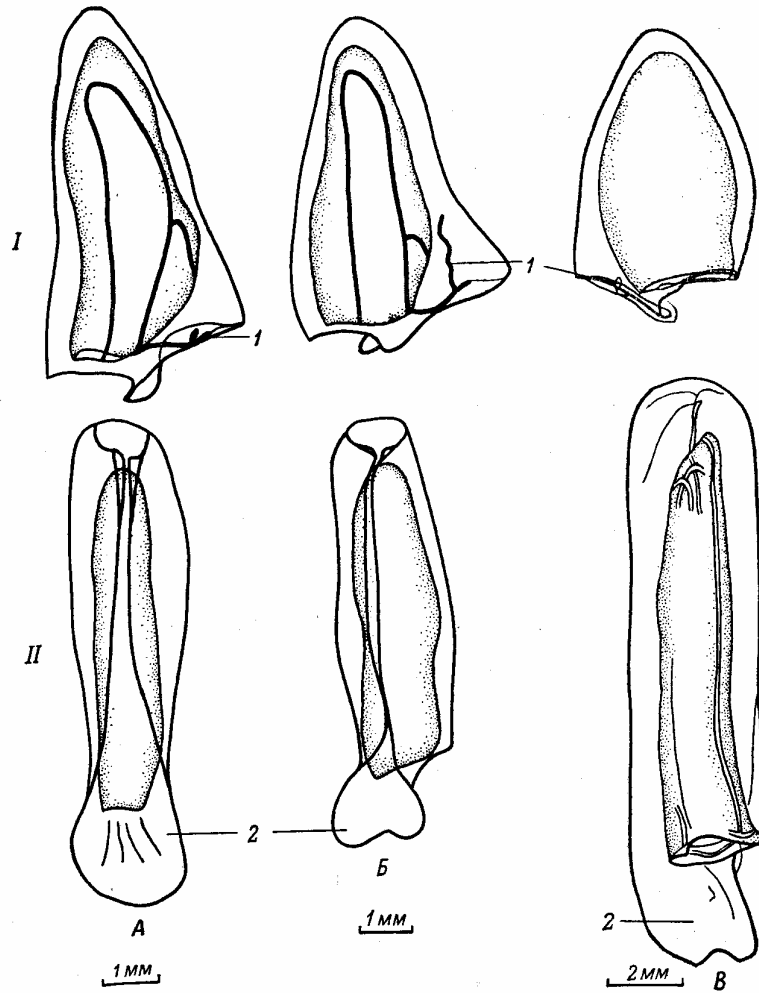
Fig. 105. Superior (I) and inferior (II) nectophores of three species, belonging to the genus *Galetta*.
A – *Galetta australis* Quoy and Gaimard; Б – *G. chuni* Lens and van Riemsdijk; В – *G. angusta* (Totton (after Totton). 1 – somatocyst; 2 – lamella.

### 1. **Galetta biloba** (M. Sars, 1846) (fig. 106)

Sars, 1846: 45, 46, pl. 7, figs. 16-21 (*Diphyes*); Haeckel, 1888b: 151 (*Galeolaria*); Chun, 1897a: 17 (*Galeolaria*); Römer, 1902: 173 (*Galeolaria*); Vanhöffen, 1906: 16 (*Galeolaria*); Lens and van Riemsdijk, 1908: 59, pl. 9, fig. 75 (*Galeolaria*); Bigelow, 1911b: 238, pl. 5, figs. 8, 9; pl. 6, figs. 1-3 (*Galeolaria australis*, in part); Moser, 1925: 145-149 (*G. australis*, in part); Candeias, 1929: 272, fig. 3 (*G. australis*); Totton, 1954: 104-107, text-figs. 49-51 (*Sulculeolaria*); 1965: 145-148, text-figs. 83-86 (*Sulculeolaria*); Totton & Fraser, 1955a: 1-4, fig. 4 (*Sulculeolaria*).

Polygastric stage. The larval nectophore is unknown. Superior definitive nectophore (4.5-13 mm in height) does not show any differences in shape from the nectophores of other species of this subfamily. The circular lobes of the lamella are one above the other. Lateral canals loop join to the ventral by commissures of which each arises from the lateral at a level of ½ the total height of the nectophore; and further, the right lateral commissure always arrives at the ventral canal slightly above

the left commissure. The ascending branch of the lateral canal join equally to the ventral canal at the level of the point where the pedicular canal arises. The somatocyst is not large (approx. ½ the height of the nectophore), in its intact state is forma an oval vesicle (fig. 106, A). The inferior definitive nectophore (reaching 14 mm in height), by its shape is no different from most of those of other species. The left lobe of the hydroecium is situated slightly higher than the right. The lamella is divided, but not entirely and has in its middle a trough-like cavity (fig. 106, Б).

Distribution. Northern parts of the Pacific Ocean (38°N and 15226' E); tropical Pacific; Atlantic Ocean (around Bermuda; North Atlantic in the region south-east of Ireland; of Shetland, and the North Sea, of the Norwegian Sea and the coasts of Norway and Greenland); Indian Ocean.
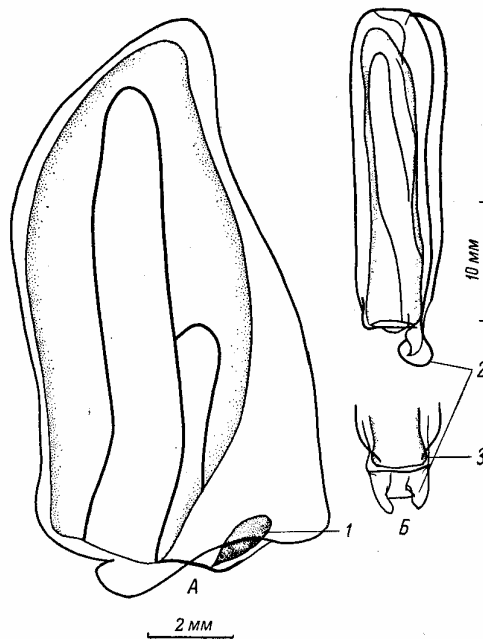
Found within the limits of 0-100 m.



Fig. 106. *Galetta biloba* (M. Sars).
А – superior definitive nectophore; Б – inferior definitive nectophore (after Totton). 1 – somatocyst; 2 – lamella (mouth plate); 3 – basal part nectophore in dorsal view.

Not found in our waters. In the collections of the ZIN AN SSSR there are some nectophores of this species collected in the northern part of the Pacific Ocean.

Subfamily **CHUNIPHYINE** Moser, 1925

**p.166**

Diphyidae with 2 definitive nectophores  **ETC**


p. 169

### 5. Genus **CLAUSOPHYES** Lens and van Riemsdijk, 1908

Lens and van Riemsdijk, 1908: 12; Bigelow, 1913: 70; Moser, 1925: 362; Totton, 1954: 133.


Superior nectophore (up to 20 mm in length) conical, smooth, without ridges and slightly flattened laterally. Base of nectophore has 2 ventral rounded processes from side of dorsal wall of hydroecium.. Hydroecium reaching up to ½ height of nectophore and, as *Chuniphyes*, has a mesogloeal process for the attachment of the inferior nectophore. The latter (up to 35 mm in length) has a pyramidal shape; having, besides the two ventral lobes, 2 weakly marked dorsal furrows and ventral spade-like process. Somatocysts runs up nectophore, and in proximal part is swollen.

Type species: *Diphyes ovata* Chun, 1897.

### 1. **Clausophyes galeata** ? Lens and van Riemsdijk (fig. 112)

Lens and van Riemsdijk, 1908: 12, pl. 1, figs. 6-8; Bigelow, 1913: 71-73, pl. VI, fig. 1,2; Totton, 1954: 134; 1965: 194, pl. XXXV, fig. 11.


Polygastric stage. Larval nectophore unknown. Superior nectophore (10-20 mm in length) conical in shape (fig. 112, A). Hydroecium shallow. Mesogloeal process at the level of the lower third of the nectosac. Itself at the level of the entrance to the hydroecium and pedicular canal. Oval lobes demarcate hydroecium, descend slightly below opening of subumbrella, their dorsal walls forming 2 quite large, rounded processes (judging by figures in literature, these exceed the length of those in *C. ovata*). Proximal, swollen part of somatocyst variable in shape from being simply oval to an elongated curve. distal part of somatocyst filiform and extends almost to the apex of the superior nectophore. Basal part of somatocyst having filiform peduncle. Posterior definitive nectophore (15-35 mm in length) pyramidal in shape (fig. 112, Б). Dorsal wall of nectophore bearing 2 dorso-lateral ridges, distinct in apical part but transitory, in "hillocks" on the convex surface running down to the base of the nectophore. Ventral lobes delimit shallow hydroecium, with flaps on inner surface basally (1 on right and 2 on left). Dorsal wall of hydroecium transforms into spade-like process below the opening of the subumbrella. Wide, sack-shaped nectosac occupying ¾ the height of the nectophore. Expanded part of somatocyst present proximally, and can extend to apex of nectophore. Filiform part (ascending and descending branches) variable in length.

Distribution. Pacific coast of Kamchatka, N.W. coast of America (region of Vancouver) between 30 and 45°N and 145 to 165°E; East China Sea, east coast of Japan, Philippines region. Malay archipelago.

Found at great depth and only a few times found as shallow as 0-300 m.

In the collections of the ZIN AN SSSR there are a few superior and posterior bells from the northern part of the Pacific Ocean.
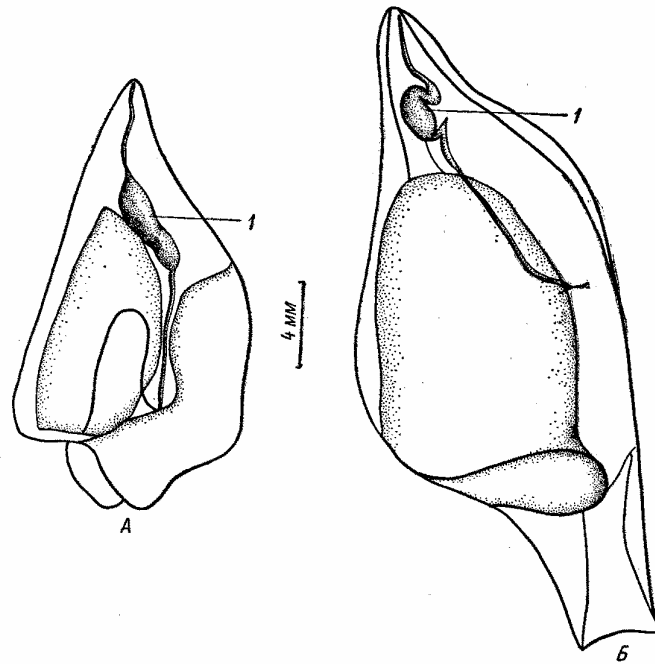
Fig. 112. *Clausophyes galeata*? Lens and van Riemsdijk.
A – superior definitive nectophore; Б – inferior definitive nectophore. 1. somatocyst.

Despite the undoubted close relationship of *C. galeata* and *C. ovata* we continue to follow the opinion of Totton (1954) regarding the independence of these species. Through comparisons of the nectophores of *C. galeata* and *C. ovata* we can draw attention to the following distinguishing characters: dorso-basal protuberance in hydroecium of superior nectophore of *C. galeata* descends below the level of the subumbrella further than that in *C. ovata*; hydroecium of *C. galeata* lacks two grooves, characteristic of *C. ovata*; right lobe of the hydroecium of inferior nectophore of *C. galeata* lacks second inner flap (no trace in all examples and not, apparently, age-related), and on left lobe of the hydroecium of the inferior nectophore of *C. galeata* there are 2 flaps (not found in *C. ovata*). Totton added the spade-like extension of the dorsal wall of the hydroecium in the inferior nectophore of *C. galeata* were very similar to the process in *C. ovata* and that the right wing of the hydroecium of the inferior nectophore of *C. galeata* was thicker than the left and had a triangular shape, not found in *C. ovata*.

In our material of the species described the spade-like process has a smooth basal part, whereas Bigelow (1913) and Lens and van Riemsdijk (1908) noted two identical teeth at the base of the lobe. These distinctions of the inferior nectophore cannot be resolved from the available material of *C. galeata*.

<div align="center">Subfamily <b>DIPHYINAE</b> Moser, 1925</div>

**p. 171**

Diphyidae with two definitive nectophores. **ETC**

Stepanyants 1967, p.185

2. **Muggiaea havock** (Totton, 1941) (Fig. 126).

Totton, 1941: 159, 160, figs 17-18 (*Lensia*); 1965: 175, 176, text-fig. 114 (*Lensia*).

Polygastric stage. Larval nectophore unknown. Single definitive nectophore (6-8 mm in height) of pyramidal form (fig. 126, A). Surface of nectophore with 7 ridges, of which the two latero-ventrals bend at the level of the hydroecium. Base of subumbrella without teeth. Shallow hydroecium reaching to only 1/4 height of nectophore and bluntly rounded in its apical part. Base of hydroecium obliquely truncated. Dorsal wall of hydroecium bent somewhat below opening of subumbrella, representing doubled, rounded lobes, having serrated ends. Ventral wall of hydroecium has deep incision (Fig. 126 Б). Knob-like appearance of somatocyst (1.4 mm in length) sits on a short pedicle. Cavity of subumbrella deep (6 mm in height). On stem of colony a bud of a second nectophore is absent.
Eudoxid: Unknown.
Distribution: Pacific Ocean in region of coast of Kurile Islands, southern part of Okhotsk Sea, region of Commander (?) Islands; Atlantic Ocean (Bermuda Island, southern Atlantic); south east part of Indian Ocean.

The horizontal distribution of this species extremely wide, from 0 to 3400 m, but as it has been found predominantly in the 500-3000 m range one can assume that adult forms of *M. havock* prefer to live at depth.

From the description of this species it follows to place it in the genus *Muggiaea*, as the presence of single nectophore (without reserve bud of second nectophore) and similar depth of hydroecium excludes its inclusion in the genus *Lensia* (Totton, 1941).
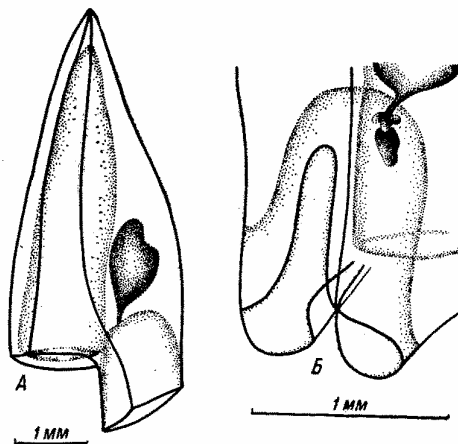


Fig. 126. *Muggiaea havock* (Totton).
А – definitive nectophore; Б – basal part of definitive nectophore (in ventral view).

Stepanyants 1967, pp. 194-197

## Subfamily **DIMOPHYINAE** Moser, 1925

Diphyidae with 2 definitive nectophores. Superior definitive nectophore conical in shape, **To translate a bit more**.

1. **Dimophyes arctica** (Chun, 1897)  (figs. 134-136)

Chun, 1897a: 19-24, 36, 98, 99, pl. 1, figs. 1-10 (*Diphyes*); 22, 23, 99 (*Diphyes borealis*); Schneider, 1898: 55, 57 (*Muggiaea*); Römmer & Schaudinn, 1900: 245 (*Diphyes*); Römmer, 1902: 174, 175 (*Diphyes*); Cleve, 1904: 84, 118, 156 (*Muggiaea atlantica*); Vanhöffen, 1906: 17, 18, text-fig. 16-18 (*Diphyes*); Linko,, 1907: 154, 155 (*Diphyes*); 1913: 11, 12 (*Diphyes*); Damas & Koefoed, 1907: 412, 413 (*Diphyes*); Broch, 1908: 1-6 (*Diphyes*); 1928: III, c3; Bigelow, 1911b: 247, 347, 369, 370 (*Diphyes*); 1913: 11, 12 (*Diphyes*); Moser, 1925: 389-397; Bernstein, 1934: 22; Rumström, 1932: 32; Leloup, 1933b: 35, 36; 1934a: 29, 31; 1935: 9; Mackintosh, 1934; 72, 86, 90, 98, 125, 127, 134, fig. 26, 20, tabl. I-VIII; Leloup & Hentschel, 1935: 266; Russell & Colman, 1935: 266; Kramp, 1942: 9-12; 1943: 9, fig. 2; 1949: 7, fig. 3;Yashnov, 1948: 75; Sears, 1950: 3; Kielhorn, 1952: 248; Totton, 1954: 123-127; 1965: 184, 185, pl. XXXIII, fig. 1, 2, 7, text-fig.. 122; Totton & Fraser 1955a: 55, 1-4, fig. 1; Stepanjants, 1963: 1867.
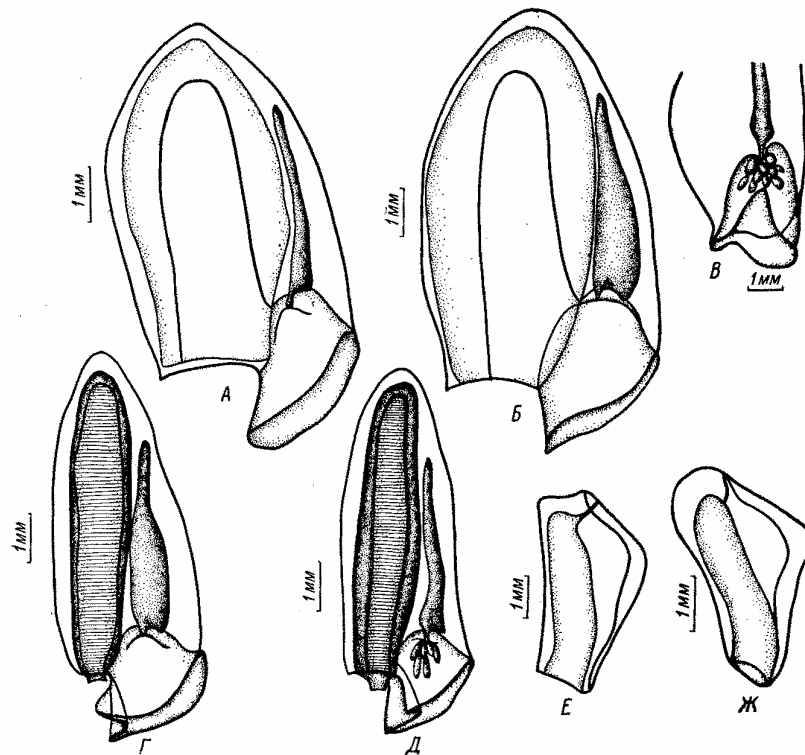


Fig. 134 *Dimophyes arctica* Chun
А, Б – Superior definitive nectophore, the walls of the nectosac of which are deprived of musculature; В – basal part of superior definitive nectophore in ventral view; Г, Д – superior definitive nectophore, the walls of the nectosac of which have powerful musculature: E - inferior nectophores.

Polygastric stage. Larval nectophore unknown. Superior, definitive nectophore (4-12 mm in height) conical in shape. The surface of the nectophore without facets, and no teeth on the subumbrella rim. Deep nectosac more or less reaching the apex and having a powerful musculature, the presence of which gives elasticity and shape to the nectophore (Fig.134, Г, Д). In some examples of *D. arctica* one often sees that the walls of the subumbrella are deprived of musculature. The mesogloea of the nectophore is still more friable, and the nectophores themselves are rather shorter and more rounded at the apex than those provided with musculature (Fig.134, А, Б). The reason for such a distinction in the nectophores of *D. arctica* is difficult to explain. It is possible to say, with assurance, only that it is not a growth stage factor, because some of the nectophores with or without musculature are of the same age (Fig.135, А, Б). The shallow hydroecium (1/3-1/4 the length of the nectophore) has an undivided dorsal wall and a significant concavity of the ventral one (Fig.134, В). The somatocyst arises from a very short stalk (pedicel), which arises from a groove in the apex of the hydroecium, with the left side of the groove somewhat higher then the right. For this reason the somatocyst has a ventral, blind swelling that is not equally pronounced in all specimens. The somatocyst is conical, more or less pointed at its apex, and reaches to the level of the upper 1/3-1/4 of the nectosac. The inferior definitive nectophore (3-5mm in height) is strongly reduced. It is narrow, somewhat curved at the base of the subumbrella, almost cylindrical in shape, with a very narrow opening. The shallow hydroecium of this nectophore is organised as two lobes is most obvious as an expansion in the apical part (Fig.134, Е, Ж).

Eudoxid: Bract (5-10mm long), helmet shaped (Fig.136). Phyllocyst present as a large vesicle with two branches. One is short, going up, and the other long, going down. A yellow gastrozooid with a tentacle, and a cylindrical gonophore comprise the remaining elements of the eudoxid.
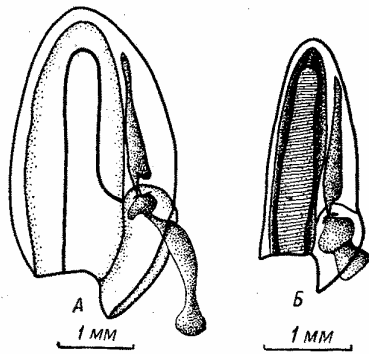


Fig. 135. Young definitive nectophore of *Dimophyes arctica* Chun
А – nectophore, with walls of nectosac deprived of musculature. Б – nectophore, with walls of nectosac with powerful musculature.
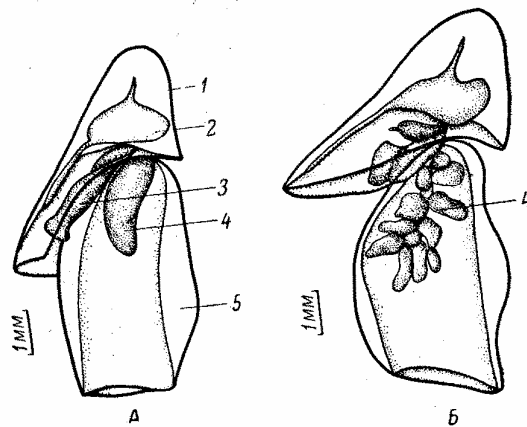
Fig. 136. Eudoxids of *Dimophyes arctica* (Chun)
А. – with androphore; Б – with gynophore. 1. – bract; 2. – phyllocyst; 3. – gastrozooid; 4. – manubrium; 5. – gonophore.

Distribution: Western coastlines of Greenland Sea, Barents Sea, area around Spitzbergen, Kara Sea, [?] Sea, northern parts of the Chuchki Sea and Arctic Basin, Bering, Okhotsk and Japan Seas, central and north-eastern parts of the Pacific Ocean, southern coast of Japan (several occurrences), North Atlantic, North Sea, in region of Straits of Gibraltar, south Atlantic (between 30°N and 30°S) (separate occurrences), Indian Ocean (south-east coast of Africa, S.E. part of Indian Ocean, around Kerguelen and Antarctic coasts, Davis Strait).

Eurythermal Species: The range of temperatures between which specimens of *D. arctica* have been found lies between -1 and 22°C (Totton, 1954), but here there is also a singular occurrence in an horizon with an unusually high temperature. To judge from the literature most occurrences are for a range of -1 to 6°C, and not higher than 12°C (Bigelow and Sears, 1937). In the basic survey of material from the central Polar Basin, Far Eastern Sea and northern part of the Pacific Ocean it is possible to infer that the optimal conditions suitable for the life and reproduction of *D. arctica* are a salinity of 33.5-35‰ and a temperature between 1.5 and 10°C, which can be found in different parts of the World at different seasons and at certain depths. The discovery that eudoxids with mature gonophores (Fig.136) were limited to the 200-400m depth zone in the Kara Sea, speaks loudly that the temperature of 2.5°C found there is that most suitable for the reproduction of *D. arctica*. However, regarding the eurythermal nectophores, *D. arctica* prefers relatively low temperatures, as is necessary for its reproduction. Evidently, therefore, in the Mediterranean Sea, where this particular layer of water is greatly warmed, *D. arctica* cannot live.

Our survey material of *D. arctica* is still available in the collections of the ZEN AN SSSR. The measurements, not so far given, regarding the morphology of the superior nectophores from the central Polar Basin and the Pacific Ocean are given in Table 7. Further studies of the complete material from the indicated areas, possibly will permit the distinction of two forms of *D. arctica*.

Comparison of size of nectophores and its parts of *Dimophyes arctica* from the Arctic Basin and Pacific Ocean.

| Region | Length of nectophore mm | Broadest width of nectophore mm | Diameter of opening of subumbrella mm | Height of somatocyst mm | Ventral bulge on somatocyst | Height of nectosac mm | Height of hydroecium mm | Height of nectosac at end of somatocyst | Free part of hydroecium mm |
|---|---|---|---|---|---|---|---|---|---|
| Japan Sea | 8-10 | 3-6 | 1.1-1.7 | 4.4-5.2 | + | 7.4-8.8 | 2.0-3.3 | ¾ | 1.0-1.8 |
| Pacific Ocean and Okhotsk & Bering Seas | 8-10.5 | 4-5 | 1.0-1.9 | 4.6-5.0 | + | 7.6-8.6 | 2.0-2.8 | ¾ | 1.3-1.8 |
| Kara Sea | 8-10 | 4-5 | 1.0-1.9 | 4.2-4.6 | + | 7.5-8.3 | 2.2-2.7 | ⅔-¾ | 1.5-1.8 |