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Edited by Doris M. Kermack and R. S. K. Barnes

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No. 29

SIPHONOPHORES AND VELELLIDS

Keys and notes for the identification of the species

P. A. KIRKPATRICK and P. R. PUGH

Institute of Oceanographic Sciences, Wormley, Surrey, UK



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A Synopsis of the Siphonophores and Velellids

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FOREWORD

To all except marine biologists, the well-known Portuguese man-o'war *Physalia* is likely to be regarded as the only British siphonophore. This is doubly unfortunate because *Physalia* is not a regular member of the British fauna and neither is it typical of the Siphonophora in general as it straddles the air/water interface (i.e. is pleustonic). Most of the fragile, beautiful and anatomically complex siphonophores are members of the plankton, seldom seen as complete organisms but nearly always as transparent fragments in plankton samples.

Included in this field-guide along with the 56 species of siphonophores is the only British "chondrophore", the 'Jack Sail-by-the-Wind' (*Velella*)—another member of the pleuston blown occasionally to our shores. Once considered to be related to the siphonophores, it has long been recognised as a somewhat parallel branch of the hydrozoan cnidarians with only a superficial resemblance to the Siphonophora.

These two groups can claim to be morphologically the most complex, specialized and polymorphic of cnidarians. Each colonial siphonophore, for example, may comprise genetically identical but structurally distinct polyps serving feeding, protective and reproductive roles and medusoid 'individuals' acting as the 'organs' of locomotion and/or buoyancy and as bracts.

We thank the authors of this *Synopsis* for the lucid manner in which they have succeeded in introducing these animals to a wider audience and for the elegance of their illustrations which capture the elusive beauty of the siphonophores.

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London

SIPHONOPHORES: ORDER SIPHONOPHORA

Introduction

Despite their inclusion together in this *Synopsis*, it should be emphasized from the outset that the siphonophores and velellids are very distinct taxa within the Class Hydrozoa, Phylum Coelenterata (Cnidaria). The velellids

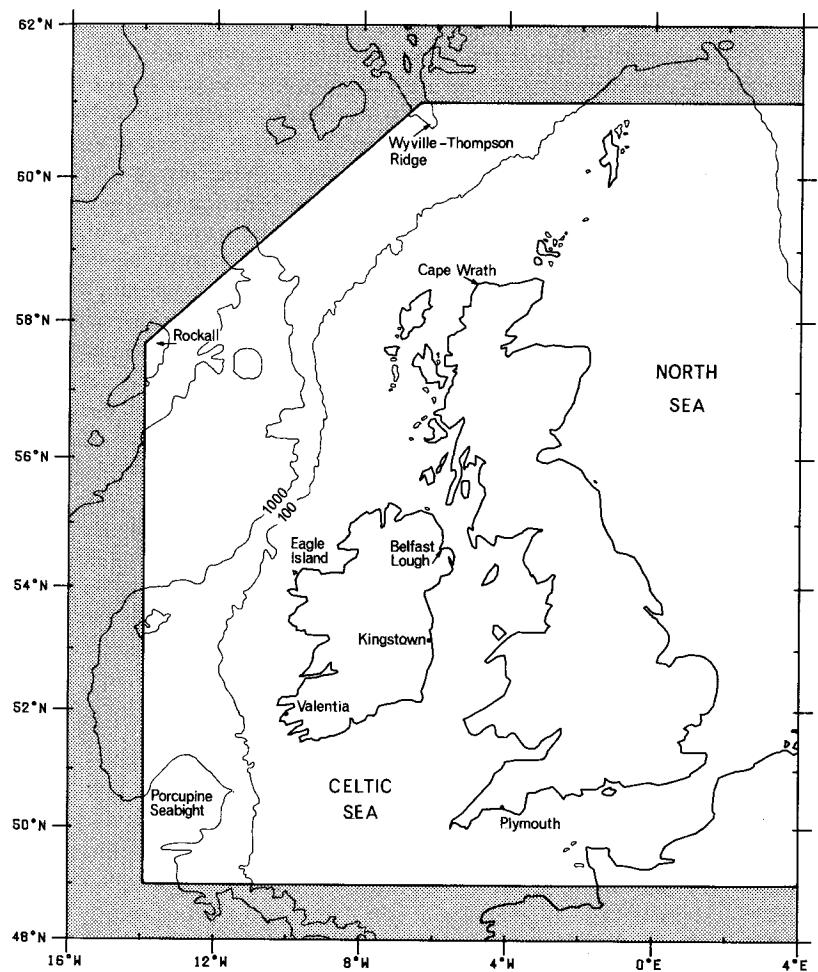


Fig. 1. Area covered by this *Synopsis* (depth in fathoms).

are included here purely as a matter of convenience since there is only a single British species, the easily recognized, pleustonic animal, *Velella velella* (Linné, 1758), commonly known as 'Jack Sail-by-the-Wind'. This species will be dealt with in a separate section towards the end of this *Synopsis*. Nonetheless the true taxonomic position of these two groups has been established only recently and in many of the classical works in these fields the velellids have tended to be included under the general heading of siphonophores, despite the fact that there are few similarities in the morphology of the two groups.

Siphonophores are highly polymorphic animals and are readily distinguishable from the medusoid, free-swimming stages of other hydrozoans; these latter medusae usually have a simple, radially symmetrical, umbrella-like form. Siphonophores are also entirely marine organisms and, with a few exceptions, appear not to be able to tolerate waters whose salinity is reduced much below 33–34%. Their presence in shallow British waters is thus due largely to the occasional intrusion of oceanic water onto the shelf or, in the case of the most famous siphonophore, the surface dwelling or pleustonic Portuguese Man O'War, to the prevailing winds resulting in the animals becoming stranded on beaches.

Approximately 150 species of siphonophores currently are recognized and 55 of these have been found in British waters. For the purpose of this *Synopsis*, British waters are chosen to be those within the area shown in Fig. 1. As can be seen this area includes not only the shelf waters but also some deeper water in the Rockall Trough and Porcupine Seabight.

General Structure

The fully developed siphonophore has a polymorphic organization, with many types of structure present, each of which has a different function. A unique terminology for these structures has evolved and it will be necessary to describe the morphology of the siphonophores in some detail in order to encompass those terms which are used most frequently in this *Synopsis*. Basically siphonophores, like all coelenterates, consist of two cell layers, the outer **ectoderm** and the inner **endoderm**, the latter forming the lining to the **gastro-vascular cavity**. These two layers are separated by a more or less thickened amorphous layer, the **mesogloea**. Unlike most other hydrozoan coelenterates, the siphonophores do not have an alternation of generations consisting of an attached polypoid stage and a free-swimming medusa, but derivatives of both stages are found attached to the stem of the free-floating animal.

The Order Siphonophora is divided into three Sub-orders on the basis of the presence or absence of either an apical, gas-filled float, the **pneumatophore** (Fig. 2A), or of swimming bells, **nectophores**, which are grouped together, towards the apex of the animal, to form a region called the **nectosome** (Fig. 2A). Thus the animals in the sub-order Cystonectae possess only the pneumatophore; the Physonectae possess both a nectosome and the pneumatophore; while the Calycophorae only develop a nectosome.

Pneumatophore. This is usually a small apical structure which is formed, during development, by an invagination at the aboral end of the larva, so that its cavity is lined by ectodermal cells. At the base of the pneumatophoral cavity, there is a specialized layer of secondary ectoderm, the **gas-gland** or **pneumadenia** (Fig. 2A) which secretes a gas, probably carbon monoxide, to inflate the cavity. The pneumadenia is usually quite small but in the surface-dwelling cystonect, the Portuguese Man O'War (Fig. 5) and species of the physonect family Rhodaliidae it is greatly enlarged. In the latter family the gas secreting area is extremely well developed and protrudes out onto the dorsal side of the pneumatophore to form a characteristic structure, the **aurophore** (Fig. 13A).

Most siphonophores possess a long stem on which are borne the various types of appendage which are organized down the stem such that two distinct regions (only one in cystonect siphonophores) can be recognized. The nectosomal region (Fig. 2A) is situated at the aboral end of the animal, i.e. just below the pneumatophore in the physonects. It bears, with one exception, only asexual, medusoid nectophores (swimming bells) whose

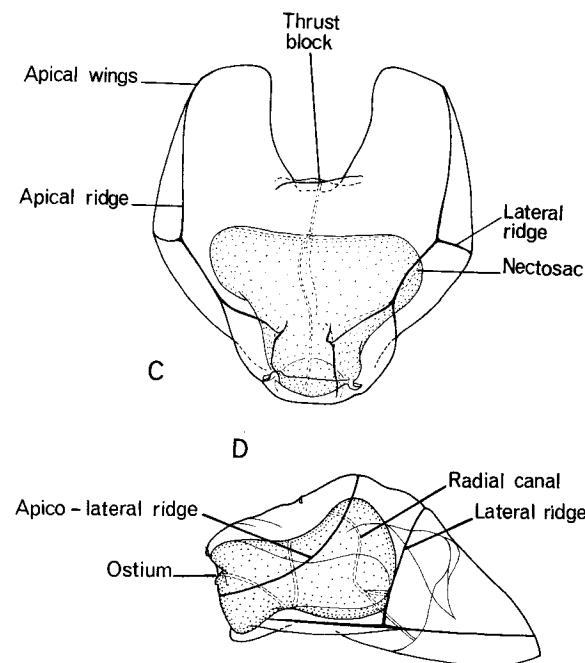
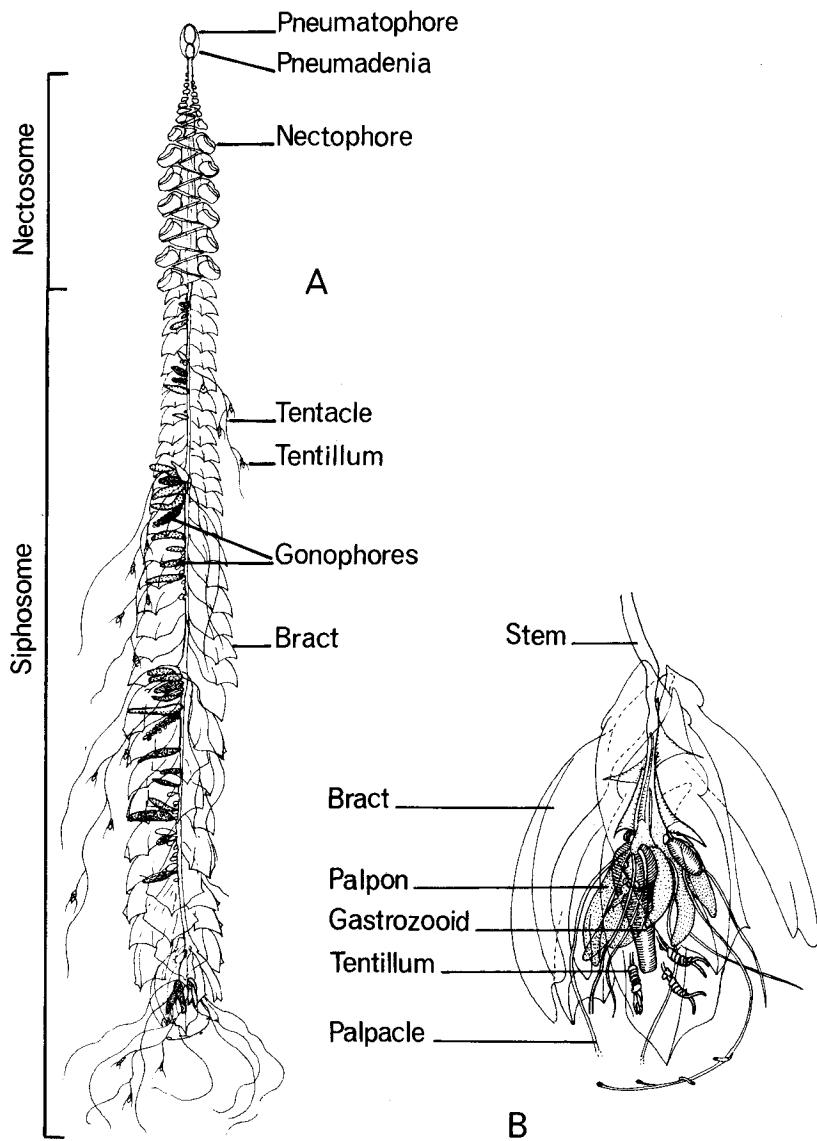


Fig. 2. General structure of a physonect siphonophore, *Agalma elegans*. A, whole animal. B, distal part of siphosome. C, nectophore (upper view) D, nectophore (lateral view). (All after Totton, 1965.)

function basically is jet propulsive locomotion but, when a large quantity of mesogloea is present within them, they also give buoyancy to the animal as a whole. Below, or orally to, the nectosome, lies the **siphosome** (Fig. 2A), a region which usually makes up the majority of the animal's length. Its stem, which is a simple tube surrounding the main gastrovascular canal, has both polypoid and medusoid structures attached to it in an orderly fashion. The fully-developed and complete animal is referred to as the **polygastric** stage as it carries numerous **gastrozooids** or feeding and digestive polyps (Fig. 2B). This polygastric stage is, according to Totton (1965), an overgrown larva which remains juvenile and asexual, but on which the true sexual medusoids are developed.

Many different terms have been applied in the past to the various organs of the siphonophores and the literature often is confused. Such confusions extend to the orientation of the animal, obscuring which part should be considered dorsal, which ventral and which anterior, which posterior. We will follow the terminology adopted by Totton (1932), who designated the ventral side as the **axial** one and thus the dorsal as the **abaxial**, or that which is farthest from the stem. The **apical** or anterior side is that which is directed

towards the aboral end of the animal, the end furthest from the oldest (larval) gastrozooid, this being the terminal, basal gastrozooid on the siphosomal stem (Fig. 2B).

Nectosome. The morphology of the nectophore is an important taxonomic character particularly as, due to the fragility of the animal as a whole, the nectophore is often the only part on which studies can be made. In the physonects, e.g. in Fig. 2C,D, the characters which are of particular taxonomic importance are:

- (a) the arrangement of the **lateral ridges**;
- (b) the course of the **radial canals** on the **nectosac**, the latter representing the sub-umbrella cavity of the original medusoid. Contractions of the muscular wall of the nectosac expel water through the basal opening or **ostium** and enable the animals to move about by this jet propulsive means.
- (c) The shape of the apico-lateral processes, or **apical wings**, which extend around the main nectosomal stem and interlock with other nectophores; and
- (d) The relative size of the **thrust block**, the region which abuts against the main nectosomal stem.

In the calycocephoran siphonophores, the nectophores are often more specialized, and their structure can vary greatly from one species to another. It is difficult, therefore, to illustrate a typical nectophore but two examples are given in Fig. 3.

1. The nectophore in Fig. 3A is a simple rounded structure that contains large volumes of mesogloea, giving buoyancy to the animal. In this type of nectophore, the nectosac usually is small and thus the animals are slow moving. The number of nectophores present, in the polygastric stage, is specifically variable, ranging from one to fifteen or more, but generally they are all of similar design.

All the nectophores possess, to a greater or lesser extent, a gutter-like furrow, the **hydroecium** (Fig. 3A,B), on their ventral side. The siphosomal stem is attached within this hydroecium which serves to protect the siphosomal budding zone. The stem itself can be withdrawn, partially or wholly, into the hydroecium both for protection and to streamline the body during locomotion. Along the dorsal surface of the hydroecium runs the **somatocyst** (Fig. 3A), which is probably a caecal extension of the original, larval gastrovascular cavity. It is the organization of the somatocyst, together with the general structure of the nectophore, which is of taxonomic importance. Basically, as is seen in the larval nectophores (see p. 54, 71), the somatocyst is a simple tube which is connected, via a **pallial canal** (Fig. 3A) to the radial canals on the nectosac. The larval nectophores usually are replaced by more-complexly structured definitive nectophores in the fully developed polygastric animal. In most definitive nectophores the somatocyst develops a basal extension beyond the point of origin of the pallial canal, called the **descending branch** (Fig. 3A). In some species an apical **ascending branch** also

is developed and this penetrates the mesoglea of the nectophore and can be complexly branched or simply terminated by a swelling (Fig. 20, 21A).

2. These calycocephoran siphonophores whose nectophores are streamlined (Fig. 3B), usually are active and rapid swimmers. In these species generally only one or two nectophores are present at any one time. One of these nectophores may be the larval one but more often this is detached during development and a definitive one replaces it. In either case, the first nectophore is apical in position and is referred to as the **anterior nectophore** (Fig. 3B). The second nectophore, if present, has a different structure and is attached behind the anterior one, being referred to as the **posterior nectophore** (Fig. 3B).

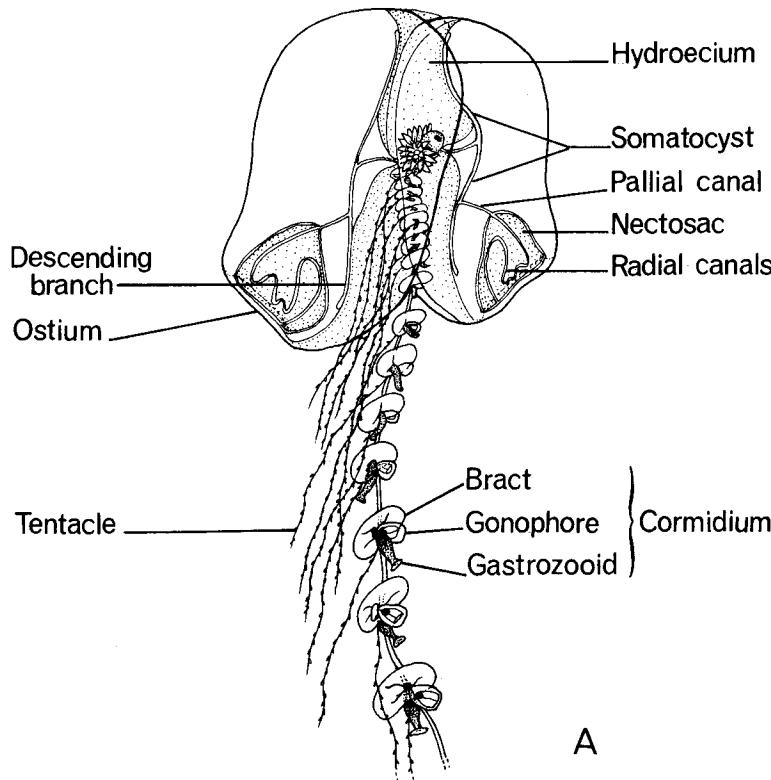
The morphological characters of importance for the specific identification of these nectophores, in particular the anterior one, are:

- (a) The pattern and number of longitudinal ridges, and, in the case of the genus *Lensia*, whether a transverse **velar ridge** (Fig. 35) is present.
- (b) the presence or absence of teeth around the ostial opening of the nectosac (e.g. Fig. 3B).
- (c) the shape of the somatocyst.
- (d) the shape of the **mouth plate** or **basal lamella** (Fig. 3B), which is a ventral process below the ostium of the nectosac; and
- (e) the angle at which the **basal facet** of the mouth plate is inclined relative to the main axis of the nectophore.

In addition, in the genus *Sulculeolaria*, the presence of **transverse commissures** (Fig. 3B) or **commissural canals** connecting the lateral radial canals to the ventral canals on the nectosac, is of taxonomic importance.

Siphosome. The siphosome generally is much longer than the nectosome and in some physonect species it can extend to many metres. The siphosomal stem bears a variety of structures, both polypoid and medusoid in origin, which have different functions. In general, representatives of each structure are grouped together in various proportions to form a **cormidium** (Fig. 3A), and the cormidia are arranged linearly down the stem. Each cormidium consists of a single gastrozooid to which is attached a **tentacle** (Fig. 3A). The tentacle is a long, highly contractile tube which often bears a number of side branches or **tentilla**, (Fig. 2B, 3B) which are powerfully armoured with **nematocysts**. The structure of the tentillum can aid in identifying some species. It may be a simple filament (unicornate) or bear a number of terminal filaments, as in the genus *Agalma*, where there are three (tricornuate). The nematocysts are used to capture prey and when discharged they may function in various ways; some penetrate the prey, injecting toxin, while others lasso and ensnare it. The nematocysts are widely distributed on other siphosomal structures but all appear to be developed in a specialized region of the gastrozooid.

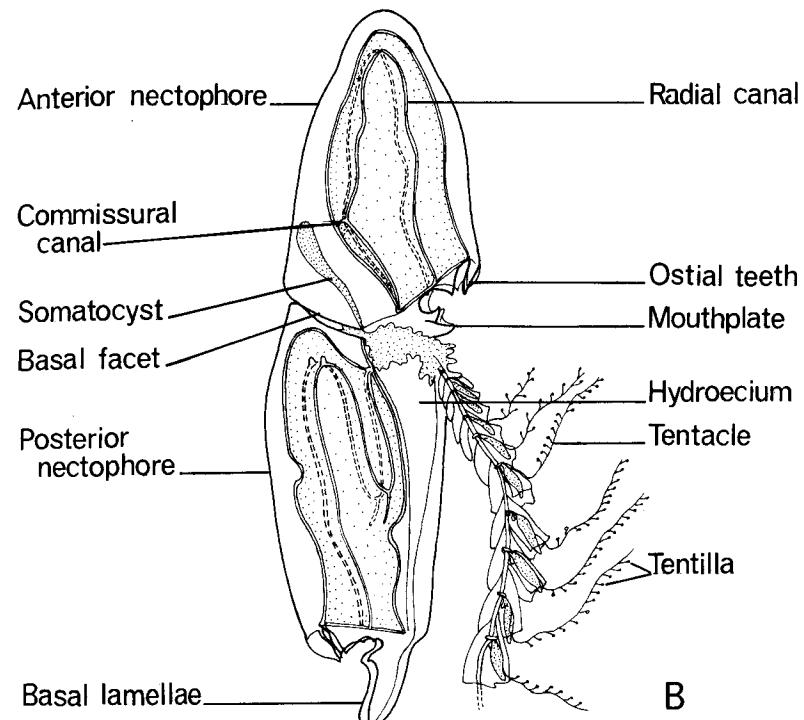
The cormidia of physonect siphonophores may contain also a number of **palpons** (Fig. 2B), which are thought to be reduced gastrozooids and, indeed,



A

may carry a small tentacle or **palpacle**. Palpons may have a sensory function and/or be used to accumulate and dispose of the animal's excretory products. They usually are attached directly to the siphosomal stem but a specialized type, the **gonopalpon**, is budded off from a **gonodendron**. The gonodendron itself originally may have been a palpon (see Totton, 1965), and it is to the gonodendron that the medusoid structures are attached. These structures can be either fully functional or reduced sexual **gonophores** (Fig. 2A), on the manubrium of which the sexual products are developed, or they may be asexual nectophores which lack a manubrium. The latter are found only on cystonect and a few calycophoran siphonophores, and may have a propulsive function.

Another cormidial element is the **bract** (Fig. 3A). Bracts are absent in cystonect siphonophores, while in the physonects they are usually leaf-like structures with a simple bracteal canal. In the calycophores the bract often is more complexly organized and forms part of the **eudoxid** or sexual stage, as described below. The bracts have a general protective function as they overlie the other cormidial elements, but, where large volumes of mesogloea are present, they can also play an important role in floatation.



B

Fig. 3. General structure of two calycophoran siphonophores. A, *Rosacea cymbiformis*: whole polygastric phase. B, *Sulculeolaria quadrivalvis*: whole polygastric phase. (A, after Totton, 1965; B, after Carré, 1979.)

Eudoxid Stage. The eudoxid or sexual stage of the calycophoran siphonophores is, in effect, a detached cormidium, consisting of a single bract and gastrozooid, with sexual gonophores. The specific identification of this stage is often difficult but is based largely on the general shape of the bract and the pattern of its canals. The diphyid bract (Fig. 34C) is conical or helmet-shaped, with a basal process known as the **neck shield**. Its canals are reduced to a simple swelling, the **phyllocyst**. In contrast, the arrangement of the canals of the prayid eudoxid bracts can be complex although there is a basic pattern of six canals, comprised of two hydroecial, two longitudinal, a dorsal and a ventral. Often the longitudinal canals, which run out in the direction of the axis of the stem of the polygastric phase, are reduced to **spur canals** (Fig. 21B), while a **central organ** or median swelling may be present at the junction of the main canals.

The eudoxid gonophores are variable in form but may bear ridges, which can be serrated or bear prominent basal teeth.

Biology

Life History

Little is known of the lifespan of an individual siphonophore, although some evidence seems to indicate that some species may live as long as ten or more years. The method of growth of these animals, in that there is a continued elongation of the siphosome, with the release, in the calycophores, of the sexual or eudoxid stage, also indicates an extended growth and reproductive period. Nonetheless, there are indications from the work of Moore (1949, 1953) that the abundance of certain siphonophore species varies seasonally, and that the actual period or periods of abundance differ between species. Further, a cyclical alternation in the preponderance of the polygastric and eudoxid stages was noted, again with the number of cycles per annum being specifically variable. Our own unpublished data for the more temperate regions of the North Atlantic Ocean indicate that there is a seasonality in the abundances of certain species but, as Bigelow and Sears (1937) earlier pointed out, one cannot always presume that these variations reflect true seasonal changes as there may be temporal changes in their depth distribution.

There is considerable specific variation in the reproductive cycle of siphonophores and it is difficult to provide a generalized account. As Totton (1965) points out, the fully grown siphonophore is an enlarged, larval nurse carrier (**his paedophore**) that itself does not become sexually mature but buds off the adult, medusoid gonophores. Individual animals usually bud off gonophores of both sexes (i.e. are monoecious), although not necessarily simultaneously. There are, however, a few species where each animal produces gonophores of the single sex (i.e. are dioecious).

In *Physalia physalis*, which is dioecious, it appears that the terminal parts of the gonodendra break off from the main body when all their gonophores have ripened. In physonect siphonophores it is the gonophore itself that usually is detached prior to release of the sexual products, while the gonophores of the calycophoran eudoxid remain attached, although the eudoxid itself is, of course, free-swimming. The female physonect gonophore contains only a single egg, while up to 30 eggs can be present in the calycophoran gonophore. In all cases fertilization is external and development proceeds rapidly to produce a planuloid larva. Only the post-larval developmental stages are known for *P. physalis* and these are described by Totton (1960). It is thought that the earlier stages may occur, as with *Velella velella* (see p. 142), in the depths of the oceans. As with this latter species it is

also not clear what determines whether the specimen will eventually become a right- or left-sailing form. In contrast there are now several studies on the development of physonect and calycophoran larvae. After gastrulation, an invagination appears at the apical pole of the physonect larva that represents the primordial pneumatophore. Later a ring of larval bracts is developed below this pneumatophore and the primary gastrozoid and tentacle appear. At this point the larva is said to have reached the **athorybia stage** (see Totton, 1965). Post-larval development results in the appearance of the definitive nectophores and the gradual elongation of the stem to form the typical polygastric animal with its linear cormidia. The development of the calycophoran larva basically differs from that of the physonect in that the apical pole is resorbed, rather than invaginated, and that a single larval nectophore is developed in place of the ring of larval bracts. This larval nectophore may be retained as the anterior nectophore in the polygastric stage or it may be replaced by a definitive one. The whole developmental period appears to last from two to three weeks. There are many exceptions to this generalized picture that cannot be considered here.

Feeding

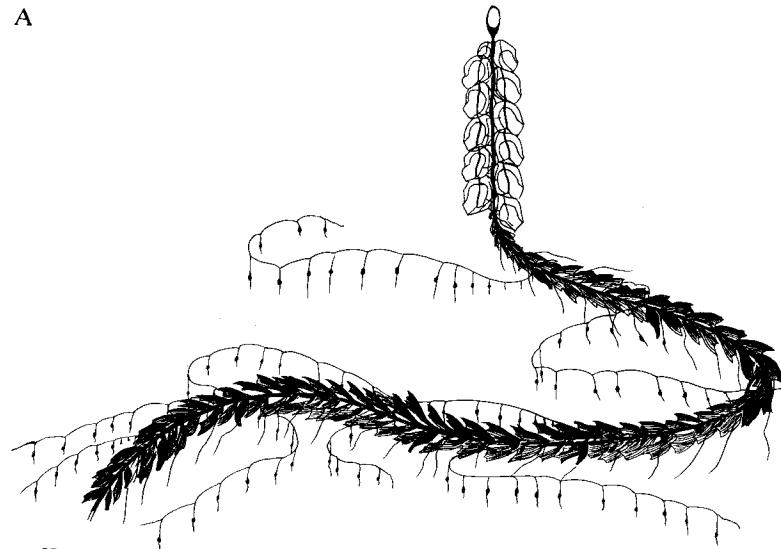
Siphonophores are carnivores, feeding chiefly on small crustaceans and larval fish and capturing their prey by means of batteries of nematocysts. These are borne on a variety of structures but particularly on the tentacles and their tentilla. The tentacles can be extended to considerable lengths relative to the size of the animal such that a small physonect, only a few centimetres long, can have a total tentacular length of 5 m or more (Mackie and Boag, 1963). An individual tentacle of the Portuguese Man O'War may reach 10–20 m in length.

Biggs (1977) has reviewed various capture methods. He suggests that the so-called fishing cycle consists of two basic phases; a fishing period, when the tentacles are spread out and the siphonophore waits for something to swim into its 'net', and a swimming phase. This latter phase is initiated either by a failure to make a capture within a certain time span or by the collapse of the tentacle 'net'. Swimming culminates in the redeployment of the fishing 'net'. The fishing posture adopted depends, for instance, on the ability to remain neutrally buoyant or on the degree to which the siphosomal stem itself can be extended. In many physonect species, the presence of large volumes of mesogloea in the bracts enables the siphosomal stem to be held horizontally or at an oblique angle, thereby preventing tentacle entanglement and allowing the 'net' to be spread more effectively (Fig. 4A). These animals may also use the palpacles of their palpons to help sense prey.

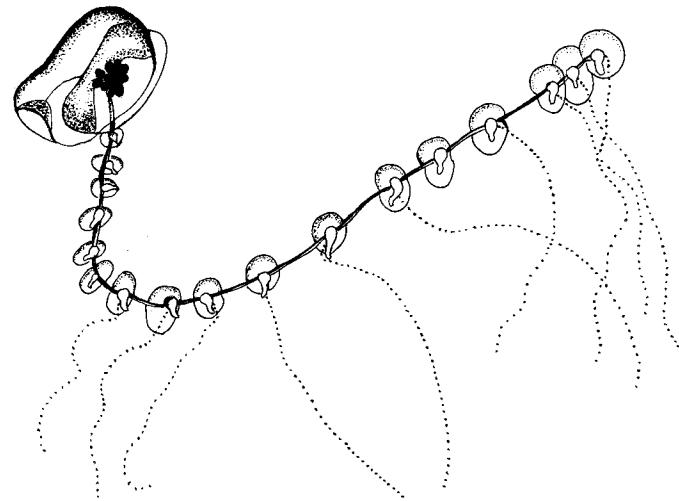
The greatest variety of fishing techniques is found amongst the calycophoran siphonophores, which have long, flexible stems. The slow-swimming forms, e.g. *Rosacea cymbiformis*, use an extended 'long-line' posture (Fig. 4B), while the active swimmers set complex 'nets'. Some use a **veronica**

movement (Mackie and Boag, 1963) that results in the tentacles spreading out from the stem, which is formed into a helix with two or three turns (Fig. 4C). Purcell (1980) suggests that additional fishing techniques can be used to increase the chances of prey capture. 'Squid-jigging' or periodic contractions of an individual tentillum, may be combined with mimicry, whereby the tentillum is organized as a lure to resemble, for instance, a copepod.

A



B



Purcell (1980, 1981a,b, 1982) has shown also that these various feeding strategies enable certain siphonophore species to be selective predators, e.g. *Hippopodius hippopus* feeds almost exclusively on ostracods.

Little is known about the role of siphonophores in the open-sea food chain. They do not represent a dead end in this chain for, despite their gelatinous nature, they are preyed upon by other organisms, particularly other gelatinous carnivores such as medusae, ctenophores and heteropods. Fish have been observed selectively to bite off the pigmented, and probably more nutritious, parts of the siphonophore stem. There is also a very interesting

C

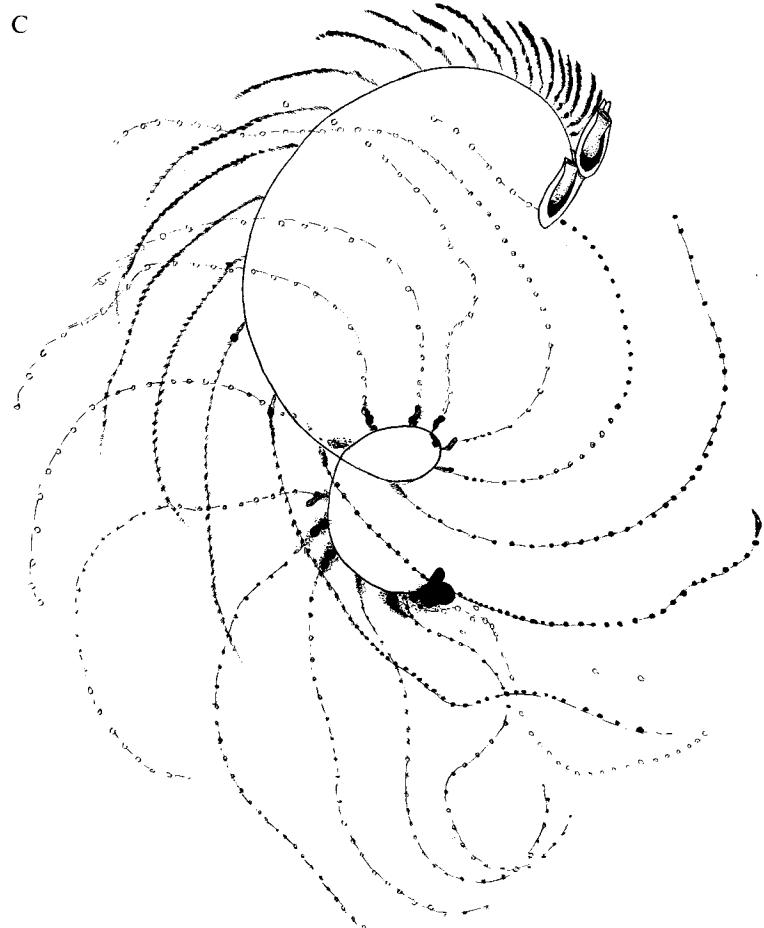


Fig. 4. A variety of fishing postures. A, *Nanomia cara*: horizontal or oblique 'net'. B, *Rosacea cymbiformis*: extended 'long-line'. C, *Sulculeolaria* sp: helical 'net'. (A, after Mackie, 1964; B, C, after Biggs, 1977.)

association between siphonophores (and indeed many other groups of gelatinous organisms), and hyperiid amphipods. Harbison, Biggs and Madin (1977) discuss in detail the associations, which sometimes are species specific, between these two groups of animals. The nature of the association can vary from simply phoresia, when the amphipod is carried about by the siphonophore, to total parasitism, particularly when a female lays her eggs on the siphonophore and the juvenile stages develop and gradually consume it.

General Ecology

All siphonophores, with the exception of the species in the families Physaliidae and Rhodaliidae, are permanently planktonic marine organisms. Representatives are present throughout the world's oceans but most species appear only rarely in inshore waters or regions where the salinity falls below approximately 33–34‰. Similarly, species diversity is reduced considerably in regions of high salinity and/or temperature, as in the Red Sea and neighbouring areas. However, a few species do appear to be largely coastal, occurring in shallow waters where the salinity is not greatly reduced. From the zoogeographical standpoint the distribution of the species can be roughly divided into boreal, tropical and equatorial categories (Margulis, 1973), but such a scheme belies the actual three-dimensional distributions. Thus, although some species clearly are restricted to the more superficial warmer waters, the deeper living, bathypelagic, species can exist at almost any latitude as the temperature at these depths does not vary greatly throughout. Some siphonophore species may have limited depth ranges, but species are present at all depths down to at least 4500 m.

The distribution of siphonophores in the warmer waters of the North Atlantic Ocean was discussed by Pugh (1977). These studies indicated that the specific composition of a siphonophore population is influenced by the various water masses in the World's oceans. Thus the population in the North Atlantic Central Water can be distinguished from that in the South Atlantic Central Water. Many species of siphonophore undergo diel vertical migrations, which can extend over a depth range of 200–250 m. The factors which might initiate these migrations and the processes involved in them are discussed by Pugh (1977, 1983). Presumably these migrations are undertaken in order that the siphonophores can maintain themselves in regions of high prey density, since their prey often migrates to more superficial waters at night. Some of the physonect species, with pneumatophores, are known to be important contributors to the deep-scattering layers.

Collection, Preservation and Examination

Most of the specimens of siphonophores which have been collected have been caught in a variety of nets, ranging from simple surface dip-nets to sophisticated deep-water trawls. The careful use of dip-nets may result in some intact specimens of siphonophores being collected, but these can be overlooked easily because of their transparency. Most nets, however, abrade the fragile specimens and fragment them into their myriad component parts.

The best, and most exhilarating, way to collect the near-surface dwelling species is by SCUBA diving. The divers take down with them jars into which, with some practice, the siphonophores can be induced to swim. The methods involved are described by Hamner (1975), and it must be emphasized that such techniques should be used only by a team of experienced divers with full safety procedures in operation. *A lone diver should NOT undertake such collecting techniques.* These techniques also demand a high degree of clarity in the water, without which it would be impossible to see these transparent organisms. However, the ability to study undamaged specimens is a necessary prerequisite to an understanding of the beauty in the organization of these polymorphic animals. It is difficult to envisage a complete specimen from its scattered fragments.

The deeper-living siphonophores have to be collected by net hauls, unless one is fortunate enough to have access to a submersible with equipment designed to collect animals. It is assumed here that nets will be the usual method by which the siphonophores are collected by the reader and so this *Synopsis* is arranged as a guide to the identification of the pieces of an individual specimen, rather than the whole. Even if specimens are collected intact, odd pieces eventually will become detached and can be used for identification.

Preservation of intact specimens is a difficult task. The careful addition of a magnesium chloride solution, drop by drop, to the sea water in which the animal is swimming should eventually anaesthetise it in a relaxed condition. If this can be achieved, then a further dropwise addition of 10–20% formalin may enable the specimen to be preserved in this state. A gradual hardening of the stem will ensue, but at all times the specimen should be treated with great care.

The fragmented specimens can be transferred to a 5% formalin solution for fixing and preservation and a change of this solution after a few days is recommended. The specimens are best examined soon after preservation as, for instance, the nectophores tend to shrink and lose their rigidity which can hamper identification. The component parts of many species have character-

istic shapes and, with a practised eye, can be readily identified. However, identification is best achieved at low magnification, using a binocular microscope fitted with a dark-background device. If this device is not available a brief exposure to a stain, such as Borax Carmine or Steedman's Triple Stain, can help to show up the ridges on certain species, such as those of the genus *Lensia*.

Classification

Order SIPHONOPHORA

Suborder CYSTONECTAE

Family PHYSALIIDAE

Physalia physalis Linnaeus

Suborder PHYSONECTAE

Family APOLEMIIDAE

Apolemia uvaria Lesueur

Family AGALMIDAE

Agalma elegans (Sars)

Halistemma rubrum (Vogt)

Marrus orthocanna (Kramp)

Nanomia cara Agassiz

Bargmannia elongata Totton

Family PHYSOPHORIDAE

Physophora hydrostatica Forskål

Family RHODALIIDAE

Stephalia corona Haeckel

Family FORSKALIIDAE

Forskalia edwardsi Köllicker

Suborder CALYCOPHORAE

Family PRAYIDAE

Subfamily AMPHICARYONINAE

Amphicaryon acaule Chun

Maresearsia praeclara Totton

Subfamily PRAYINAE

Rosacea plicata *sensu* Bigelow

Rosacea cymbiformis (Chiaje)

Praya dubia (Quoy and Gaimard)

Prayoides intermedia Leloup

Desmophyes annectens Haeckel

Subfamily NECTOPYRAMIDINAE

Nectopyramis diomedae Bigelow

Nectopyramis thetis Bigelow

Nectopyramis spinosa Sears

Family HIPPOPODIIDAE

Hippopodius hippopus (Forskål)

Vogtia spinosa Keferstein and Ehlers

Vogtia pentacantha Köllicker

Vogtia serrata (Moser)

Vogtia glabra Bigelow

Family DIPHYIDAE

Subfamily SULCULEOLARIINAE

Sulculeolaria quadrivalvis Blainville

Sulculeolaria biloba (Sars)

Sulculeolaria turgida (Gegenbaur)

Subfamily DIPHYINAE

Lensia conoidea (Keferstein and Ehlers)

Lensia multicristata (Moser)

Lensia hotspur Totton

Lensia subtilis (Chun)

Lensia meteori (Leloup)

Lensia achilles Totton

Lensia lelouveteau Totton

Lensia fowleri (Bigelow)

Lensia havock Totton

Lensia exeter Totton

Lensia hostile Totton

Lensia grimaldi Leloup

Muggiae a kochi (Will)

Muggiae atlantica Cunningham

Dimophyes arctica (Chun)

Chelophyses appendiculata (Eschscholtz)

Eodoxoides spiralis (Bigelow)

Family CLAUSOPHYIDAE

Clausophyes ovata (Keferstein and Ehlers)

Clausophyes massiliiana Patriti

Chuniphyes multidentata Lens and van Riemsdijk

Crystallophyses amygdalina Moser

Heteropyramis maculata Moser

Thalassophyes crystallina Moser

Family SPHAERONECTIDAE

Sphaeronectes gracilis (Claus)

Family ABYLIIDAE

Subfamily ABYLINAE

Ceratocymba sagittata (Quoy and Gaimard)

Subfamily ABYLOPSINAЕ

Abylopsis tetragona (Otto)

Bassia bassensis (Quoy and Gaimard)

Enneagonum hyalinum Quoy and Gaimard

Systematic Part

The distinguishing features of the three siphonophore suborders have been discussed above. The Cystonectae is subdivided into two families, one of which contains a single surface-dwelling species, the Portuguese Man O'War, while the other has four wholly planktonic species with relatively small, vertical pneumatophores. The seven families of the suborder Physonectae are distinguished by a variety of characters, such as the presence or absence of tentacles on the nectosome or of an aurophore on the pneumatophore, the shape of the siphosome and the general structure and arrangement of the nectophores. Finally, the six calycophoran families are classified according to the number and structure of the nectophores and the organization of the somatocyst within these nectophores.

The classification used in this *Synopsis* is based almost entirely on Totton (1965). Totton's works and that of Bigelow (1911), for instance, have done much to sort out the previously highly confused taxonomy, rendering it unnecessary to list synonyms in this *Synopsis*.

Although a key to the British families of siphonophores is given below, and other keys are interspersed within the text, it should be noted that no concise key to the siphonophores can be entirely satisfactory due to the polymorphic nature of the animals and the fact that there are so many exceptions to the rule. Thus, for the present purpose, the keys will be concerned only with the most commonly observed components of the siphonophores.

Key to the British Families of Siphonophora

1. Pneumatophore present 2
Pneumatophore absent Suborder Calycophorae 7
2. Nectophores organized to form nectosome; usually numerous bracts present Suborder Physonectae 3
Nectosome absent; reduced nectophores present only on gondendra; pleustonic animal with enormous purplish pneumatophore Suborder Cystonectae Family Physaliidae (p. 26)
3. Tentacles present between nectophores on nectosome; nectophores deeply hollowed out axially Family Apolemidae (p. 28)
Nectosomal tentacles absent; nectophores not hollowed out axially 4

4. Nectosome and siphosome elongate forming a narrow stem 5
Nectosome and/or siphosome contracted or reduced
5. Nectophores bilaterally symmetrical in shape with squared or rounded apices and arranged biserially on nectosome
..... Family Agalmidae (p. 31)
Nectophores asymmetrical in shape and dorsoventrally flattened; multiserial arrangement on nectosome Family Forskaliidae (p. 46)
6. Nectosome and siphosome contracted to form a solid corm; with a large pneumatophore and an aurophore Family Rhodaliidae (p. 44)
Nectosome elongated; siphosome shortened to form a sac on which cormidia are arranged spirally; bracts absent but ring of much enlarged palpons Family Physophoridae (p. 42)
7. Four or less, commonly one or two, nectophores present; bracts present on siphosome 8
Up to 15+ closely applied nectophores present; bracts absent
..... Family Hippopodiidae (p. 71)
8. Rounded nectophores and eudoxid bracts 9
Nectophores pointed, toothed or of irregular shape 10
9. Nectophore with long, thin, often branched somatocyst and large, deep hydroecium Family Prayidae (p. 48)
Small fragile individual nectophore with a simple somatocyst and a narrow hydroecium Family Sphaeronectidae (p. 126)
10. Posterior nectophore with a somatocyst; anterior nectophore with extensive opening of hydroecium on ventral surface
..... Family Clausophyidae (p. 113)
Posterior nectophore without somatocyst; hydroecium of anterior nectophore with small basal opening 11
11. Conical, stream-lined anterior nectophore; posterior nectophore usually apically truncated and of similar size to or smaller than anterior one Family Diphyidae (p. 79)
Anterior nectophore angular with inflated somatocyst; posterior nectophore larger than anterior Family Abylidiae (p. 129)

Key to the Eudoxid Bracts of the British Calycophorae

1. Bracts smooth-walled and rounded 2
Bracts pointed or of irregular shape 3
2. Bracts large with 2 to 6 branches to the canal system
..... Family Prayidae (p. 48)
Bracts small and fragile; single bracteal canal
..... Family Sphaeronectidae (p. 126)

- 3. Phyllocyst enlarged; two branch canals extend into the neck shield
 - Family Clausophyidae (p. 113)
 - At most only one branch from phyllocyst extending into neck shield 4
- 4. Bracts conical in shape Family Diphyidae (p. 79)
 - Bracts angular in shape and rigid in structure ... Family Abylidiae (p. 129)

Suborder CYSTONECTAE

This suborder is represented by a single British species.

Family PHYSALIIDAE

Cystonect siphonophore with a horizontal pneumatophore. There is a single genus.

Genus *PHYSALIA* Lamarck, 1801

Monotypic genus for *P. physalis* (L), 1758

Physalia physalis (L), 1758
(Fig. 5)

This species is the only pleustonic siphonophore. It possesses a huge, asymmetric, bluish pneumatophore, up to 30 cm in length, which lies horizontally on the sea surface. The cormidial elements are attached on one side of the float, at its oral end. The tentacles can stretch out to many metres below the float and can inflict a painful sting on an unsuspecting bather. A longitudinal crest runs along the top of the float and can be raised to act as a sail. The effect of the wind on this sail is to move the left-handed specimens to the right of the wind direction and *vice versa* for the right-handed ones.

Although the 'Portuguese Man O'War' is the best known of all British siphonophores, it normally inhabits the tropical and sub-tropical regions of the World's oceans. There are, however, hundreds of records for strandings of the animals on the south west coasts of England, Wales and Ireland. Wilson (1947) has shown that such strandings particularly occur during periods of strong south-westerly and westerly winds, but are not necessarily indicators of the northward spreading of warmer Atlantic waters.

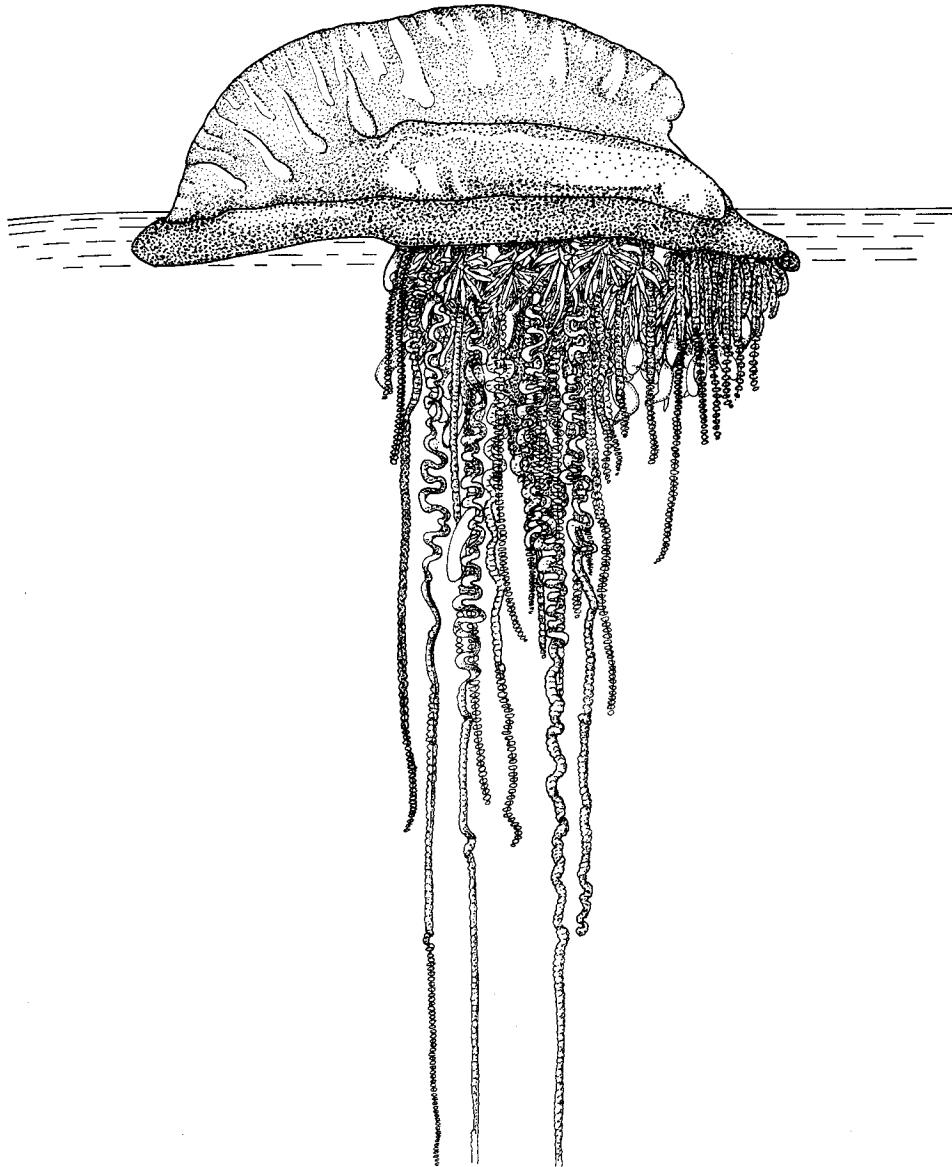


Fig. 5. *Physalia physalis*. (Portuguese Man O'War.) Whole animal (after Totton, 1965).

Suborder PHYSONECTAE

Siphonophores with an apical pneumatophore and, beneath it, a series of nectophores arranged to form a nectosomal region. Asexual nectophores are not present on the siphosome.

Family APOLEMIIDAE

The only physonect siphonophores whose nectophores are separated from each other by a cluster of 4–6 short nectosomal tentacles. The siphosomal tentacles are filiform, without tentilla.

Genus APOLEMIA Eschscholtz, 1829

Monotypic genus for *A. uvaria* (Lesueur, ?1811)

Apolemia uvaria (Lesueur, ?1811)

(Fig. 6)

Pneumatophore. Bulb-shaped, widest near its apex and often flecked maroon.

Nectophore. (Fig. 6A,B) 15–20 mm in size, resembling a half-walnut. The deep apical wings wrap around the base of the nectophore above. Large nectosac, often reddish-brown in colour, with strongly S-shaped lateral radial canals which occasionally bear short side branches.

Bracts. Flimsy, the younger ones being semi-circular in shape, bearing opaque patches of nematocysts on the surface.

The siphosome can extend to a length of 20 m or more and terminal cormidial groups can become detached to lead a separate existence.

Apolemia uvaria is well known from the Mediterranean Sea and there are several records from the Atlantic Ocean, although the systematics of the apolemidids is not well established. The British records are distributed widely, from the Celtic Sea and the South West Shelf edge to the northern part of the North Sea. The species occurs in the top 100 m of water but there are no records of its presence in shallow or less saline waters.

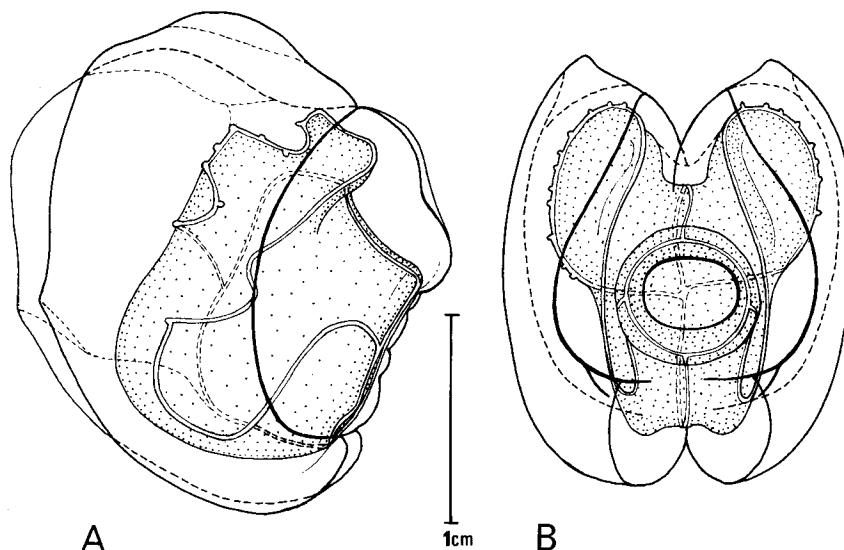


Fig. 6. *Apolemia uvaria*. A, B, nectophore (lateral and ostial views).

Family AGALMIDAE

Physonect siphonophores with a biserial arrangement of nectophores in the nectosome and a long, usually contractile, siphosome. It is a diverse family whose species show a wide variety of form. The exact systematic position of one species, *Bargmannia elongata*, Totton, 1954, is uncertain but we follow Stephanyants (1967) in including it as an agalmid.

Key to the British species of Agalmidae

(based mainly on the characters of the nectophores)

- | | |
|--|-----------------------------|
| <ol style="list-style-type: none"> 1. Nectosac with straight lateral radial canals..... | 2 |
| Nectosac with looped lateral radial canals | 3 |
|
 | |
| <ol style="list-style-type: none"> 2. Nectophore elongated, pointed apically, with narrow nectosac and lateral ridges (Fig. 11A) | Bargmannia elongata (p. 40) |
| Nectophore truncated with large, expanded nectosac; lateral ridges absent (Fig. 9A) | Marrus orthocanna (p. 36) |
|
 | |
| <ol style="list-style-type: none"> 3. Nectophore with two distinct lateral ridges | 4 |
| Nectophore with a single lateral ridge (Fig. 10) | Nanomia cara (p. 38) |
|
 | |
| <ol style="list-style-type: none"> 4. Nectophore with large thrust block and short lateral processes; tentilla unicornuate (Fig. 8) | Halistemma rubrum (p. 34) |
| Nectophore without distinct thrust block; with long lateral processes; tentilla tricornuate (Fig. 7) | Agalma elegans (p. 32) |

Genus AGALMA Eschscholtz, 1825

Agalmid siphonophores with tricornuate tentilla consisting of a central swelling and two, highly contractile, lateral filaments. There is a single British species.

Agalma elegans (Sars, 1846) Fewkes, 1880
(Fig. 2, 7)

Pneumatophore. Small, ovoid, usually with red-pigmented cap (Fig. 2).

Nectophore. (Fig. 7A) Up to 7 mm in length, with large truncated lateral processes which surround the nectosomal stem. Latero-vertical ridge runs perpendicularly up from the infra-lateral ridge and delimits a triangular facet on the outer side of each lateral process. Apico-lateral ridge divides from apical ridge and runs along side of nectophore in its distal half.

Bracts. (Fig. 7B) Thin and leaf-like, ending in three small projections.

The siphosomal stem is highly contractile. The post-larva, or *Athorybia* stage, bears 4–6 small, thick triangular larval bracts with serrated edges, below which is a single gastrozooid. It is usually less than 4 mm in length.

This is a cosmopolitan species in the World's oceans but records are infrequent. In British waters it has been found in the deeper, western waters, in the northern North Sea and in the western English Channel. Its presence in shallower waters probably is associated with the incursions of oceanic waters on to the Continental Shelf.

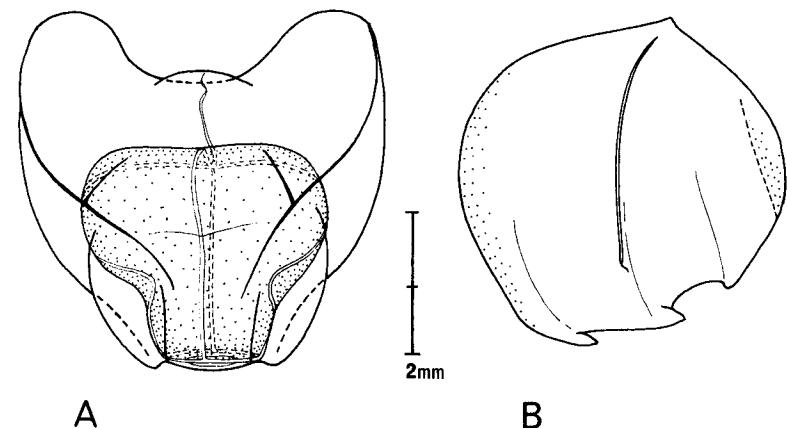


Fig. 7. *Agalma elegans*. A, nectophore (upper view). B, bract (after Totton, 1965).

Genus HALISTEMMA Huxley, 1859

Agalmid siphonophores with unicornuate tentilla, and with distinctively looped lateral radial canals on the nectosac of the nectophores. There is one British species.

Halistemma rubrum (Vogt, 1852)
(Fig. 8)

Stephanomia rubra Bigelow, 1911; Totton, 1954

Pneumatophore. Oval, 3–4 mm in height.

Nectophore. (Fig. 8A,B) Variable in shape, usually squared and rigid in appearance, up to 20 mm in height. Central thrust block usually larger than the lateral process. Two lateral ridges, often incomplete. The pattern of the looped lateral radial canals on the large nectosac is characteristic (Totton, 1954).

Bracts. (Fig. 8C) Thin and leaf-like, variable in shape but usually with two short lateral processes and a larger central one.

A widespread species in warmer waters. The only British records are from deep water in the Porcupine Seabight at depths between 10 and 1000 m.

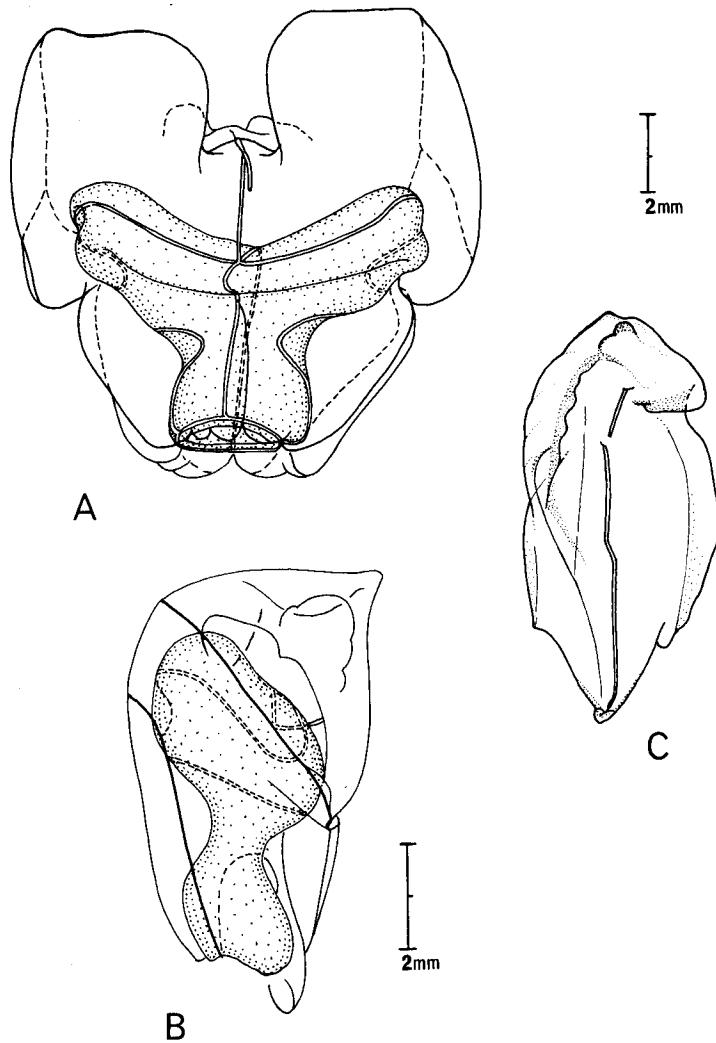


Fig. 8. *Halistemma rubrum*. A, B, nectophore (views from below and laterally).
C, bract (after Totton, 1954).

Genus MARRUS Totton, 1954

Agalmid siphonophores whose nectophores are truncated apically and whose nectosacs possess straight, unlooped lateral radial canals. The tentilla are unicornuate. There is a single British species.

Marrus orthocanna (Kramp, 1942)
(Fig. 9)

Pneumatophore. Parsnip-shaped.

Nectophore. (Fig. 9A) Longer than broad, up to 15 mm in length, with no distinct lateral ridges. The apical ridges divide close to the ostium and delimit two narrow, triangular distal facets. Thrust block well-developed and longer than the rounded lateral processes. Nectosac triangular.

Bract. (Fig. 9B) Roughly triangular with a flimsy, tacky appearance.

In general this is a rare high-arctic agalmid, in the Atlantic sector only, but it has been recorded also from the deeper waters west of Britain (our unpublished data). Fraser (1967) found it in the deep waters of the Rockall Trough at depths between 600 and 2000 m, and it is present also at 645–700 m in the Porcupine Seabight.

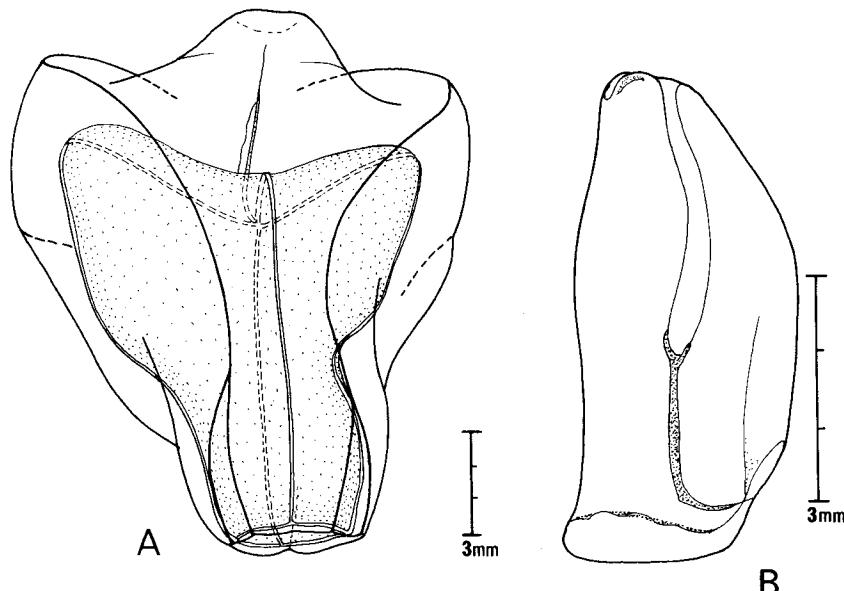


Fig. 9. *Marrus orthocanna*. A, nectophore (upper view). B, bract.

Genus NANOMIA Agassiz, 1865

Agalmid siphonophores whose male and female gonophores are arranged to form an alternating paired series down the siphosome at the base of the palpons. Tentillum unicornuate. There are two species, both of which have been said to occur in British waters although Totton (1954) points out that the literature is confused and probably only one species actually has been found. This conclusion is adhered to here.

Nanomia cara Agassiz, 1865
(Fig. 4A, 10)

Stephanomia cara Bigelow, 1911

Pneumatophore. Small, ovoid, with a red-pigmented cap and a short stalk.
Nectophore. (Fig. 10) Compact, up to 10 mm in length. A complete diagonal latero-ventral ridge divides the lateral surface into two distinct facets. The short apico-lateral ridge divides close to the ostium and appears as an extension of the apical ridge. Stout, obliquely truncated lateral processes are separated by a very small thrust block. Nectosac Y-shaped with lateral radial canals looping extensively in a characteristic manner.

Bract. Thin and leaf-like, of general agalmid form.

Almost exclusively a boreal North Atlantic species which Margulis (1978) described as transitional, occurring in the region between the North Atlantic current and the sub-Arctic circle. It is moderately common in the northern North Sea and other Scottish regions, and additional records come from the South West coast of Ireland, the Celtic Sea and the English Channel. Russell (1933) recorded exceptional numbers (under the name *Stephanomia bijuga*) in catches made off Plymouth in 1930.

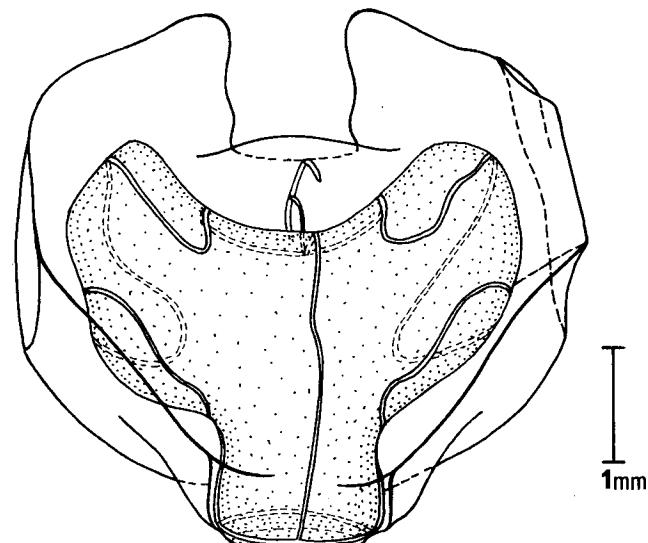


Fig. 10. *Nanomia cara*. Nectophore (upper view) (after Totton, 1965).

Genus BARGMANNIA Totton, 1954

The exact systematic position of this physonect genus is uncertain but we follow Stephanyants (1967) and include it within the Agalmidae. The genus is monotypic for *B. elongata* Totton, 1954.

Bargmannia elongata Totton, 1954
(Fig. 11)

Pneumatophore. Long, ovoid with central constriction, and borne on thin stalk.

Nectophore. (Fig. 11A,B) Elongated, reaching 25 mm in length, apically pointed, with a distinctive pattern of lateral ridges. Lateral processes short and central thrust block triangular. The long, narrow nectosac appears undulated in lateral view, and bears straight radial canals.

Bract. Broad and rounded, leaf-like, with many spots (?pigment) on the surface.

A well known species from the Atlantic, North Pacific and Indian Oceans, it generally is found in deep water between 300 and 600 m, or deeper, and so rarely appears in British waters. The only such records are from the Porcupine Seabight (our unpublished data).

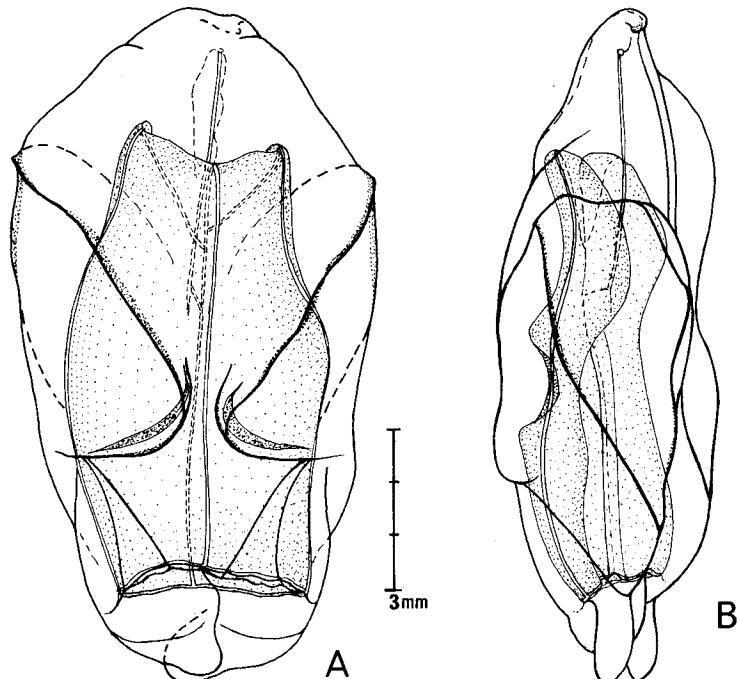


Fig. 11. *Bargmannia elongata*. A, B, nectophore (upper and lateral views).

Family PHYSOPHORIDAE

Physonect siphonophores with a laterally expanded siphosome forming a spiral sac on which the loosely packed, bractless cormidia are borne.

Genus PHYSOPHORA Forskål, 1775

Monotypic genus for *P. hydrostatica*. Forskål, 1775

Physophora hydrostatica Forskål, 1775

(Fig. 12)

Pneumatophore. Up to 5 mm in length with a deep red-pigmented cap.

Nectophore. (Fig. 12B) Up to 20 mm in height, flimsy, with no apparent ridges, and arranged in two rows, approximately 12 in each, down the nectosome. The part closest to the stem is hollowed out (compare *Apolemia uvaria*). Extensive Y-shaped nectosac has characteristically looped lateral radial canals; the dorsal and ventral canals are sinuous.

Siphosome. (Fig. 12C) Palpons greatly enlarged, covering and protecting the other cormidial elements on the bag-like siphosome. They are pinkish-blue in life, and possess long, fine palpacles.

A well known species from the World's oceans, commoner, in the Atlantic, in more temperate waters. There are several records from British waters in the Scottish Shelf region, from the Faroes to the northern North Sea. Jeal and West (1970) reported it from a rockpool on the west coast of Ireland.

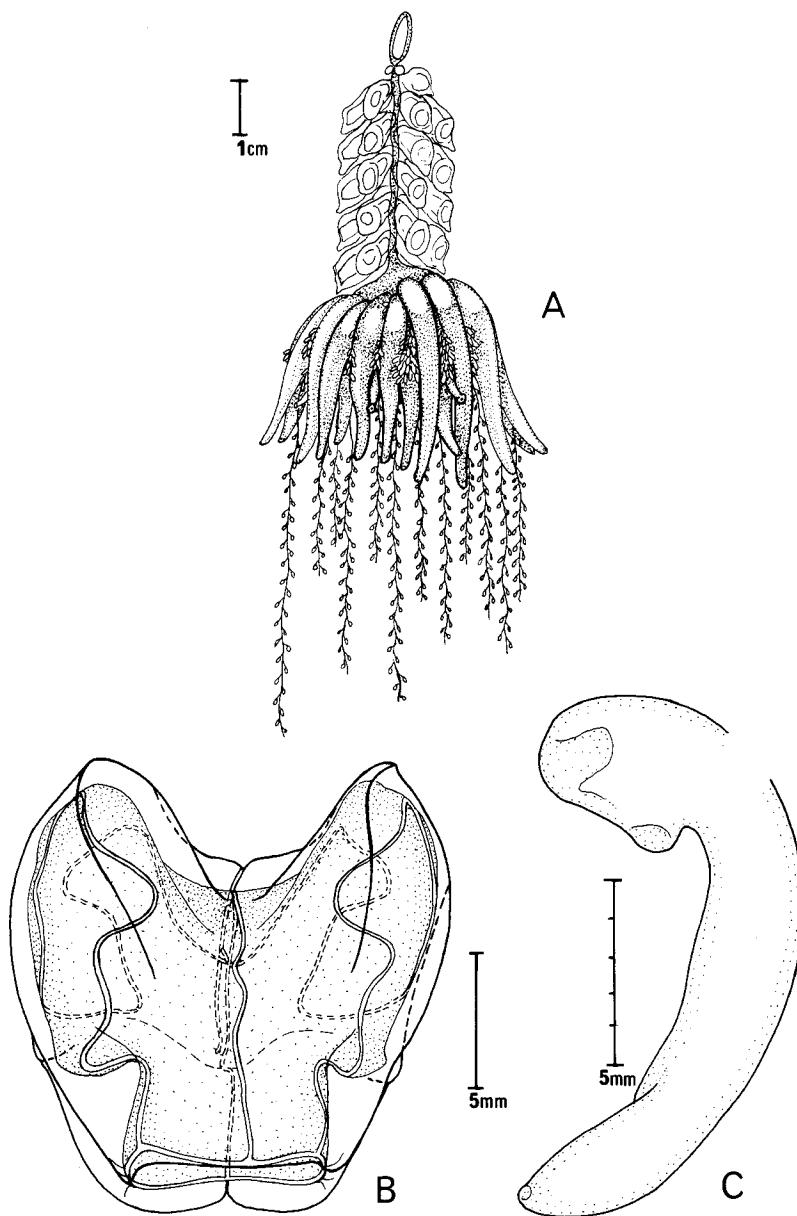


Fig. 12. *Physophora hydrostatica*. A, whole polygastric animal. B, nectophore (upper view). C, palpon.

Family RHODALIIDAE

A very unusual physonect family whose nectosome and siphosome are contracted to form a globular **corm** below the enlarged pneumatophore. The gas-secreting area is developed greatly to form a characteristic structure, the **aurophore**, extending from the baso-dorsal surface of the pneumatophore. The animals are benthic, attaching themselves to the sea-bed by their tentacles. The family recently has been reviewed by Pugh (1983).

Genus STEPHALIA Haeckel, 1888

Rhodaliid siphonophore with smooth-walled aurophore and pneumatophore. Cavity present within the nectosome, while solid siphosome includes an extensive network of gastrovascular canals, including a major canal system. One British species.

Stephalia corona Haeckel, 1888

(Fig. 13)

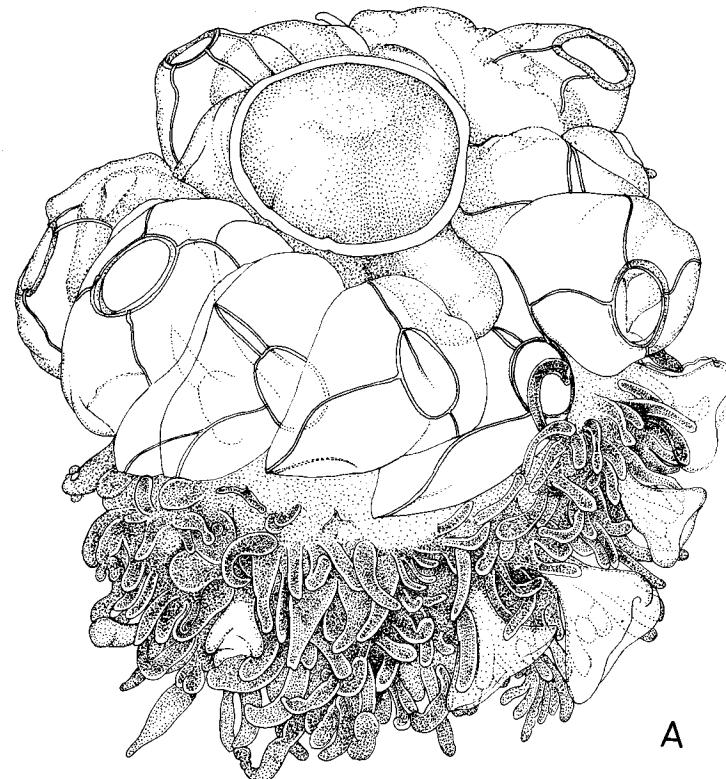
The specimens basically are spherical in form, measuring up to 25 mm or more in diameter (Fig. 13A). Most of the cormidial elements and nectophores are lost during collection.

Pneumatophore. 5–11 mm in diameter, orange-red in colour.

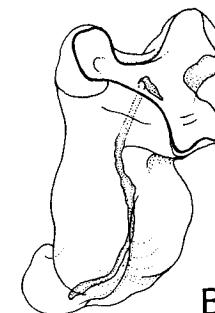
Nectosome. Narrow apical part, immediately below pneumatophore, contains a shallow cavity. Below, it broadens out on to the main body of the corm, whilst internally a series of chambers separated by septa are present. 8–22 flimsy nectophores, depending on size of specimen, with orange radial canals, form a corona under the pneumatophore.

Siphosome. A series of gelatinous protuberances, which bear up to four cormidia, are arranged in spiral whorls, generally two, around the periphery of the corm. Two types of gastrozooid are present, one with a reduced tentacle without tentilla; the other with a tentacle bearing tentilla. Characteristically shaped, trefoil-headed bracts are present (Fig. 13B).

The rhodaliids are a little known physonect family probably because of their benthic existence. *Stephalia corona* has been found at two localities, one off the coast of West Africa (Mauretania) and the other close to the Wyville-Thomson Ridge to the north west of Scotland. In the latter case the depth of collection was approximately 1000 m.



A



B

1mm

Fig. 13. *Stephalia corona*. A, whole animal. B, bract.

Family FORSKALIIDAE

Long-stemmed physonect siphonophores with numerous, multiserially arranged nectophores forming a cone-shaped or cylindrical nectosome. There is a single genus.

Genus FORSKALIA Köllicker, 1853

Only one British species.

Forskalia edwardsi Köllicker, 1853

(Fig. 14)

Pneumatophore. Ovate, sometimes with red-pigmented cap.

Nectophore. (Fig. 14A) Asymmetrical and dorsoventrally flattened, up to 10 mm in length. The domed nectosac, reaching to about two fifths of the nectophoral height, has straight radial canals.

Bract. (Fig. 14B) Variable in shape, being pyramidal, bolster-shaped, triangular in cross-section or knee-shaped with small, distal teeth.

Abundant in the Mediterranean Sea and known from all the oceans. The only records for British waters are from Belfast Lough and Kingstown Harbour, Ireland (under the name *Forskalia contorta*) (Stephens, 1904).

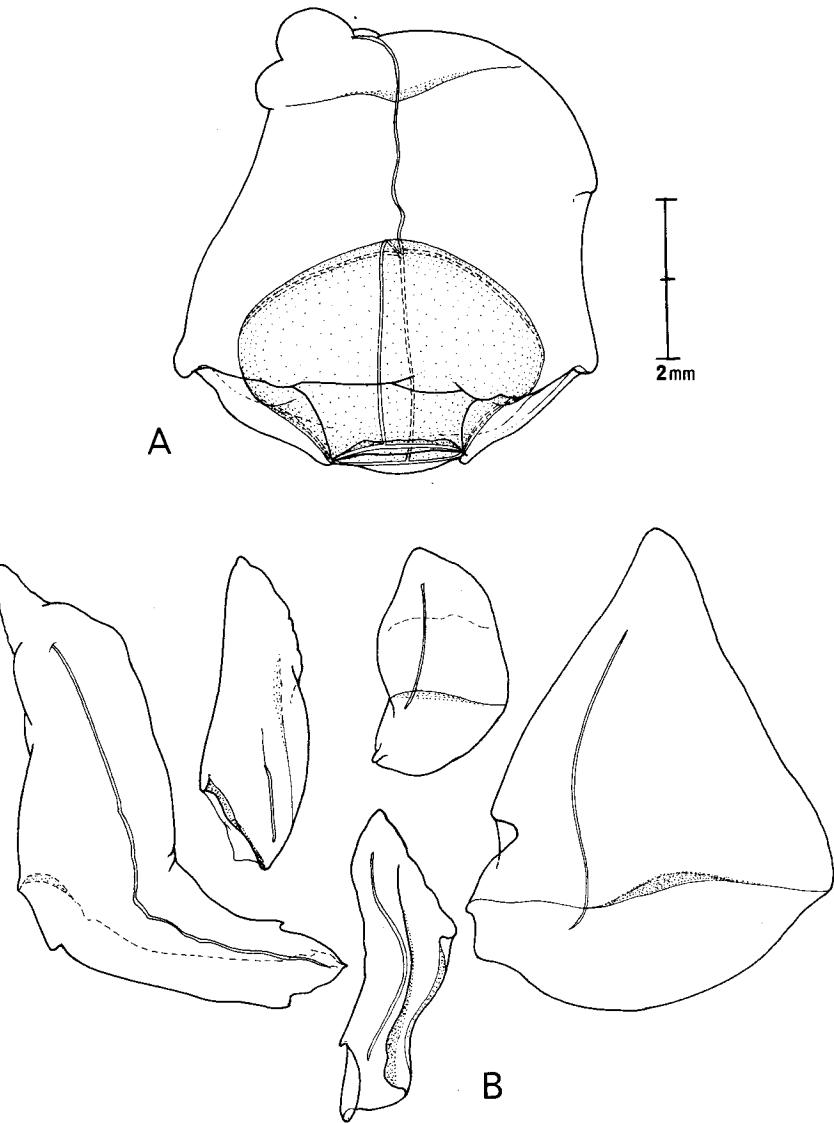


Fig. 14. *Forskalia edwardsi*. A, nectophore (upper view). B, various bracts.

Suborder CALYCOPHORAE

Siphonophores possessing nectosomal and, in some cases, siphosomal asexual nectophores, but an apical pneumatophore is absent. A single bract is developed on each cormidial unit, with the exception of the family Hippopodiidae where bracts are absent. Usually, the cormidial units are detached successively from the main siphosomal stem and become the free-swimming eudoxid, or sexual, stage.

Family PRAYIDAE

The nectophores are relatively large and usually rounded, containing large quantities of mesoglea. The larval nectophore sometimes is retained during the polygastric stage, or may be replaced by from one to four definitive nectophores, whose somatocysts are often complexly branched. The eudoxid bracts are rounded and unridged.

The following key to the British species is based mainly on the characters of the nectophores present in the polygastric stage. The eudoxid stages of the three prayid subfamilies are readily distinguished.

Key to the British species of Prayidae

1. 1–4 rounded nectophores present, with simple or complex somatocyst 2
A single nectophore present which bears ridges, angles or serrations; eudoxid bracts very similar in form to nectophore (Nectopyramidinae) 8
2. Two nectophores of different sizes present; eudoxid bracts very small with simple canals (Amphicaryoninae) 3
2–4 nectophores of similar size present; eudoxid bracts with 4 main and 2 reduced spur (longitudinal) canals (Prayinae) 4
3. Nectosac of smaller nectophore without external opening; lateral canals on nectosac of larger nectophore simple, with distinct right-angle bend (Fig. 15A) *Amphicaryon acaule* (p. 50)
Nectosac of smaller nectophore functional; lateral canals on nectosacs of both nectophores branched (Fig. 16A,B) *Maresearsia praeclara* (p. 52)
4. Somatocyst in nectophores simple and unbranched 5
Somatocyst in nectophores complexly branched (Fig. 19) *Praya dubia* (p. 58)
5. Lateral canals in nectosac sinuous; somatocyst without an ascending 'branch' 6
Lateral canals in nectosac either straight or complexly bifurcated; somatocyst with an ascending 'branch' which extends into mesogloea 7

6. Deep, gutter-like hydroecium running entire length of nectophore; dorsal canal of eudoxid bract arises proximal to spur on left hydroecial canal (Fig. 18) *Rosacea cymbiformis* (p. 56)
Hydroecium extends for up to 3/4 length of nectophore; nectosac is basal; dorsal canal of bract arises distal to spur on left hydroecial canal (Fig. 17) *Rosacea plicata* (p. 54)
7. Somatocyst of nectophore ends in an apical swelling; lateral canals on nectosac straight; eudoxid bract has swollen central organ (Fig. 21A,B) *Desmophyes annectens* (p. 62)
Ascending 'branch' of somatocyst simple; lateral canals on nectosac bifurcating; eudoxid stage unknown (Fig. 20) *Prayoides intermedia* (p. 60)
8. Nectophores with toothed ridges; somatocyst simple (Fig. 24)
..... *Nectopyramis spinosa* (p. 68)
Nectophores without distinct ridges; somatocyst divided 9
9. Branches of somatocyst bear several side branches; without a central organ and with a relatively small hydroecium (Fig. 22)
..... *Nectopyramis diomedae* (p. 64)
Branches of somatocyst without side branches; central organ present; hydroecium extensive (Fig. 23) *Nectopyramis thetis* (p. 66)

Genus AMPHICARYON Chun, 1888

Prayid siphonophores with two dissimilar nectophores; the larger, which is possibly the retained larval nectophore, partly encloses the reduced or vestigial (?) definitive nectophore. The nectosac of the latter does not have an external opening. The eudoxid bract has a pair of lateral hydroecial canals. There is a single British species.

Amphicaryon acaule Chun, 1888
(Fig. 15)

Nectophores. (Fig. 15A) The larger is ovoid, up to 10 mm in diameter; the partly enclosed vestigial is disc-shaped. The nectosacs of both possess four simple canals, and the lateral canals on the functional nectosac of the larger nectophore make a characteristic right-angled bend apically.

Eudoxid. (Fig. 15B) Small and thin, with two straight canals. It is folded to form a shield to the bell-shaped gonophores.

A common species in the World's oceans, most often encountered in warmer waters, but rarely found in the Mediterranean Sea. It has been recorded in the deeper waters to the west of Ireland, but the single known record for British waters comes from the region of the Wyville-Thomson ridge at a depth of 20 m (Fraser, 1961).

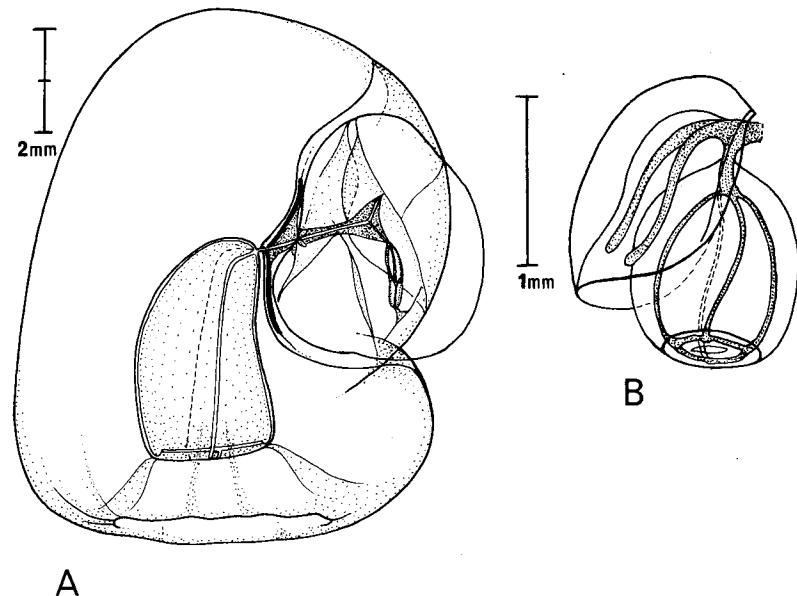


Fig. 15. *Amphicaryon acaule*. A, nectophores of polygastric stage. B, eudoxid stage (after Bigelow, 1911).

Genus MARESEARSIA Totton, 1954

Amphicaryonine siphonophores whose two large, but dissimilar nectophores possess functional nectosacs. There is a single British species.

Maresearsia praecleara Totton, 1954

(Fig. 16)

Nectophores. (Fig. 16A,B) The two nectophores together form a sphere, about 15–20 mm in diameter, with the larger partly enclosing the smaller. Both have flask-shaped nectosacs, whose radial canals are branched characteristically. The somatocyst of the smaller nectophore is tiny, lying over the stem attachment point, while that of the larger can be quite swollen.

Eudoxid. (Fig. 16C) Bract small and hemispherical with two narrow, recurved canals. The gonophores are bell-shaped.

There are few published records for this species, although our unpublished data indicate that it is widespread in the warmer waters of the North Atlantic Ocean, and occurs as far north as 53°N. The single record for British waters comes from the Porcupine Seabight at a depth of 700 m.

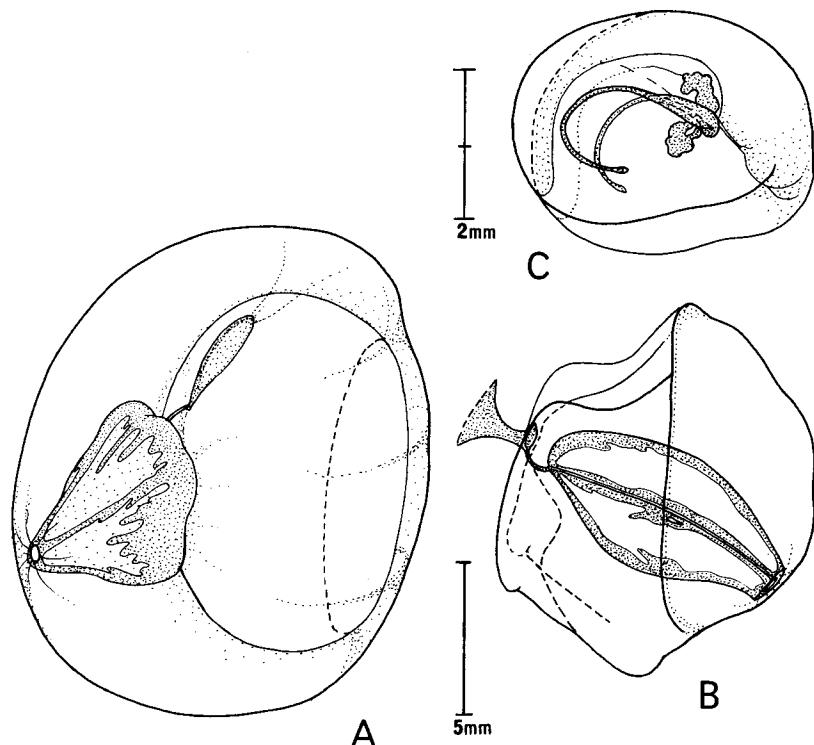


Fig. 16. *Maresearsia praecleara*. A, larger nectophore. B, smaller nectophore. C, eudoxid bract.

Genus ROSACEA *sensu* Bigelow, 1911

Polygastric phase usually with two unridged definitive nectophores, which have sinuous lateral radial canals on their nectosacs. Eudoxid bracts relatively large, with the basic prayine arrangement of canals. There has been much confusion in the past regarding the taxonomy of prayine siphonophores, and we follow Totton (1965) in using the generic name *Rosacea* in the sense which Bigelow (1911) applied to it. There are two British species.

Rosacea plicata *sensu* Bigelow, 1911
(Fig. 17)

Nectophore. The small, globular larval nectophore resembles that of the hippopodiids (see p. 71) except that its somatocyst is kinked and a central organ usually is present (see Totton, 1965). This nectophore is replaced by two elongated definitive nectophores (Fig. 17A), up to 30 mm in length, which contain large quantities of mesoglea. The hydroecium extends along approximately 3/4 of the ventral surface reaching neither apex nor base, and the simple somatocyst runs along the mid-line of the dorsal surface. The nectosac is basal.

Eudoxid. (Fig. 17B) Bract kidney-shaped and compact. The longitudinal bracteal canals are reduced to spurs, and the dorsal canal arises distal to the spur on the left hydroecial canal. The gonophores are simple and bell-shaped.

A well-known and common species throughout the World's oceans, but most commonly found in temperate waters in the 200–500 m depth range. There are many records of its presence in western British waters but it is not known to have penetrated into the English Channel or the North Sea.

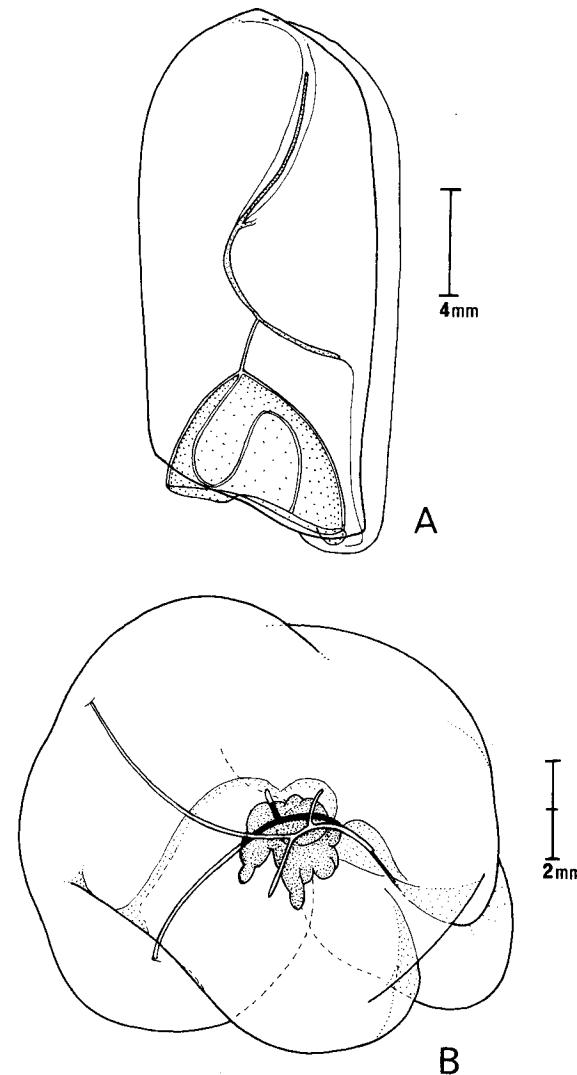


Fig. 17. *Rosacea plicata*. A, nectophore (lateral view). B, eudoxid bract (dorso-lateral view) (both partly after Totton, 1965).

Rosacea cymbiformis (Chiaje, 1822)
 (Fig. 3A, 4B, 18)

This species closely resembles *R. plicata* and it may be difficult to distinguish them.

Definitive nectophore. (Fig. 18A) Generally less rounded and slightly more flattened than those of *R. plicata*. The deep, gutter-like hydroecium extends the length of the ventral surface, resulting in the relatively small nectosac being displaced dorsally.

Eudoxid. (Fig. 18B) Bract less compact than that of *R. plicata*, with the dorsal bracteal canal arising proximal to the spur on the left hydroecial canal.

This species is known from the Mediterranean Sea and North Atlantic Ocean and probably is more common than records suggest, due to the identification difficulties. Specimens often have been caught by SCUBA divers close to the surface (G. R. Harbison, personal communication) indicating that it may be a shallower-living species than *R. plicata*. Fraser (1950, 1961) gives records for specimens caught off the coasts of Scotland.

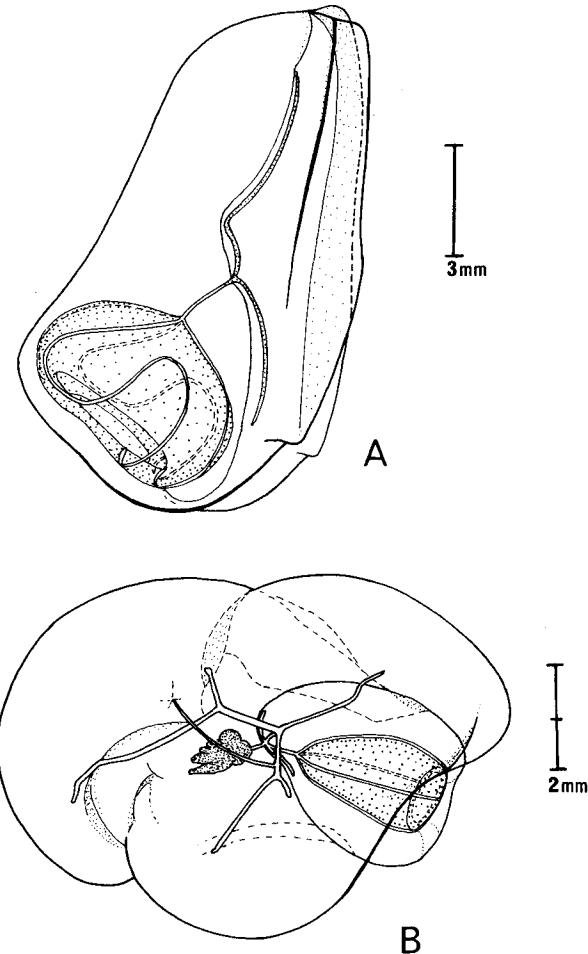


Fig. 18. *Rosacea cymbiformis*. A, nectophore (lateral view). B, eudoxid (dorsal view).

Genus PRAYA Quoy and Gaimard, in Blainville, 1834

Polygastric phase includes two large definitive nectophores and, frequently, one or two reserve bells. The somatocyst is divided complexly and the radial canals in the nectosac are branched. There is a single British species.

Praya dubia (Quoy and Gaimard (1833) 1834)
(Fig. 19)

Nectophore. (Fig. 19A,B) Both larval and definitive nectophores have bifurcating canals on their nectosacs, the larval otherwise resembling those of *Rosacea* spp. Definitives large, up to 100 mm in length, and cylindrical with a baso-ventral extension beneath the baso-dorsal opening of the nectosac. The groove-like hydroecium extends the full length of the ventral surface. The somatocyst divides apically into three branches: a simple dorsal canal and two long, branching laterals, which recurve and run down the sides of the nectophore.

Eudoxid. (Fig. 19C) Bract kidney-shaped, with two reduced spur (longitudinal) canals. The dorsal canal arises from the left spur. Gonophores bell-shaped with a characteristically three-pronged, anchor-like, mantle canal.

A widespread species, more common in tropical and sub-tropical waters, at depths of 300 to 500 m or shallower. It has not been recorded in the Mediterranean Sea. There are three records for British waters; off the north west of Cape Wrath (Fraser, 1967), south of the Wyville-Thomson Ridge (Fraser, 1963) and in the Porcupine Seabight (our unpublished data).

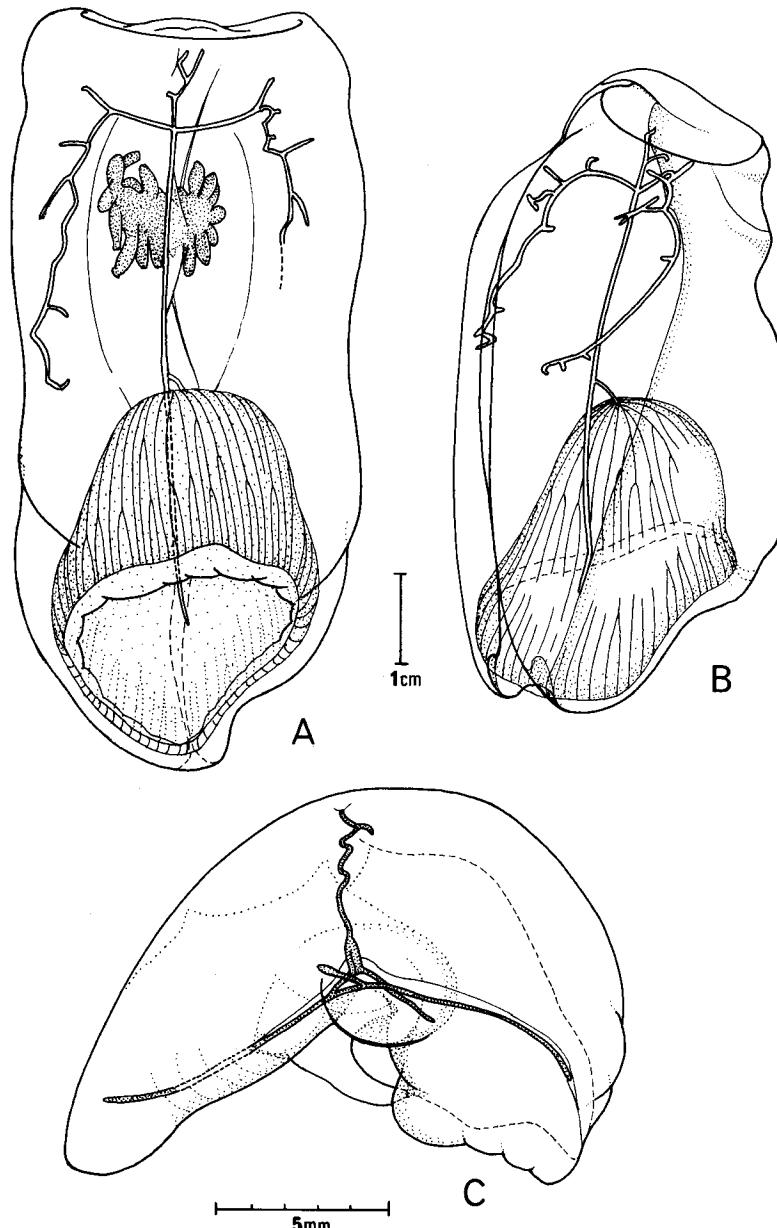


Fig. 19. *Praya dubia*. A, B, nectophore (dorsal and lateral views). C, eudoxid bract (lateral view).

Genus PRAYOIDES Leloup, 1934

Monotypic genus for *P. intermedia* Leloup, 1934*Prayoides intermedia* Leloup, 1934

(Fig. 20)

Nectophore. (Fig. 20) Larval nectophore probably retained, usually remaining firmly attached, near its apex, to a single definitive one. Both are very flimsy structures, whose nectosacs bear bifurcating canals. The somatocysts are simple with thin apical 'ascending' or dorsal canals, although these may be difficult to discern. The 'descending' canal, which extends basally beyond the point of origin of the pallial canal, is present only in the definitive nectophore.

The eudoxid stage has not been identified.

A little known species, although our unpublished data indicate its presence in the temperate waters of the North East Atlantic Ocean and in the Porcupine Seabight, in the 300–500 m depth range.

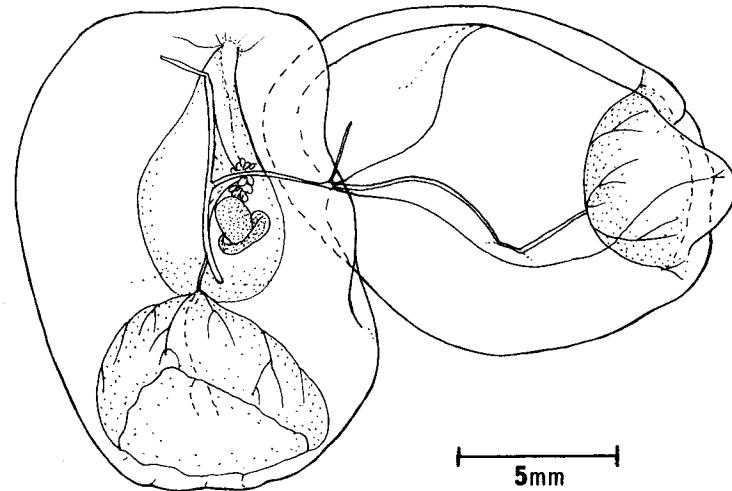


Fig. 20. *Prayoides intermedia*. Nectophores of polygastric stage.

Genus DESMOPHYES Haeckel, 1888

Monotypic genus for *D. annectens*, Haeckel, 1888

Desmophyes annectens Haeckel, 1888
(Fig. 21)

Rosacea plicata Kawamura, 1915 (non *sensu* Bigelow, 1911)

Nectophore. (Fig. 21A) Usually two flimsy, ovoid nectophores, up to 40 mm in length, although up to six biserially arranged nectophores have been reported (Haeckel, 1888). Nectosac small and shallow, with four straight radial canals. The unbranched somatocyst has a distinctive whitish swelling at its apex.

Eudoxid. (Fig. 21B) Bracts small, compact and kidney-shaped, characterized by the presence of a large white spherical or ovoid central organ, giving rise to the thin dorsal bracteal canal. An asexual nectophore is thought to be present, and the gonophores are fragile and reduced.

Little has been published on the distribution of this species although it is quite common in our 'Discovery' material, especially close to the surface in the North West African upwelling region and at greater depths in temperate North East Atlantic waters, including the Porcupine Seabight.

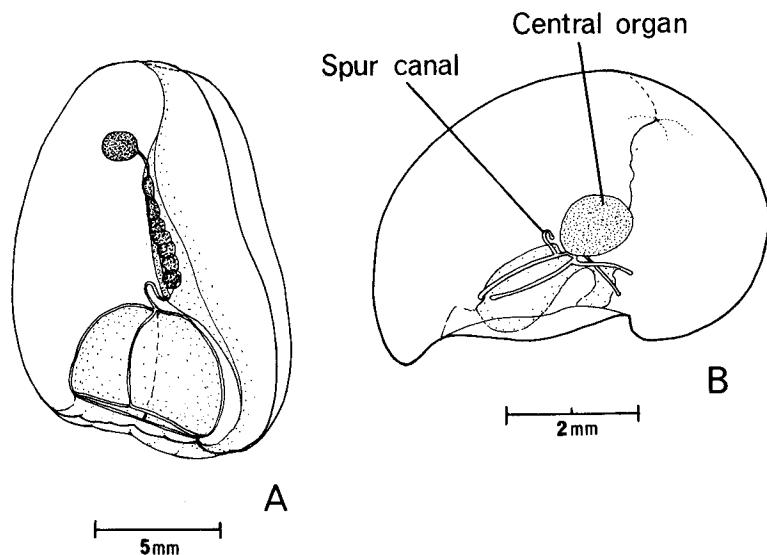


Fig. 21. *Desmophyes annectens*. A, nectophore (lateral view). B, eudoxid bract (lateral view).

Genus NECTOPYRAMIS Bigelow, 1911

An unusual group of prayid siphonophores with asymmetric nectophores, bearing rounded ridges or serrations. The eudoxid bracts resemble the nectophores in appearance, and may bear special nectophores. The genus requires revision, but here we distinguish the species listed by Totton (1965). There are three British species.

Nectopyramis diomedaeae Bigelow, 1911
(Fig. 22)

Nectophore. Only one definitive nectophore is developed, roughly pyramidal or rhomboidal in shape, up to 60 mm in height, with rounded edges and a faint pattern of surface ridges (Fig. 22A). The small nectosac is offset to one side of the base, and the deep narrow hydroecium lies immediately above it. The somatocyst is branched complexly (Fig. 22B).

Eudoxid. (Fig. 22C) Pyramidal bract, up to 40 mm in height, resembling the nectophore in appearance but more flattened. The canal system conforms to the basic prayid pattern, but each canal has several branches. The large special nectophore may be the first gonophore retained after the sexual products are released.

The scant published records for this species were reviewed by Pugh (1974). Our unpublished data show it to be widespread in the North Atlantic Ocean from the equator to 60°N, but more common in the warmer waters at mesopelagic depths. In British waters, Fraser (1961, 1967) records it in the Rockall Trough and our data indicate its presence in the vicinity of the Porcupine Seabight.

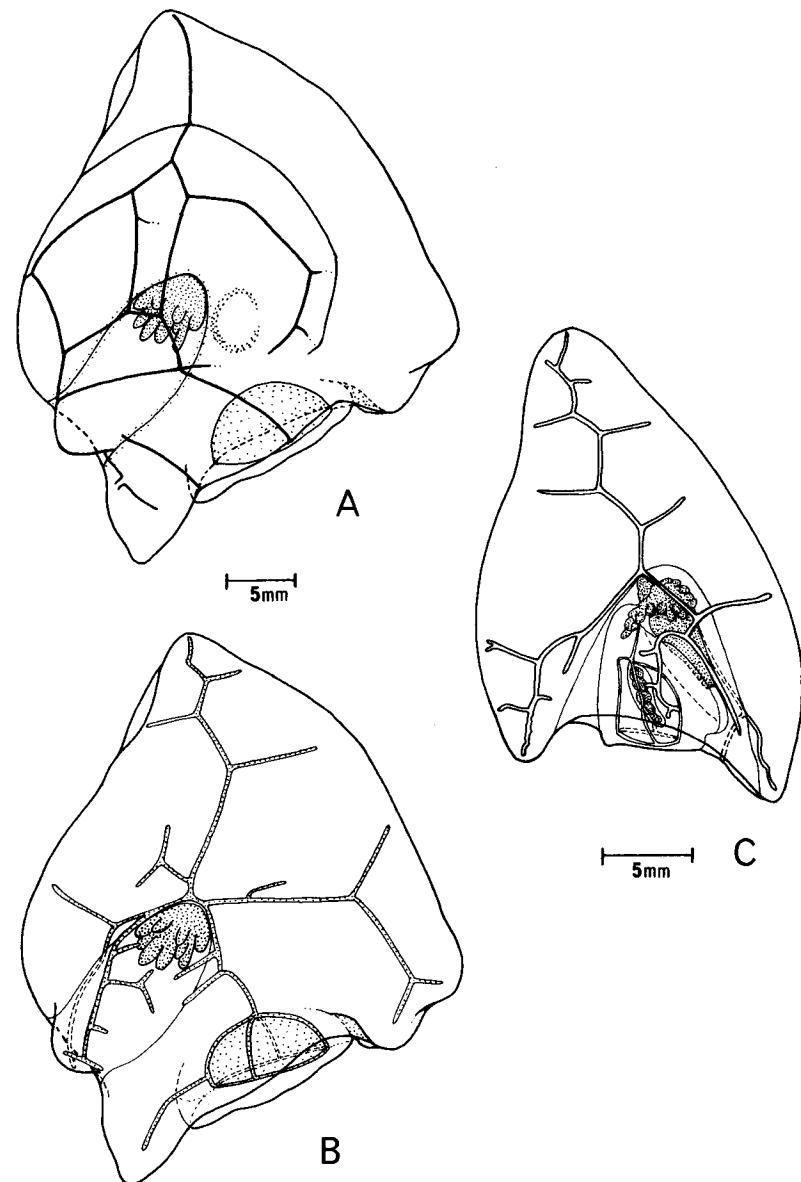


Fig. 22. *Nectopyramis diomedaeae*. A, nectophore showing external ridges. B, nectophore, showing somatocyst and canal system. C, eudoxid stage, excluding external ridges (after Bigelow, 1911) (all lateral view).

Nectopyramis thetis Bigelow, 1911
 (Fig. 23)

Nectophore. (Fig. 23A) A single, pyramidal definitive nectophore, up to 20 mm in height, is developed. The deep but narrow hydroecium extends almost the length of the ventral surface. The shallow nectosac has thick enclosing lips around its ostium, and its radial canals arise separately from the somatocyst. The latter also has two hydroecial branches, which themselves divide further, arising close to a central organ.

Eudoxid. (Fig. 23B) Bract resembles nectophore in shape and canal system. The dorsal canal is forked characteristically near its apex, and there is a prominent central organ. The large (?) asexual nectophore is nearly enclosed by the bract.

This species is best known from the North Atlantic Ocean (Pugh, 1974 and our unpublished data), but records exist for the Indian and Pacific Oceans. It occurs at mesopelagic depths, commonly between 400 and 700 m. There are several British records from the deeper waters to the north west of Scotland and from the region of the Porcupine Seabight.

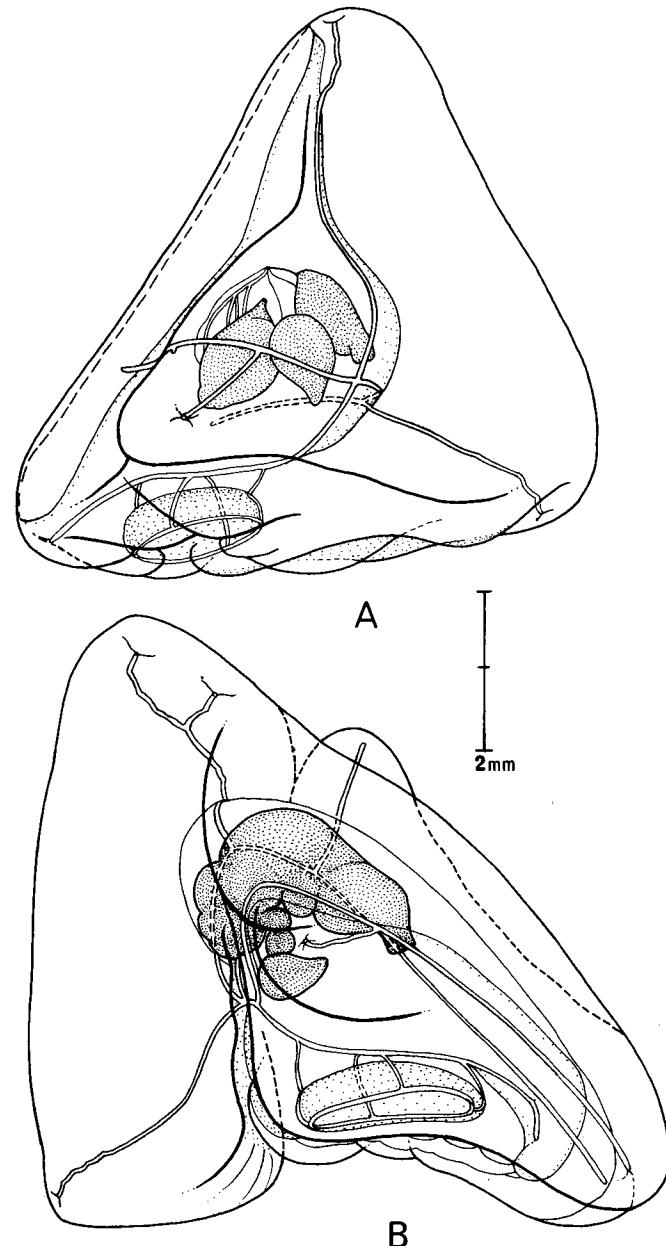


Fig. 23. *Nectopyramis thetis*. A, nectophore. B, eudoxid stage (both lateral view).

Nectopyramis spinosa Sears, 1952
 (Fig. 24)

Nectophore. Two types of small nectophore (up to 10 mm) have been described. They are nearly spherical and have toothed ridges whose pattern recalls that on a tennis ball. Both have a deep, narrow hydroecium, a central organ and a simple somatocyst which bends basally through a right-angle. The so-called larval nectophore (see Totton, 1965) has a vestigal nectosac (Fig. 24) supplied by two small canals arising separately from the somatocyst. The other type of nectophore has a functional nectosac with a canal system resembling that in *N. thetis*.

Eudoxid. Unknown. It is definitely not that described by Totton (1965) under the name *N. spinosa*.

The earlier records for this species were reviewed by Pugh (1974). More recent data show that, like the other nectopyramidines, it is a mesopelagic species. It usually occurs in the 200–700 m depth range, throughout the North Atlantic Ocean from the Equator to 60°N, but there are only two British records, both probably for the 'larval' nectophore, from the region of the Wyville-Thomson Ridge (Fraser, 1961) and Porcupine Seabight (our unpublished data).

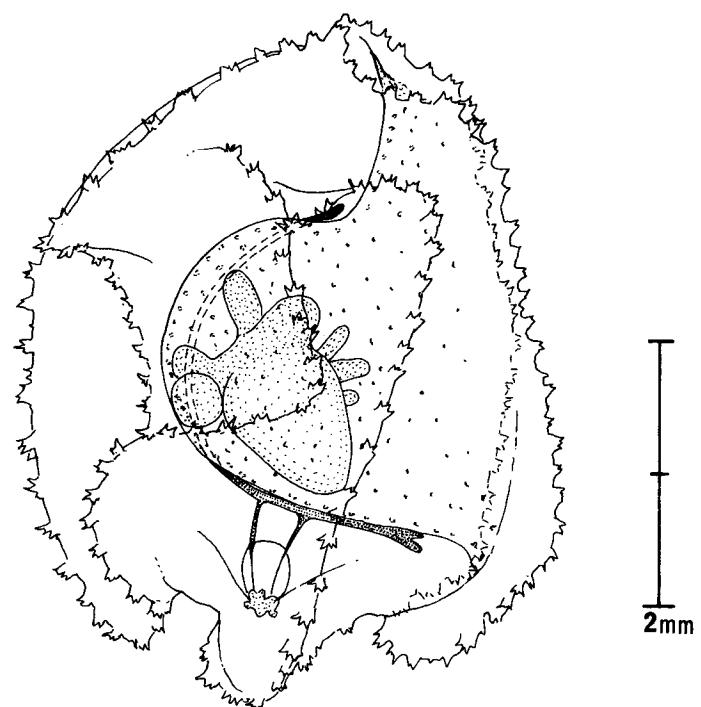


Fig. 24. *Nectopyramis spinosa*. Nectophore ('larval').

Family HIPPOPODIIDAE

Calycophoran siphonophores with a biserial arrangement of up to sixteen or more flattened definitive nectophores in varying stages of development, the youngest being apical, fitting tightly together around a thin stem which can be retracted between them. In the fully-developed polygastric stage nectophores are added continuously but their number is kept constant by a corresponding loss of the oldest ones. No bracts are developed and the gonophores arise directly from the siphosomal stem, being released on maturation. The rounded larval nectophore (Fig. 25C) resembles that of the prayine siphonophores, but can be distinguished by the shape of the somatocyst which curves smoothly over the mid-dorsal surface of the hydroecium and is without a central organ, though a slight swelling may be present.

The family is divided into two genera although, as Totton (1965) points out, all the species may well be congeneric.

Key to the British species of Hippopodiidae

(based on structure of the definitive nectophores)

1. Nectophores rounded or horseshoe-shaped 2
Angular nectophores with serrations, gelatinous teeth or ridges 3
2. 4 dorsal knobs forming an arc above ostium of nectosac; apex of nectophore rounded (Fig. 25A) *Hippopodius hippopus* (p. 72)
2 dorsal knobs; younger nectophores slightly pointed (Fig. 29)
..... *Vogtia glabra* (p. 76)
3. Nectophores with serrations or gelatinous teeth 4
Nectophores ridged with smooth facets (Fig. 28) *Vogtia serrata* (p. 74)
4. Nectophores with numerous serrations on ridges and protuberances on facets (Fig. 26) *Vogtia spinosa* (p. 74)
Nectophores with small gelatinous teeth on ridges, and smooth facets (Fig. 27) *Vogtia pentacantha* (p. 74)

Genus HIPPOPODIUS Quoy and Gaimard, 1827

Monotypic genus for *H. hippopus* (Forskål)

Hippopodius hippopus (Forskål, 1776)
(Fig. 25)

Nectophore. (Fig. 25A,C) Nectosac of larval nectophore has only two radial canals. The horseshoe-shaped definitive nectophores, up to 20 mm in diameter, often go opaque when preserved. The four rounded dorsal knobs vary in size and the inner two may be almost imperceptible (or absent, as in the very first definitive nectophore to be developed (Carré, 1968)). The nectosac is relatively large, and a réte, which is largest in the younger nectophores, is present on the ventral canal. The nectophores emit bright bioluminescent flashes when stimulated.

This species has a widespread distribution throughout the World's oceans and the Mediterranean Sea, and complete polygastric phases (Fig. 25B) often are found in net collections. It is an epiplanktonic species, mainly occurring at depths down to 300 m. There are numerous records for British waters ranging from the Porcupine Seabight to the northern North Sea.

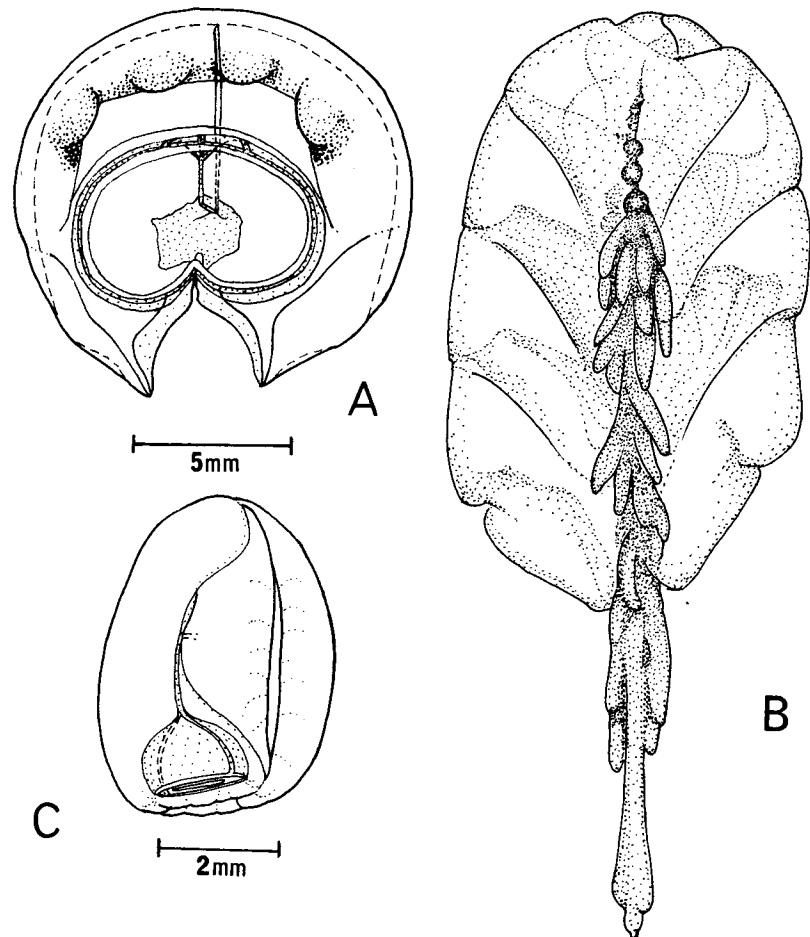


Fig. 25. *Hippopodius hippopus*. A, definitive nectophore. B, whole polygastric stage. C, larval nectophore (lateral view).

Genus VOGTIA Köllicker, 1853

The nectosac of the larval nectophore has four radial canals, cf. *Hippopodius*, but they are frequently difficult to discern. There are four British species.

Vogtia spinosa Keferstein and Ehlers, 1861
(Fig. 26)

Nectophore. (Fig. 26) Roughly five-pointed and flattened, up to 20 mm in diameter. Numerous gelatinous teeth are arranged along the ridges and on the dorsal and lateral facets. Up to sixteen nectophores are present in the polygastric stage, but they fit loosely together and are easily broken off.

A widespread species occurring mainly at depths between 300 and 500 m by day. There are many British water records, mainly from the Porcupine Seabight and along the shelf break to the west of Ireland and Scotland.

Vogtia pentacantha Köllicker, 1853
(Fig. 27)

Nectophore. (Fig. 27) Five-pointed, up to 15 mm in diameter, with small gelatinous teeth on the ridges, but with smooth facets except for occasional protuberances near the central ridge. Nectosac comparatively small. The polygastric stage is fragile and seldom found intact in net collections.

Not so well known as the other *Vogtia* species, but has a widespread distribution, most often in the 200–500 m depth range. There are several British records at similar localities to those for *V. spinosa*.

Vogtia serrata (Moser, 1925)
(Fig. 28)

Nectophore. (Fig. 28) Roughly triangular, up to 40 mm in diameter, with two small flaps at centre of base. Neither the distinctive ridges nor the facets bear protuberances, and a small, deep hollow exists beneath each lateral process. This species has a widespread distribution and usually is the deepest-living of all the hippopodiids. Pugh (1974) found it, by day, mainly between 600 and 650 m although it has been recorded down to 4000 m. In British waters it occurs in the deeper waters from the Porcupine Seabight to off the north west of Scotland.

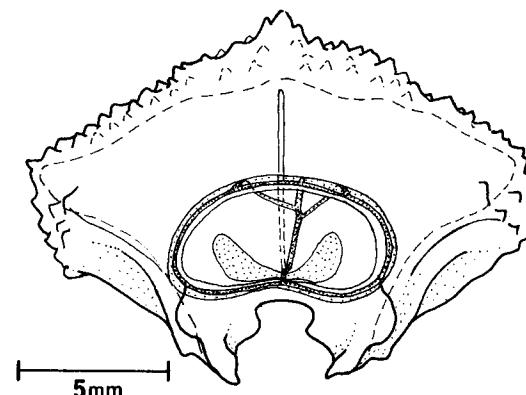


Fig. 26. *Vogtia spinosa*. Definitive nectophore, dorsal view.

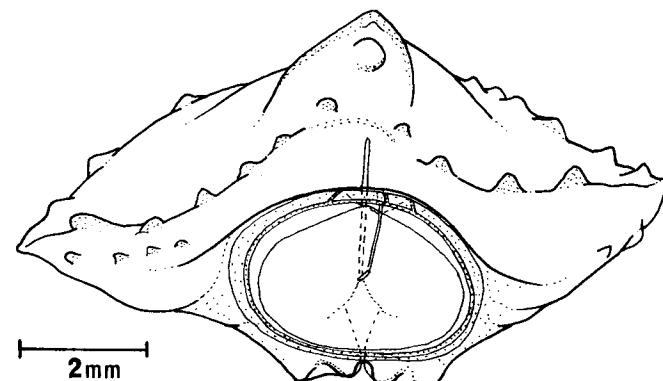


Fig. 27. *Vogtia pentacantha*. Definitive nectophore, dorsal view.

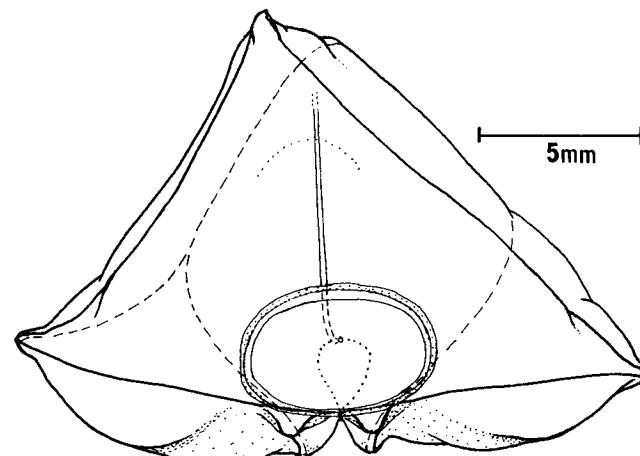


Fig. 28. *Vogtia serrata*. Definitive nectophore, dorsal view.

Vogtia glabra Bigelow, 1918
 (Fig. 29)

Nectophore. (Fig. 29A,B) Usually horseshoe-shaped, up to 30 mm in diameter, but the younger ones tend to be slightly pointed at their apex. There are two latero-dorsal, rounded knobs above the nectosac.

A common, widespread species often at depths between 200 and 600 m. Its distribution in British waters is similar to the other *Vogtia* species, i.e. off the west coasts beyond the shelf break.

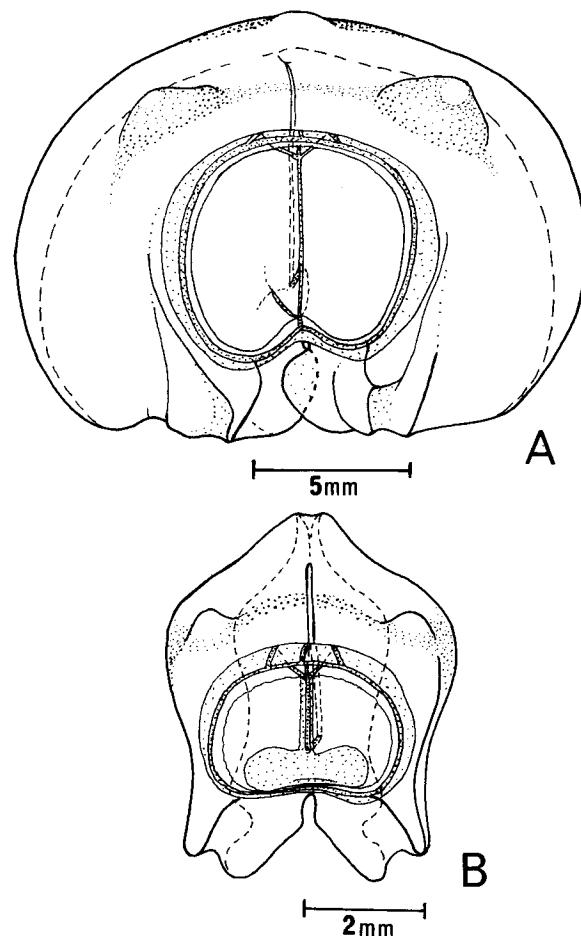


Fig. 29. *Vogtia glabra*. A, B, definitive nectophores, dorsal view (B, young stage).

Family DIPHYIDAE

The polygastric stage usually includes two dissimilar streamlined definitive nectophores arranged serially. The larval nectophore is found rarely and will not be considered here. The anterior or first definitive nectophore possesses a somatocyst, while the second or posterior (if developed) does not. The somatocyst often contains oil droplets which may aid in buoyancy control. The hydroecium generally is reduced in the anterior nectophore. A nectosac occupies most of the nectophore and, with the overall streamlining, enables the animals to be fast and active swimmers.

The Diphyidae is the largest family of siphonophores, and is split into two subfamilies, the Sulculeolariinae and the Diphyinae. In the Sulculeolariinae the anterior nectophore is smooth and rounded, without ridges, while in the posterior nectophore the lateral radial canals loop extensively over the nectosac surface. In contrast the diphyine species usually have ridged nectophores and, in the posterior one, unlooped radial canals. In addition the bracts of the Sulculeolariinae are thin, leaf-like structures which may not be released as part of a eudoxid, while the bracts of the free-living diphyine eudoxids are distinctive helmet-shaped structures.

Key to the British Species of Diphyidae

1. Anterior nectophore blunt and unridged; posterior nectophore has extensively looped lateral radial canals on nectosac Sulculeolariinae 2
- Anterior nectophore pyramidal, usually ridged or folded; posterior nectophore (if developed) has unlooped lateral radial canals on nectosac Diphyinae (p. 84)
2. Somatocyst short or minute; nectosac of posterior nectophore unconstricted; ostial teeth absent 3
- Somatocyst at least one third length of anterior nectophore; nectosac of posterior nectophore has 2 constrictions; ostial teeth usually present (Fig. 30) *Sulculeolaria quadrivalvis* (p. 80)
3. Somatocyst short; both nectophores have divided mouthplate (Fig. 31) *Sulculeolaria biloba* (p. 82)
- Somatocyst minute; posterior nectophore has undivided mouthplate (Fig. 32) *Sulculeolaria turgida* (p. 82)

Subfamily SULCULEOLARIINAE Totton, 1954

Contains a single genus *Sulculeolaria* Blainville, 1834

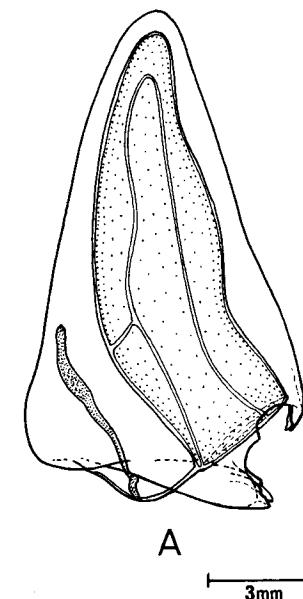
Genus SULCULEOLARIA Blainville, 1834

The anterior or posterior nectophore, which are of similar size, may be replaced if lost, a process which can be repeated at least four times. Occasionally an anterior and two posterior nectophores are present together. The morphology of successive nectophores can vary markedly and this has led to much confusion regarding the taxonomy of this genus (see Carré, 1979). In the anterior nectophore the hydroecium is so reduced as to be virtually absent, while the characteristic feature of the posterior one is the extensive looping of the lateral radial canals. The two or possibly three British species can be easily distinguished on the basis of the presence or absence of ostial teeth, and the shape of the somatocyst.

Sulculeolaria quadrivalvis Blainville, 1834
(Fig. 3B, 30)

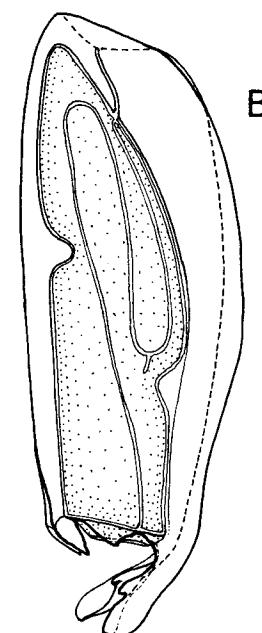
Anterior nectophore. (Fig. 30A) Up to 20 mm in height with two lateral and two dorsal ostial teeth. These teeth are most prominent in the first definitive nectophore, but are reduced in size or disappear in successive replacement nectophores. The long, sinuous somatocyst reaches one third to two fifths of the nectophoral height. The mouthplate is divided into two rounded lobes.

Posterior nectophore. (Fig. 30B) Also with lateral and dorsal ostial teeth. The nectosac has two characteristic constrictions, at right-angles to each other. A common species in the warmer waters of the World's oceans, and in the Mediterranean Sea, living close to the surface. Totton (1954) describes the presence of this species in Valentia Harbour, Ireland and this appears to be the only record within the designated area for British waters.



A

3mm



B

Fig. 30. *Sulculeolaria quadrivalvis*. A, anterior nectophore. B, posterior nectophore.
(Lateral views.)

Sulculeolaria biloba (Sars, 1846)
(Fig. 31)

Anterior nectophore. (Fig. 31A) Up to 20 mm in height, but without ostial teeth. The short, ovoid somatocyst is obliquely inclined. The mouthplate is divided into two elongated lobes.

Posterior nectophore. (Fig. 31B,C) Characterised by the shape of the mouthplate, which bears two side processes and a central thickening.

Another warm water species living close to the sea surface, and rarely found in temperate waters. Both this and the succeeding species have been described under the name *Galette australis* and it is difficult to sort out some of the earlier records, as Totton (1954) discusses. Totton and Fraser (1955) refer only to *S. biloba* in the northern waters of the Atlantic, and the British records stretch from the English Channel, up the western continental shelf as far as the north of Scotland.

Sulculeolaria turgida (Gegenbaur, 1853)
(Fig. 32)

Anterior nectophore. (Fig. 32A) Up to 15 mm in height, with a minute somatocyst and no ostial teeth.

Posterior nectophore. (Fig. 32B) Bears a thin, rounded mouthplate.

As discussed above it is not absolutely certain that this species occurs in British waters. It is assumed, however, that the specimens of *Galette australis* referred to by Leloup (1955) belong to *S. turgida*, and several of these records lie in deeper waters off the western coastline of the British Isles. As with the other species of *Sulculeolaria*, *S. turgida* is found more frequently close to the surface in tropical waters.

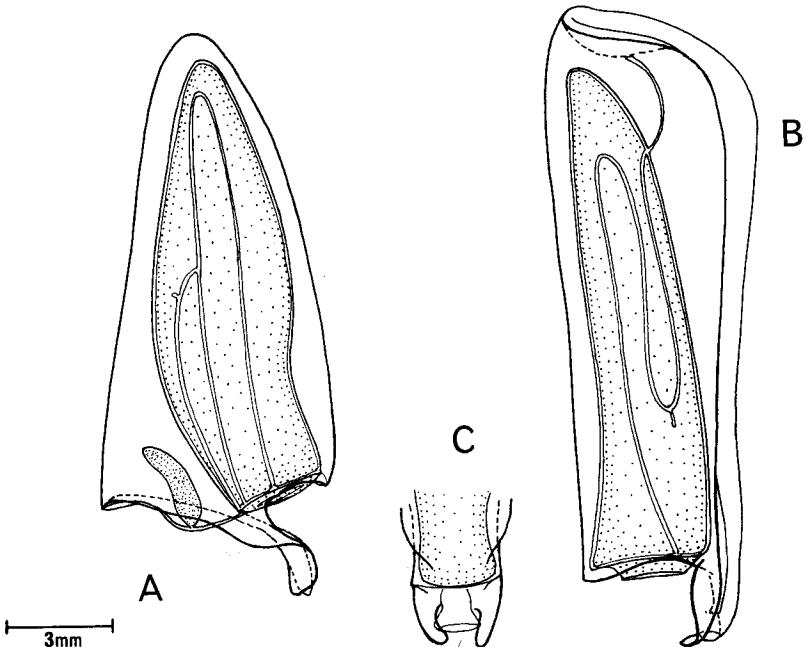


Fig. 31. *Sulculeolaria biloba*. A, anterior nectophore (lateral view). B, posterior nectophore (lateral view). C, mouthplate detail of B (dorsal view) (C, after Totton, 1965).

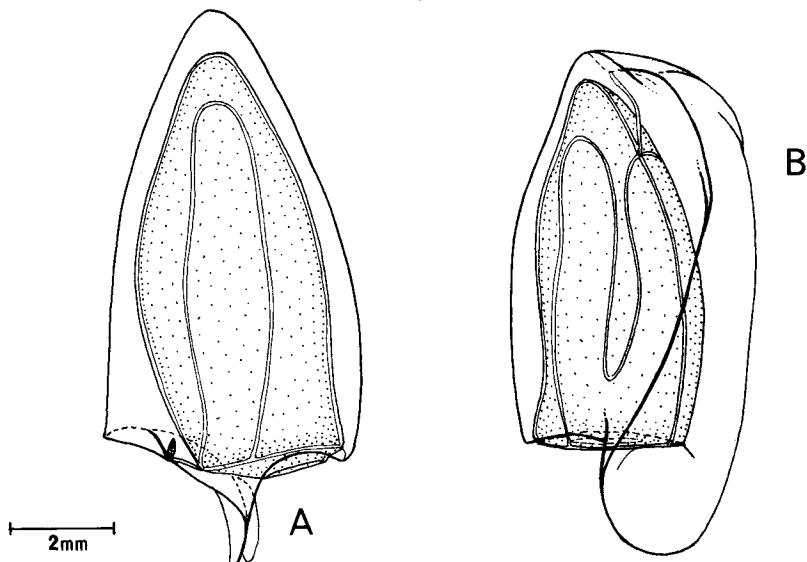


Fig. 32. *Sulculeolaria turgida*. A, anterior nectophore. B, posterior nectophore (lateral views).

Subfamily DIPHYINAE Moser, 1925

A single anterior and posterior nectophore are produced, and the latter may be reduced or suppressed altogether. The anterior nectophore is pyramidal and usually sharply pointed apically. The free-swimming eudoxid stage usually has helmet-shaped bracts. There are seventeen British species of which twelve belong to a single genus. The following key to the British diphyines is based solely on the characters of the anterior nectophores, as in the majority of cases the posterior nectophores and eudoxid stages have not been described.

Key to the British Diphyinae

1. Mouthplate undivided (Fig. 47) *Dimophyes arctica* (p. 106)
Mouthplate divided 2
2. Ridges on nectophore spirally twisted; hydroecium pointed apically (Fig. 49) *Eodoxoides spiralis* (p. 110)
Ridges straight or slightly curved 3
3. 5 distinct ridges at base, but dorsal ridge incomplete at apex; hydroecium claw-shaped (Fig. 48) *Chelophyses appendiculata* (p. 108)
Arrangement of ridges and hydroecium not as above 4
4. One pair of lateral ridges (sometimes indistinct); 5 ridges in all 5
More than one pair of lateral ridges, not all may reach ostium 12
5. 5 non-crested ridges, laterals very indistinct 6
5 distinct, crested ridges 7
6. Somatocyst globular on long stalk (Fig. 44) *Lensia subtilis* (p. 102)
Somatocyst laterally expanded on short stalk (Fig. 41) *Lensia meteori* (p. 98)
7. Deep hydroecium, one quarter to one third the height of nectophore; somatocyst long and thin 8
Hydroecium not extending above base of nectosac 9
8. Lateral ridges bend dorsad at base; somatocyst approximately 50% height of nectophore (Fig. 45A) *Muggiae kochi* (p. 104)
Lateral ridges relatively straight at base; somatocyst reaching to apex of nectosac (Fig. 46) *Muggiae atlantica* (p. 104)
9. Somatocyst relatively long, extending above base of nectosac 10
Somatocyst short or spherical not reaching to level of base of nectosac 11
10. Lateral ridges bend dorsad at base; hydroecium reaches to level of ostium (Fig. 33) *Lensia achilles* (p. 86)
Lateral ridges straight; hydroecium very small; somatocyst long (Fig. 34) *Lensia conoidea* (p. 88)

11. Somatocyst oblique and ovate, with short stalk (Fig. 40)
..... *Lensia hotspur* (p. 96)
Somatocyst globular (Fig. 36A) *Lensia fowleri* (p. 92)
12. Nectophores with 7 distinct ridges
..... Nectophores with several additional lateral ridges 13
13. Ventro-lateral ridges bend ventrad at base and run on to mouthplate; hydroecium deep; somatocyst short (Fig. 38)
..... *Lensia havock* (p. 94)
Ventro-lateral ridges straight but reach neither apex nor base; very small hydroecium; somatocyst long and thin (Fig. 43)
..... *Lensia multicristata* (p. 100)
14. Velar ridge present
..... Velar ridge absent (Fig. 39) *Lensia hostile* (p. 96)
15. Lateral ridges extend below velar ridge; somatocyst kidney-shaped (Fig. 41) *Lensia lelouvetteau* (p. 98)
Lateral ridges do not extend below velar ridge 16
16. Somatocyst long and spindle-shaped (Fig. 35) *Lensia exeter* (p. 90)
Somatocyst short and club-shaped (Fig. 37A) *Lensia grimaldi* (p. 94)

Genus LENSIA Totton, 1932

Small, pyramidal anterior nectophores with a variable number and arrangement of ridges. Hydroecium usually shallow, rarely stretching above the ostial level. The shallow mouthplate is divided; ostial teeth are absent. Posterior nectophores, when found, are truncated proximally and have rounded mouthplates. Eudoxid bracts are simple helmet-shaped structures.

More than thirty species have been described (see Daniel, 1974), twelve of which occur in British waters.

Lensia achilles Totton, 1941
(Fig. 33)

Anterior nectophore. Up to 15 mm in height with five complete ridges, the basal portion of the laterals bending sharply dorsad. The basal facet is broad, and the hydroecium extends up to the level of the ostium. Somatocyst is elongated, a quarter to a half the height of nectophore, and variable in shape. The posterior nectophore and eudoxid phase have not been described.

A widespread species throughout the Atlantic Ocean from 60°N (our unpublished data) to 34°S (Totton, 1941). It is found most commonly at depths between 400 and 600 m. There are several records from the deeper waters to the west of the British Isles.

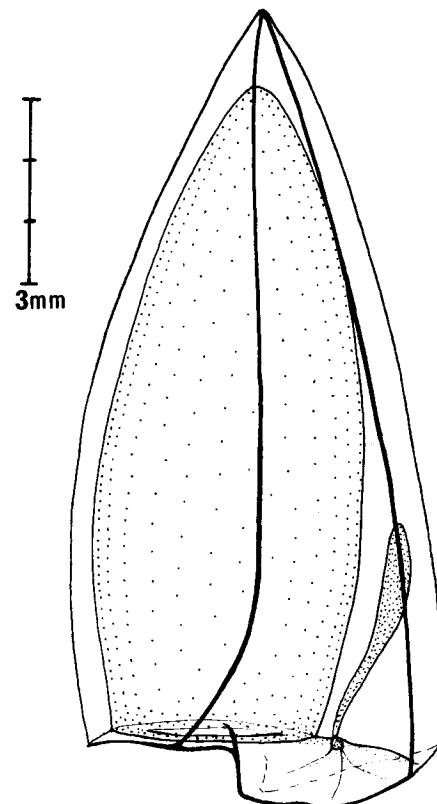


Fig. 33. *Lensia achilles*. Anterior nectophore (lateral view).

Lensia conoidea (Keferstein and Ehlers, 1860)
(Fig. 34)

Anterior nectophore. (Fig. 34A) Large, up to 20 mm in height, with five complete ridges and a minute, basal hydroecium. The mesogloea is thickened ventrally and surrounds the long thickened somatocyst, which extends to half the height of the nectophore.

Posterior nectophore. (Fig. 34B) Five ridged, reaching 20 mm in length, with an asymmetrical mouthplate which is indented centrally. The lateral radial canals are not looped as in *Sulculeolaria* spp.

Eudoxid. (Fig. 34C) The eudoxid bract is conical, approximately 4 mm in height, with a long, swollen phyllocyst. The gonophores possess a mouth-plate. (The gonophores of all *Lensia* spp. are difficult to identify specifically and will not be described in detail. Reference should be made to Totton, 1965.)

This is a common and cosmopolitan species most frequently encountered in the North Atlantic Ocean, in temperate waters north of 40°N and at depths between 200 and 600 m. There is also some evidence (our unpublished data) for a deeper-living population. There are many records for this species in British waters, mainly from the deeper western waters, but also from the northern North Sea (Russell, 1939).

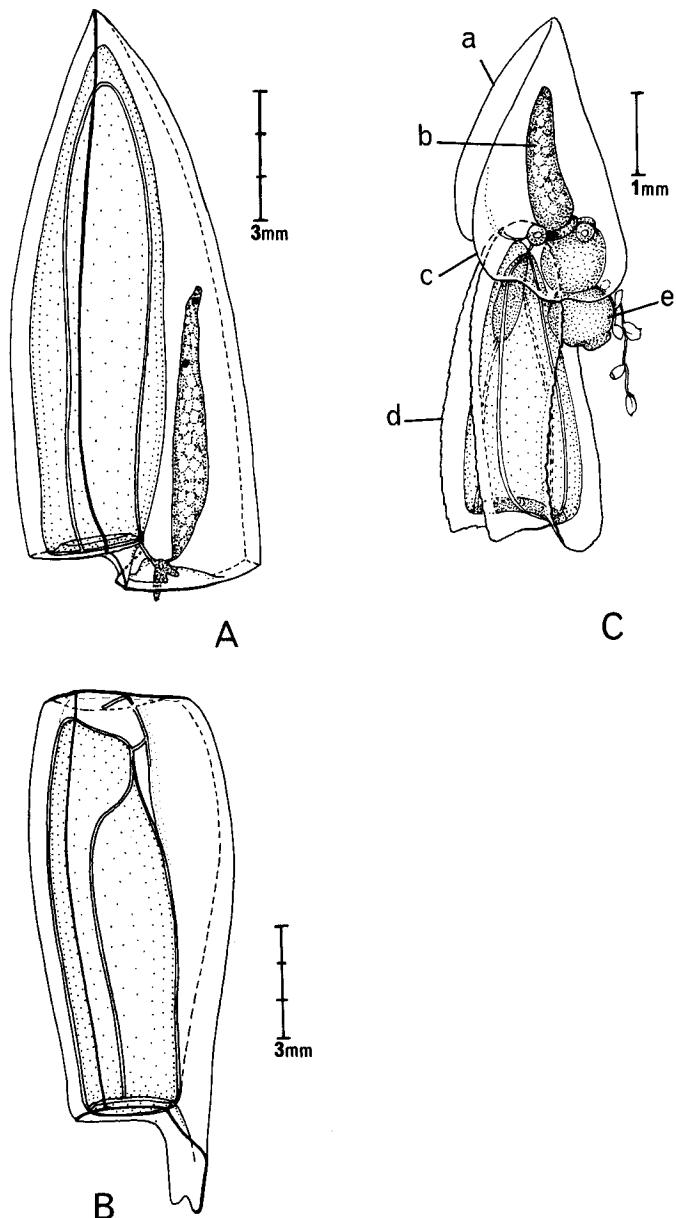


Fig. 34. *Lensia conoidea*. A, anterior nectophore. B, posterior nectophore. C, eudoxid stage (all lateral view) (A, C, partly after Totton, 1965; B, after Bigelow and Sears, 1937). (a, bract; b, phyllocyst; c, neck-shield; d, gonophore; e, gastrozooid).

Lensia exeter Totton, 1941
 (Fig. 35)

Anterior nectophore. Up to 10 mm in height and multi-ridged, although only five ridges meet at the apex. The latero-dorsal ridges on each side connect with a transverse velar ridge, lying 1–2 mm above the ostium. Dorsally these velar ridges bend and run to the ostial level without joining the dorsal ridges. The mouthplate is relatively large, and the hydroecium, which is open to the ventral surface, extends up to the ostial level. The long, slender somatocyst reaches to one third of the height of the nectophore.

Neither the posterior nectophore nor the eudoxid stage have been identified.

This is a little known siphonophore identified only from the Atlantic Ocean. Our unpublished data show it to be present at stations ranging in position from the equator to 60°N, including three from the Porcupine Seabight, and at depths usually between 400 and 700 m.

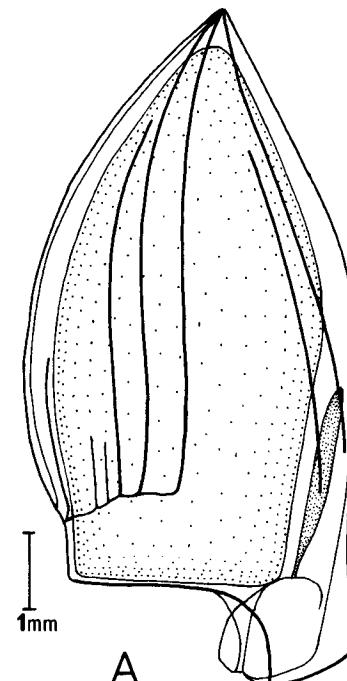


Fig. 35. *Lensia exeter*. Anterior nectophore, lateral view (note transverse velar ridge) (partly after Totton, 1965).

Lensia fowleri (Bigelow, 1911)
(Fig. 36)

Anterior nectophore. (Fig. 36A) Large, up to 20 mm in height, with five complete ridges. The globular somatocyst lies below the ostial level, within an extensive mouthplate.

Posterior nectophore. (Fig. 36B) Smaller and more delicate than anterior nectophore. The hydroecium is delimited by two triangular-shaped wings. The small, rounded mouthplate is undivided.

Eudoxid. The bract (Fig. 36C) is elongated, up to 4.5 mm in height, and rounded apically, with a wide neck shield which bears a marginal notch. The phyllocyst is small and globular. The gonophore apparently has no mouth-plate.

This species is distributed widely in the Atlantic and other oceans, and also occurs in the Mediterranean Sea. Peaks of abundance occur in warmer waters at depths from the surface to 250 m (Pugh, 1974), but specimens have been found up to 61°N (Margulies, 1971). Records for this species in British waters are numerous and range from the Porcupine Seabight (our unpublished data) to the north west of Scotland (Fraser, 1961, 1967, 1968).

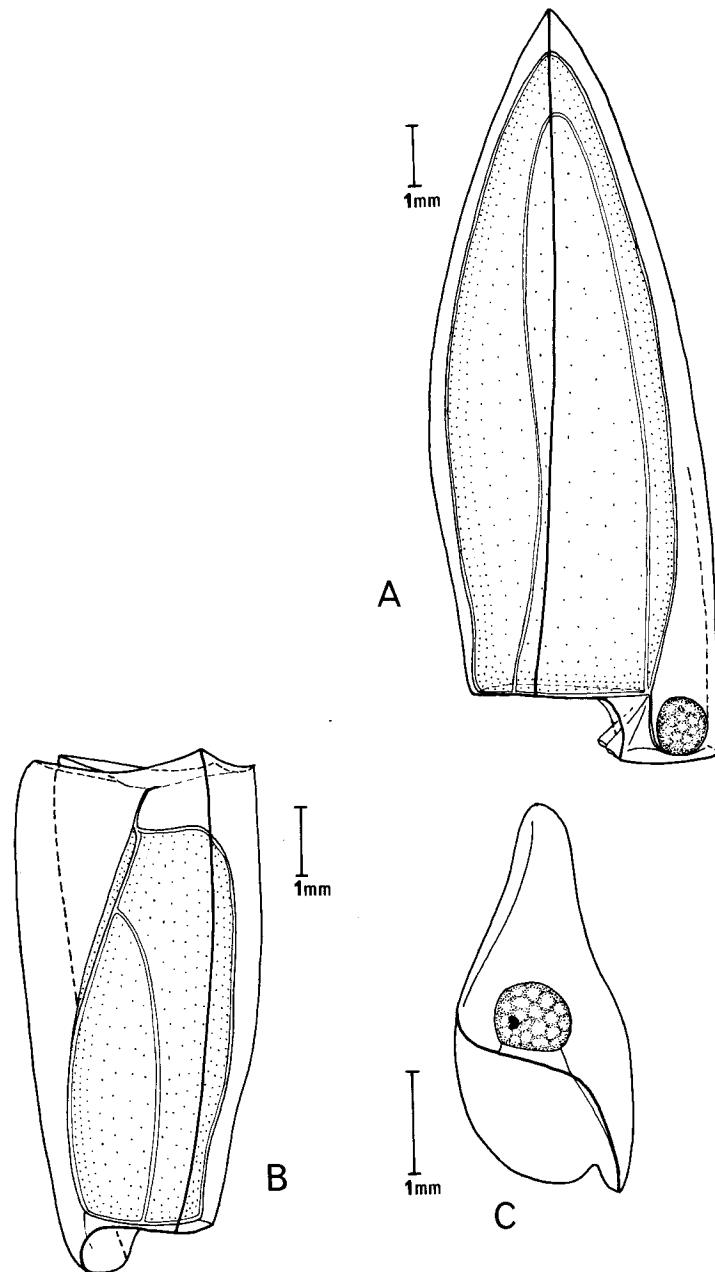


Fig. 36. *Lensia fowleri*. A, anterior nectophore. B, posterior nectophore. C, eudoxid bract (all lateral view) (C, after Patriti, 1965).

Lensia grimaldi Leloup, 1933
 (Fig. 37)

Anterior nectophore. (Fig. 37A) Small and fragile, usually less than 8 mm in height, with several ridges of somewhat variable number. Only five of these ridges reach the apex and only the ventrals join the base of the nectophore. The latero-dorsal ridges bend dorsally near their bases and bifurcate (Fig. 37B). The hydroecium is open ventrally and extends to slightly above the ostial level. The somatocyst is short and club-shaped.

The posterior nectophore and eudoxid stage are not known.

This is an uncommon siphonophore, although widely distributed throughout the Atlantic Ocean from 53°N (our unpublished data) to 34°S (Totton, 1941), usually in the 300–600 m depth range. It has been found twice in the Porcupine Seabight.

Lensia havock Totton, 1941
 (Fig. 38)

Anterior nectophore. Up to 15 mm in height with seven distinct and complete ridges. The ventro-lateral ridges bend ventrad basally and run down on to the mouthplate. The hydroecium is relatively large, extending to well above the ostial level, and is open to the ventral surface for most of its height. The somatocyst is short and expanded, usually club-shaped, but its full extent is often difficult to discern.

The posterior nectophore and eudoxid stage have not been identified.

The systematic position of this species was discussed by Pugh (1974). It is a rare, deep-living species with a widespread distribution throughout the Atlantic from 53°N (our unpublished data) to 57°S (Totton, 1941). There are only a few records for the Indian and Pacific Oceans. It has been found once in the Porcupine Seabight at a depth of 1000–1525 m.

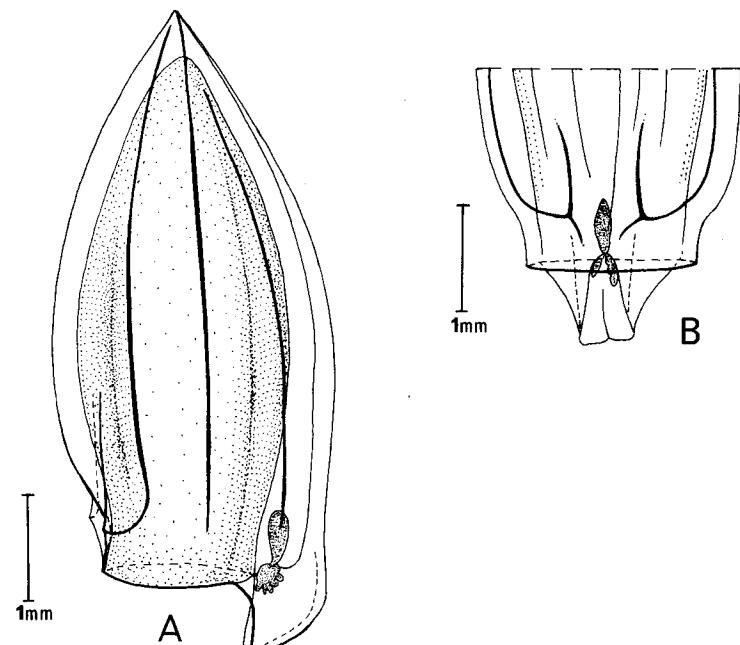


Fig. 37. *Lensia grimaldi*. A, anterior nectophore (lateral view). B, detail of A, ostial region (dorsal view) (B, after Totton, 1965).

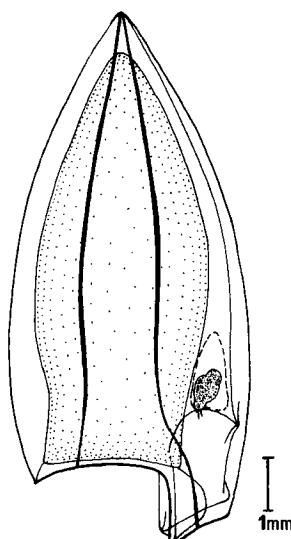


Fig. 38. *Lensia havock*. Anterior nectophore (lateral view).

Lensia hostile Totton, 1941
(Fig. 39)

Anterior nectophore. Up to 15 mm in height, fragile and multiridged, 3 or 4 of the laterals on each side being complete. The number of other ridges is variable, but there is no velar ridge (cf. *L. exeter*). The deep hydroecium reaches to a level slightly above the ostium and is open ventrally. The somatocyst has an inverted heart shape but, as in *L. havock*, its true outline may be difficult to see.

The posterior nectophore and eudoxid stage are not known. Little information has been published on this species, but it is widely distributed in the North Atlantic Ocean from the equator to 60°N (Pugh, 1974 and our unpublished data). It occurs within the 500–600 m depth range (Margulis, 1971) and also below 950 m. The records for British waters all come from 'Discovery' stations in the Porcupine Seabight area.

Lensia hotspur Totton, 1941
(Fig. 40)

Anterior nectophore. Small, usually less than 10 mm in height, with five complete ridges. The hydroecium is reduced to a small depression in the mouthplate. The short, ovate somatocyst is angled obliquely and has a short stalk.

Posterior nectophore. Difficult to distinguish from that of other *Lensia* species, but it has a rounded notch on the mouthplate.

The eudoxid stage has not been identified.

This species has a widespread distribution in the warmer waters of the Atlantic Ocean, occurring mainly in the top 250 m of water (Pugh, 1974). In British waters, Fraser (1967) reports it from the region to the north west of Scotland, and it has been noted in the Porcupine Seabight area (our unpublished data).

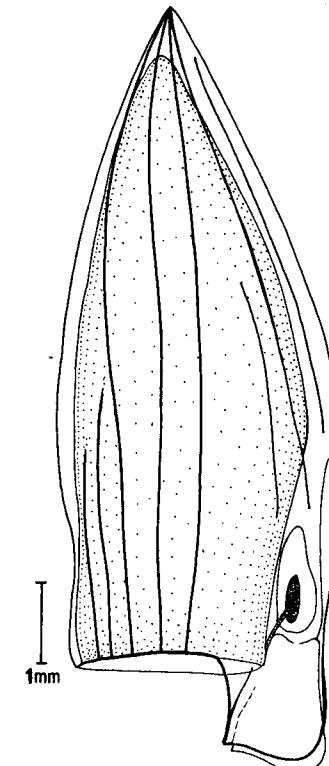


Fig. 39. *Lensia hostile*. Anterior nectophore (lateral view) (after Totton, 1965).

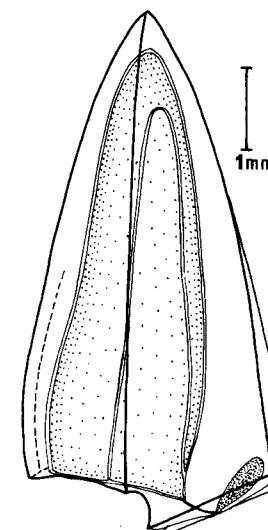


Fig. 40. *Lensia hotspur*. Anterior nectophore (lateral view) (partly after Totton, 1965).

Lensia lelouveteau Totton, 1941
 (Fig. 41)

Anterior nectophore. Distinctive, small and fragile, up to 7 mm, with numerous longitudinal ridges, most of which are complete. These ridges are linked by a cross ridge, the velar ridge. The somatocyst is short and laterally expanded, resembling a mushroom.

The posterior nectophore and eudoxid phase have not been found.

An uncommon bathypelagic siphonophore with a widespread distribution, from 60°N to 33°S in the Atlantic Ocean, at depths greater than 900 m (Pugh, 1974). There are four British records, three from the Porcupine Seabight and one to the north west of Eagle Island, Ireland.

Lensia meteori (Leloup, 1934)
 (Fig. 42)

Anterior nectophore. Small and fragile, up to 7 mm in height, and apparently unridged. The small somatocyst is expanded laterally and born on a small stalk. The basal facet is almost vertical so as to appear as part of the ventral surface.

The posterior nectophore and eudoxid stage have not been discovered.

A cosmopolitan species occurring, in the Atlantic Ocean, between 51°N and 39°S (Margulis, 1971) over a wide depth, although more concentrated in the top 300 m. The two records for British waters are both from the south west of Ireland (Totton, 1954 and our unpublished data).

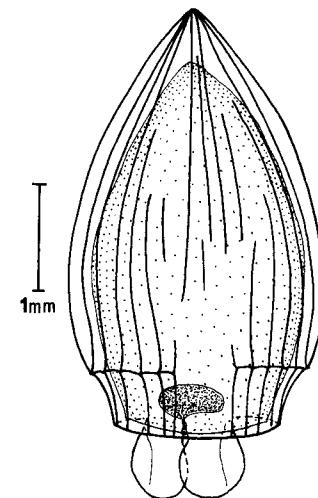


Fig. 41. *Lensia lelouveteau*. Anterior nectophore (dorsal view) (partly after Totton, 1965).

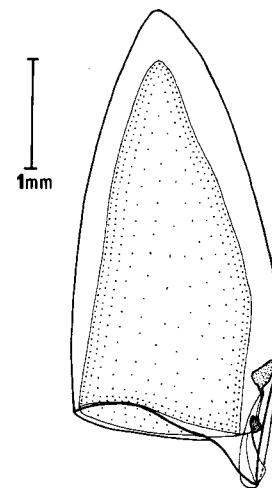


Fig. 42. *Lensia meteori*. Anterior nectophore (lateral view) (partly after Totton, 1965).

Lensia multicristata (Moser, 1925)
(Fig. 43)

Anterior nectophore. (Fig. 43A) Up to 15 mm in height, with seven longitudinal ridges. The lateral ridges end slightly above the ostium and the ventro-laterals reach neither base nor apex. The long, thin somatocyst extends one third to one half of the height of the nectophore. The hydroecium is a shallow groove at the base of the mouthplate.

Posterior nectophore. (Fig. 43B) Five-ridged, with the laterals not reaching the ostium. The broad, shallow mouthplate bears a small median tooth.

Eudoxid. Although not identified positively, the eudoxid stage may be that described by Patriti (1965) as *Eodoxia tenuis*. The elongated bract (Fig. 43C) of this latter species has a long, club-shaped phyllocyst which extends to three quarters of the height of the bract.

This species is widespread and cosmopolitan throughout the World's oceans. It is found most commonly in the 250–450 m depth range (Pugh, 1974). There are several British records from the deeper waters. Fraser (1961, 1968) found it in the region of the Rockall Trough, and other records come from the Porcupine Seabight area (our unpublished data).

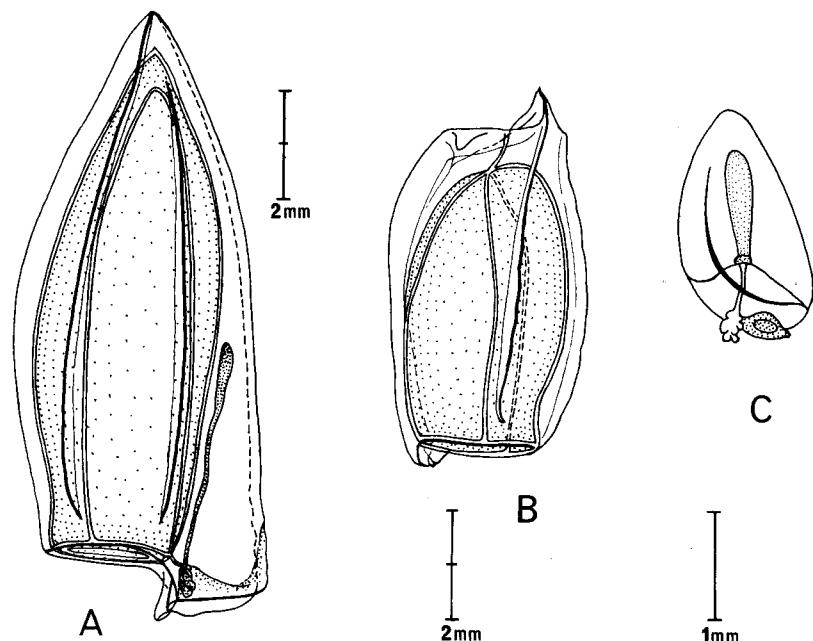


Fig. 43. *Lensia multicristata*. A, anterior nectophore. B, posterior nectophore. C, eudoxid bract. (All lateral view; A, partly after Totton, 1965; B, C, after Leloup, 1955.)

Lensia subtilis (Chun, 1886)
(Fig. 44)

Anterior nectophore. (Fig. 44A) A small, fragile, apparently unridged nectophore, up to 10 mm in height. Four longitudinal folds are present. There is a resemblance to the anterior nectophore of *L. meteori*, except that the somatocyst is globular, set on a long, thin stalk. The basal facet of the mouthplate runs obliquely up towards the ventral surface.

Posterior nectophore. (Fig. 44B) Similar in size to the anterior nectophore, with five ridges and a very small, rounded mouthplate.

Eudoxid. Bract small and rounded with a short phyllocyst (Fig. 44C). The gonophore has hydrocial folds only on the proximal part.

This species is quite common in the warmer waters of the major oceans, and in the Mediterranean Sea. It is a near surface dweller, although occasional specimens are found at depths in excess of 100 m. The few records for British waters come from the Celtic Sea continental slope region (our unpublished data).

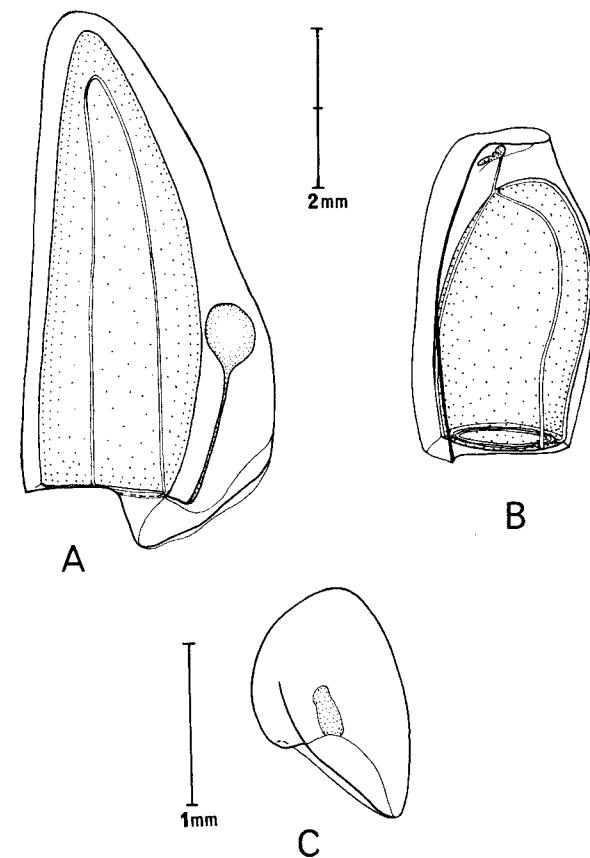


Fig. 44. *Lensia subtilis*. A, anterior nectophore. B, posterior nectophore. C, eudoxid bract. (All lateral view; C. after Totton, 1965.)

Genus MUGGIAEA Busch, 1851

Diphyd siphonophores which do not develop a posterior nectophore. The anterior has a complete dorsal ridge. The very deep hydroecium and the positioning of the somatocyst very close to the nectosac wall are distinctive features (cf. genus *Lensia*). There are two British species, both of which are neritic and thus are found rarely in the open ocean.

Muggiae kochi (Will, 1844)
(Fig. 45)

Anterior nectophore. (Fig. 45A) Small, up to 7 mm in height, with five complete longitudinal ridges. The lateral ridges bend dorsad as they approach the ostium. The hydroecium is shallower than in *M. atlantica* and the somatocyst reaches to only half the height of the nectophore.

Eudoxid. (Fig. 45B) The bract is roughly conical, with a flattened facet, an asymmetrical basal process, and a very shallow hydroecial depression. The phyllocyst is club-shaped. The gonophore has four longitudinal ridges which spiral to the right. There is a short, curved mouthplate.

This species is common in the shallower waters of the Atlantic Ocean and Mediterranean Sea. There are numerous British records, and it has been found frequently in the western part of the English Channel and the Celtic Sea.

Muggiae atlantica Cunningham, 1892
(Fig. 46)

Anterior nectophore. Of similar size to *M. kochi*, with five complete but relatively straight longitudinal ridges. The deep hydroecium extends to about one third of the height of the nectophore. The long, thin somatocyst reaches the apex of the nectosac.

The eudoxid phase is indistinguishable from that of *M. kochi* (see Fig. 45B).

The distribution of this species is similar to that of *M. kochi*, and it is rarely found in deep water. In British waters it is supposed to be an indicator of the incursion of warmer waters on to the Continental Shelf, although peaks of abundance have been noted at all times of the year. Russell (1934, 1935) commented on an alternation in the occurrences of this species and *M. kochi* in the English Channel. Fraser (1968) has noted the presence of *M. atlantica* in the northern North Sea.

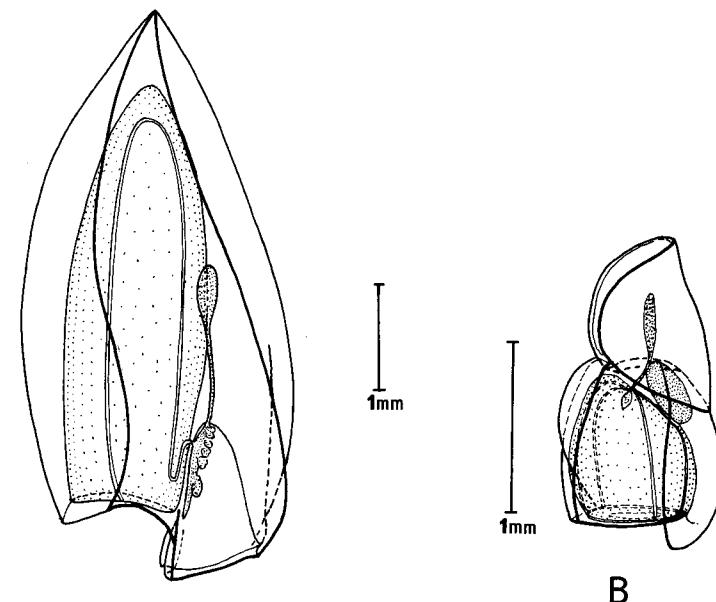


Fig. 45. *Muggiae kochi*. A, anterior nectophore, lateral view (after Totton, 1965).
B, *Muggiae* sp: eudoxid stage, lateral view (after Russell, 1938).

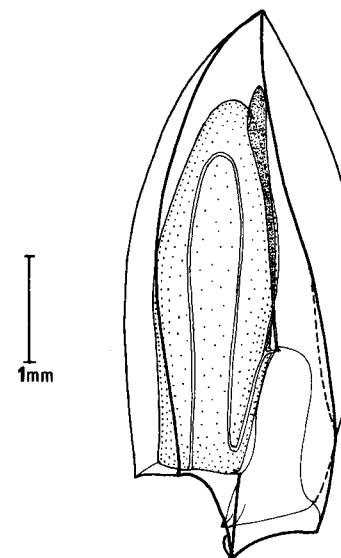


Fig. 46. *Muggiae atlantica*. Anterior nectophore, lateral view (after Totton, 1965).

Genus **DIMOPHYES** Moser, 1925
Monotypic genus for *D. arctica* (Chun, 1897)

Dimophyes arctica (Chun, 1897)
(Fig. 47)

Anterior nectophore. (Fig. 47A) Up to 15 mm in height, without lateral ridges. The nectosac often becomes opaque on preservation. The prominent undivided mouthplate is triangular in shape and the large hydroecium extends above the ostial level. The carrot-shaped somatocyst is about two thirds of the height of the nectophore.

Posterior nectophore. (Fig. 47B) Seldom found and much reduced. The deep hydroecium is bounded by two broad wings. The nectosac opens on to the baso-dorsal surface.

Eudoxid. (Fig. 47C) Up to 10 mm in height. The bract is conical with an extensive, thin neck shield. The phyllocyst has apical and lateral horns and a fine basal process, which passes down the neck shield. The gonophore has a very small mouthplate and only traces of a hydroecium.

Totton (1954) discussed the prevalence of this species in colder waters, although more recent information indicates a widespread distribution (Margulies, 1978), mainly at depths of 200–600 m or below 900 m. There are numerous British records, mainly from the deep, western waters from the Porcupine Seabight to the Wyville-Thomson Ridge. Russell (1939) noted its presence in the northern North Sea.

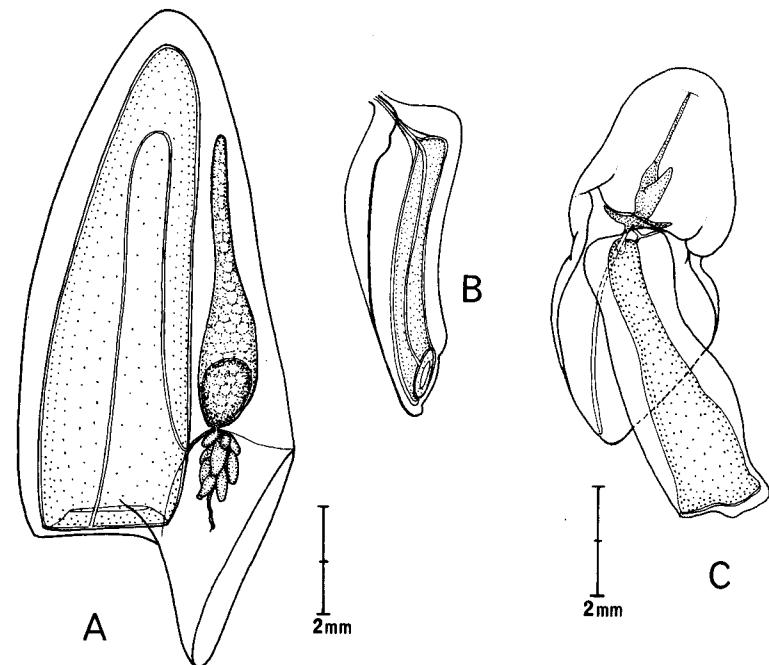


Fig. 47. *Dimophyes arctica*. A, anterior nectophore. B, posterior nectophore. C, eudoxid stage. (All lateral view; B, after Totton, 1965.)

Genus CHELOPHYYES Totton, 1932

Medium-sized diphynine siphonophores whose anterior nectophores have five ridges. The dorsal ridge extends only a short distance from the ostium. There is a single British species.

Chelophyses appendiculata (Eschscholtz, 1829)
(Fig. 48)

Anterior nectophore. (Fig. 48B) Up to 20 mm in height and very rigid in construction. Only three ridges reach the apex, one of the laterals as well as the dorsal being incomplete. The angular mouthplate is divided. The hydroecium is claw-shaped, extending to approximately one sixth of the nectophoral height. The somatocyst arises at the apex of the hydroecium, and is long and spindle-shaped. The nectophores often become opaque on preservation.

Posterior nectophore. (Fig. 48C,D) Slightly asymmetrical, with one baso-ventral process longer than the other. The basal parts of the ventral ridges are strongly serrated, each with a small but obvious tooth approximately at the ostial level. The apex of the nectophore is pointed.

Eudoxid. (Fig. 48E) Bract roughly conical with a small neck-shield, and a thickened, elongated phyllocyst. The gonophore has four longitudinal ridges which bear small serrations basally.

This is probably the commonest species of siphonophore, and is abundant in the warmer waters of the World's oceans, particularly in the top 300 m of water. In the North East Atlantic this species is found rarely north of the frontal region (approximately 42°–46°N) which represents the boundary between those waters with a permanent thermocline, to the south, and the northerly waters where only a seasonal thermocline is developed. The occasional incursions of warmer waters on to the European Continental Shelf bring with them several siphonophore species including *C. appendiculata*. Consequently there are several records for this species around the British Isles, particularly in the Porcupine Seabight and along the southwestern shelf edge.

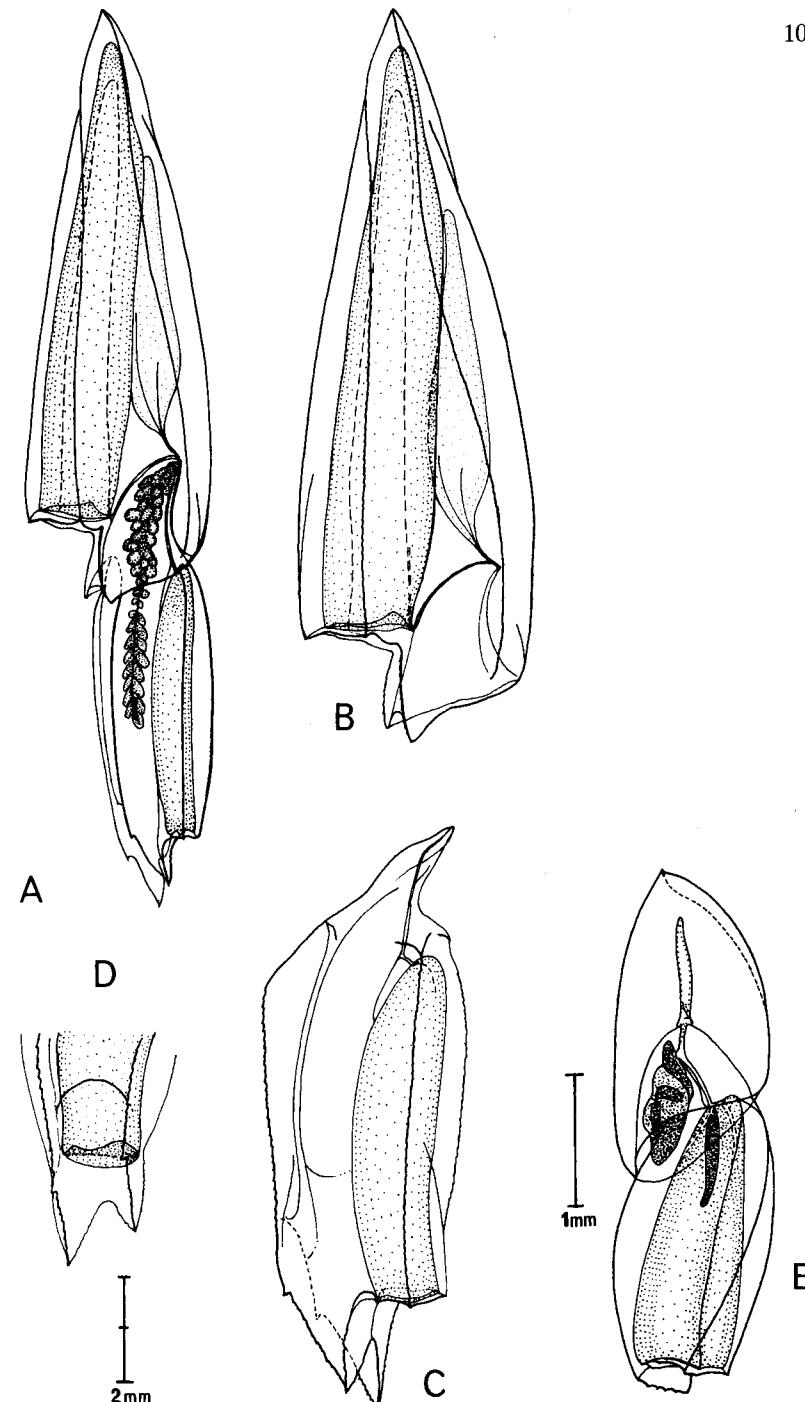


Fig. 48. *Chelophyses appendiculata*. A, whole polygastric stage. B, anterior nectophore. C, posterior nectophore. D, mouthplate detail of C (dorsal view). E, eudoxid stage.
(All lateral view except D; E, after Totton, 1965.)

Genus EUDOXOIDES Huxley, 1859

Small rigid nectophores, the anterior one having five ridges, of which the dorsal is complete. The ridges usually are serrated but there are no conspicuous ostial teeth. There is a single British species.

Eudoxoides spiralis (Bigelow, 1911)
(Fig. 49)

Anterior nectophore. (Fig. 49A) Up to 12 mm in height, with a characteristic spiral twist to the ridges. The ventral ridges unite close to the apex. The divided mouthplate is long and pointed. The hydroecium is claw-shaped, and the thickened somatocyst extends to about half the nectophoral height.

A posterior nectophore is not developed.

Eudoxid. (Fig. 49B) Bract, approximately 4 mm in height, roughly conical with two lightly serrated ridges and a wide, deep neck-shield. The phyllocyst is stout and long, reaching almost to the apex. The gonophore is twisted characteristically, its four ridges being lightly serrated.

A common, cosmopolitan species in the Atlantic Ocean (Pugh, 1974), although more often found in the warmer near-surface waters. There are a few records in British waters, ranging from the Celtic Sea shelf edge to the north west of Scotland.

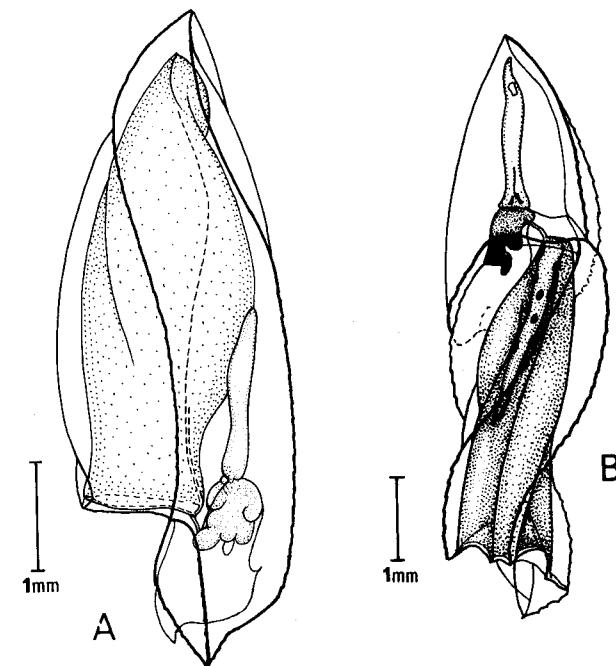


Fig. 49. *Eudoxoides spiralis*. A, anterior nectophore. B, complete eudoxid. (Both lateral view; B, after Totton, 1965.)

Family CLAUSOPHYIDAE

Both anterior and posterior nectophores possess a somatocyst. Totton (1965) suggests that the anterior nectophore may be the larval one which has been retained, so that the posterior, being thus the first definitive nectophore, would be expected to develop a somatocyst. However, this is not the case in the family Abylidae (see p. 129). The nectophores are stream-lined, although the hydroecium is more prominent than in the diphyids. The phyllocyst of the eudoxid bracts characteristically bears two fine basal branches extending down into the neck shield. There are five genera, all of which are represented in the British siphonophoran fauna.

Key to the British species of Clausophyidae

(based on the characters of the anterior nectophores)

1. Nectosac greater than half height of nectophore..... 2
Nectosac less than or equal to half height of nectophore 5
2. Hydroecium reaches to apex of nectophore (Fig. 53).....
..... *Crystallophyes amygdalina* (p. 120)
Hydroecium does not reach apex of nectophore 3
3. Somatocyst swollen at base, with pronounced lateral processes (Fig. 52) *Chuniphyes multidentata* (p. 118)
Somatocyst slightly swollen towards apex genus *Clausophyes* 4
4. Nectosac occupying most of nectophore; hydroecium not descending to ostial level (Fig. 51) *Clausophyes massiliana* (p. 116)
Nectosac occupying approximately two thirds of nectophore; hydroecium reaches ostial level (Fig. 50) *Clausophyes ovata* (p. 114)
5. Opaque pigment spots at apex and on lateral ridges (Fig. 54A)
..... *Heteropyramis maculata* (p. 122)
Without pigment spots (Fig. 55A) *Thalassophyes crystallina* (p. 124)

Genus CLAUSOPHYES Lens and van Riemsdijk, 1908

Smooth, unridged, laterally flattened nectophores. The anterior, which is usually smaller than the posterior, possesses a long, thin somatocyst which has an elongated swelling towards its apex. There are two British species.

moserae (Marenz., 1928)
Clausophyes ovata (Kersten and Ehlers, 1860)
 (Fig. 50)

The nectophores often show an iridescence.

Anterior nectophore. (Fig. 50A) Up to 20 mm in height, roughly triangular but rounded at its base. The deep hydroecium reaches to about the height of the nectophore and is open at the ostial level.

Posterior nectophore. (Fig. 50B) Up to 30 mm in height, with a large, notched mouthplate. The hydroecium extends the length of the nectophore and is bounded by large lateral wings. The somatocyst is long and narrow. Net catches usually contain more posterior than anterior nectophores.

Eudoxid. (Fig. 50C) Bract conical, up to 8 mm in height, with a rounded apex and an extensive neck-shield. The phyllocyst, slightly swollen basally, reaches the apex. The gonophore is unknown.

There are surprisingly few records for this species in the literature. Nonetheless it has a widespread bathypelagic distribution throughout the Atlantic Ocean from 60°N (our unpublished data) to 54°S (Totton, 1954). It is found most frequently in the 500–900 m depth range. There are several records for British waters, mainly from the Porcupine Seabight, but also from the shelf edge farther to the north (our unpublished data).

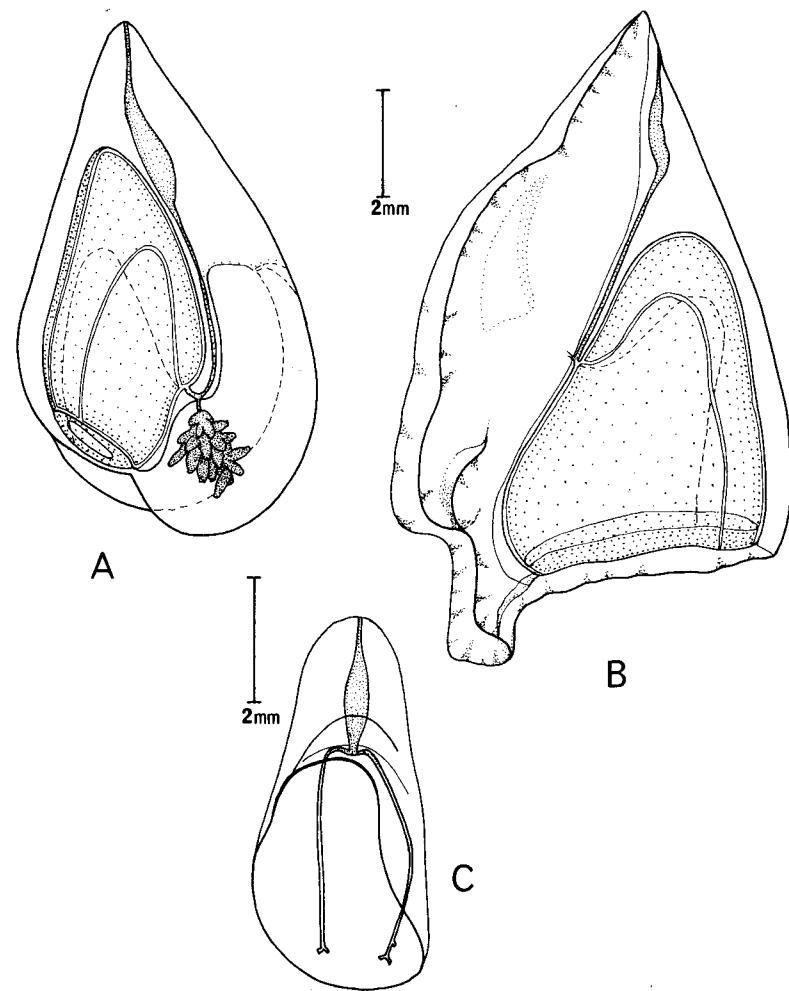


Fig. 50. *Clausophyes ovata*. A, anterior nectophore. B, posterior nectophore. C, eudoxid bract. (A, B, lateral view; C, ventral view; all after Totton, 1965.)

ovata (K&E, 1860)

Clausophyes massiliiana Patriti, 1969
(Fig. 51)

Anterior nectophore. (Fig. 51A) Oblong, up to 12 mm in height. The extensive nectosac has sinuous lateral radial canals. The deep hydroecium reaches to the nectophoral height but does not open basally.

Posterior nectophore. (Fig. 51B) Roughly triangular, up to 15 mm in height, without a distinct mouthplate. The hydroecium is variable in depth but has characteristically shaped lateral processes.

Eudoxid. (Fig. 51C,D) The bract is similar to that of *C. ovata* but the neck-shield is larger and the phyllocyst may be more swollen. The conical gonophore, up to approximately 5 mm in height, has two shallow longitudinal wings and a small, undivided mouthplate.

Patriti (1969) found this species in the western Mediterranean Sea at depths between 500 and 1000 m. Pugh (1975) found specimens at 32°N in the North Atlantic Ocean and more recent data indicate that it has a widespread distribution from the equator to 60°N. It is found mainly in the 500–600 m depth range, but also at depths down to 4200 m. There are two British records from the Porcupine Seabight (our unpublished data).

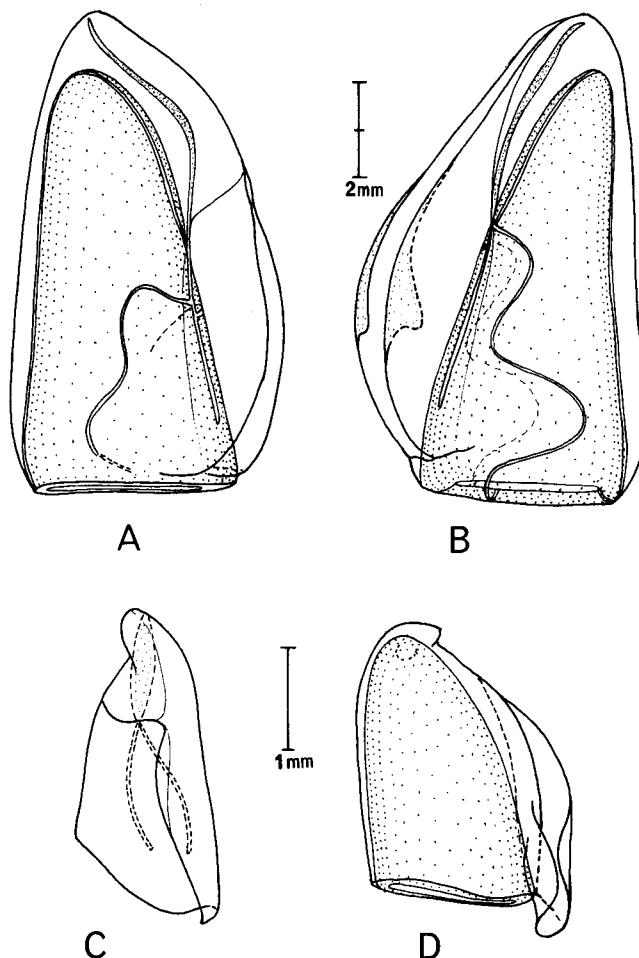


Fig. 51. *Clausophyes massiliiana*. A, anterior nectophore. B, posterior nectophore. C, eudoxid bract. D, gonophore.

Genus CHUNIPHYES Lens and van Riemsdijk, 1908

Nectophores with ridges which end in distinct basal teeth. There is a single British species.

Chuniphyes multidentata Lens and van Riemsdijk, 1908
(Fig. 52)

The nectophores are rigid in structure.

Anterior nectophore. (Fig. 52A) Up to 35 mm in height with four ridges at apex. The dorsal and the two laterals bifurcate just below the apex; the ventral continues undivided to the opening of the hydroecium about half way down the nectophore. The dorso-lateral ridges end basally in prominent teeth. The nectosac reaches just over half the nectophoral height; the deep hydroecium is shorter. The somatocyst has two broad wings at its base and a median tube reaching the apex.

Posterior nectophore. (Fig. 52C) Up to 40 mm in height, with three ridges at apex, each dividing below and ending basally in a distinct tooth. Ventro-lateral teeth are most pronounced and delimit an asymmetrical mouthplate. The shallow hydroecium, which extends to the apex, is bounded by two unequal wings.

Eudoxid. (Fig. 52E,F) Bract much reduced and flattened; phyllocyst laterally expanded with a short apical process. Gonophore five-ridged at apex, the laterals ending in prominent teeth. The point of attachment to the bract lies on the mid-ventral surface.

This species is well-known in the Atlantic Ocean, most commonly at depths of 400–600 m or greater than 900 m. There are many records from the deeper waters to the west of the British Isles.

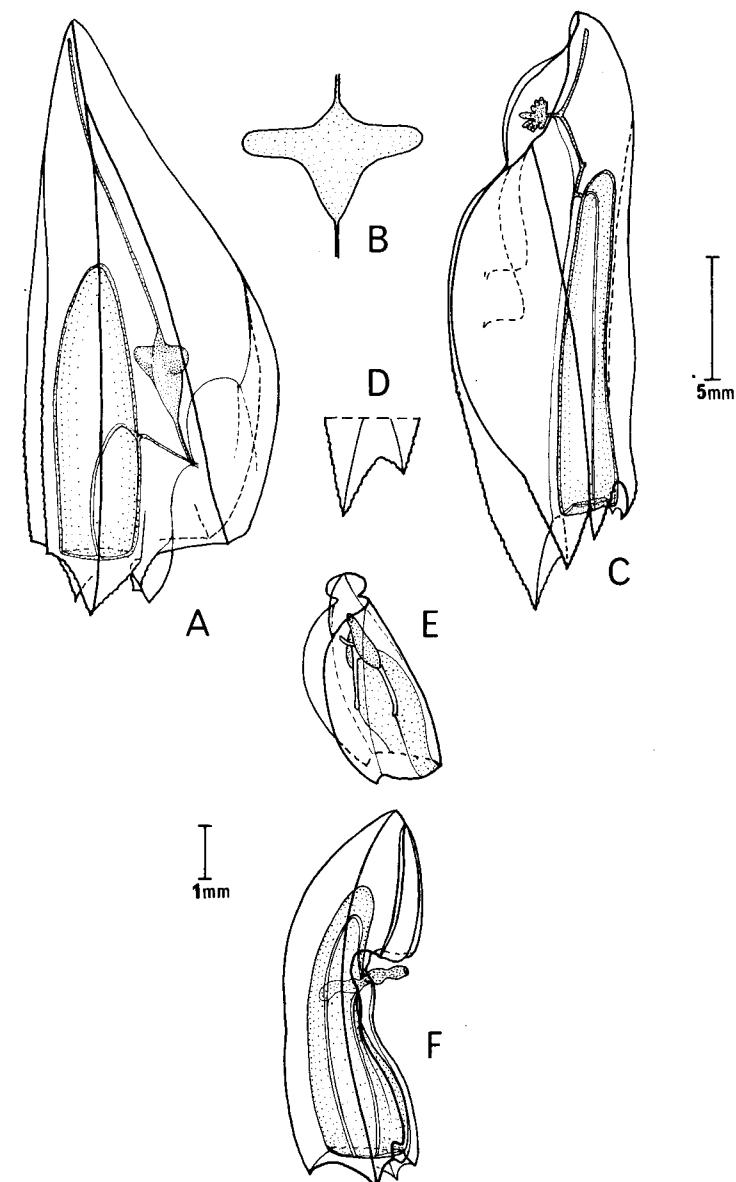


Fig. 52. *Chuniphyes multidentata*. A, anterior nectophore. B, detail of somatocyst (dorsal or ventral view). C, posterior nectophore. D, mouthplate detail of C (ventral view). E, eudoxid bract; F, gonophore. (All lateral view except B, D; E, F after Leloup, 1955.)

Genus CRYSTALLOPHYES Moser, 1925
Monotypic genus for *C. amygdalina* Moser, 1925

Crystallophyes amygdalina Moser, 1925
(Fig. 53)

The nectophores are small and delicate.

Anterior nectophore. (Fig. 53A) Up to 7 mm in height, with five complete ridges; the laterals are sharply recurved basally. The nectosac extends to about three quarters of the height of the nectophore and the shallow hydroecium almost reaches the apex. The somatocyst is swollen for much of its length.

Posterior nectophore. (Fig. 53B,C) Up to 8 mm in height, with five ridges, the laterals and ventrals joining close to the apex. The hydroecium extends the full length of the nectophore and the hydroecial folds bear small pointed flaps. The somatocyst is long and thin.

The eudoxid phase is not known.

This species was described originally from the Antarctic Ocean but Margulis (1978) has found specimens as far north as 65°N, usually in the 200–500 m depth range. It is an uncommon species in the 'Discovery' collections for the North East Atlantic Ocean, but there are six records in British waters, all from the vicinity of the Porcupine Seabight (our unpublished data).

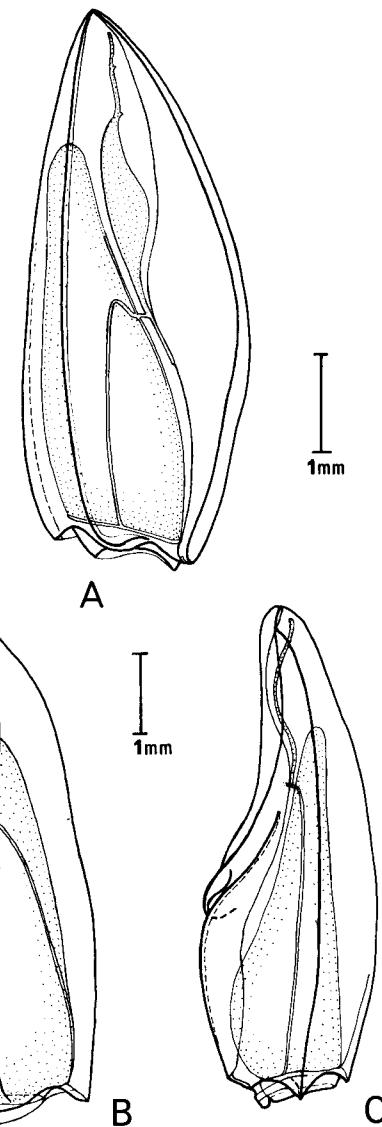


Fig. 53. *Crystallophyes amygdalina*. A, anterior nectophore. B, C, posterior nectophore. (A, C, lateral view; B, ventral view.)

Genus HETEROPYRAMIS Moser, 1925
 Monotypic genus for *H. maculata* Moser, 1925

Heteropyramis maculata Moser, 1925
 (Fig. 54)

Anterior nectophore. (Fig. 54A) Pyramidal, up to 12 mm in height, with five ridges at the apex. Nectosac occupies less than half nectophore, but the deep hydroecium extends to two thirds of the height. Somatocyst is thick and slanting basally with a narrow apical extension. Opaque spots on the dorso-lateral ridges and at the apex are characteristic, usually numbering seven or nine.

The posterior nectophore has not been identified.

Eudoxid. (Fig. 54B,C) Bract pyramidal, up to 3 mm in height, with four ridges and pigment spots at the base of the dorsals and at the apex. Gonophore rectangular with spots at opposite corners.

An uncommon species, but widespread in the Atlantic from 62°N (Margulis, 1978) to 34°S (Totton, 1954); most commonly found in the 300–1500 m depth range (our unpublished data). There is a single British record, from the Porcupine Seabight, although Fraser (1961, 1967) found it to the north west of Scotland just outside the designated area for British waters.

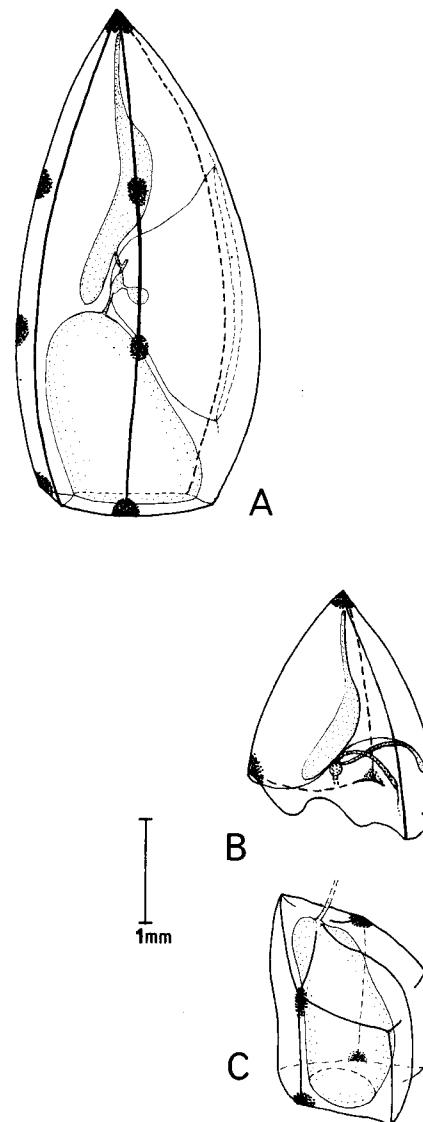


Fig. 54. *Heteropyramis maculata*. A, anterior nectophore. B, eudoxid bract. C, gonophore. (All lateral view.)

Genus THALASSOPHYES Moser, 1925
 Monotypic genus for *T. crystallina* Moser, 1925

Thalassophyes crystallina Moser, 1925
 (Fig. 55)

This species is very similar to, if not identical with, *Heteropyramis maculata*, except that it does not possess opaque pigment spots. As with the latter species the posterior nectophore has not been identified. The eudoxid stage may be confused with *H. maculata*, in which the spots sometimes are indistinct.

A rare species which occurs in the North Atlantic between 0° and 11°N, and, more often between 40° and 60°N (our unpublished data). It has a wide depth distribution from 300 to 2500 m. The four British records are from the deeper western waters, while Fraser (1961, 1967) also recorded it from just outside the designated area.

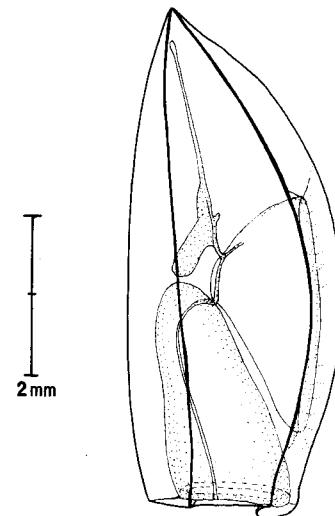


Fig. 55. *Thalassophyes crystallina*. Anterior nectophore (lateral view).

Family SPHAERONECTIDAE

The single genus, *Sphaeronectes* Huxley, 1859, contains several species which retain the larval nectophore as the only nectophore in the polygastric stage (see Carré, 1969).

Genus SPHAERONECTES Huxley, 1859

Larval nectophore is rounded, small and fragile; often lost or damaged during net collection. There is a single British species.

Sphaeronectes gracilis (Claus, 1873, 1874) (Fig. 56)

Nectophore. (Fig. 56A) Spherical, up to 8 mm in height, with large nectosac reaching to half its height. Four straight radial canals arise at the apex of the nectosac, over which bends the long, narrow hydroecium. Somatocyst short and curved, with a slight distal swelling.

Eudoxid. (Fig. 56B) Small and hemispherical with a minute, basal neck-shield. The phyllocyst is long, obliquely angled and club-shaped. The gonophore is a simple bell, thickened towards its apex.

Usually found in warmer waters close to the surface. It is common in the western Mediterranean Sea (Carré, 1969). The several records for British waters presumably resulted from incursions of warmer waters on to the Continental Shelf. There is a single record for the English Channel and several to the north and west of Scotland (Fraser, 1961, 1967, 1968).

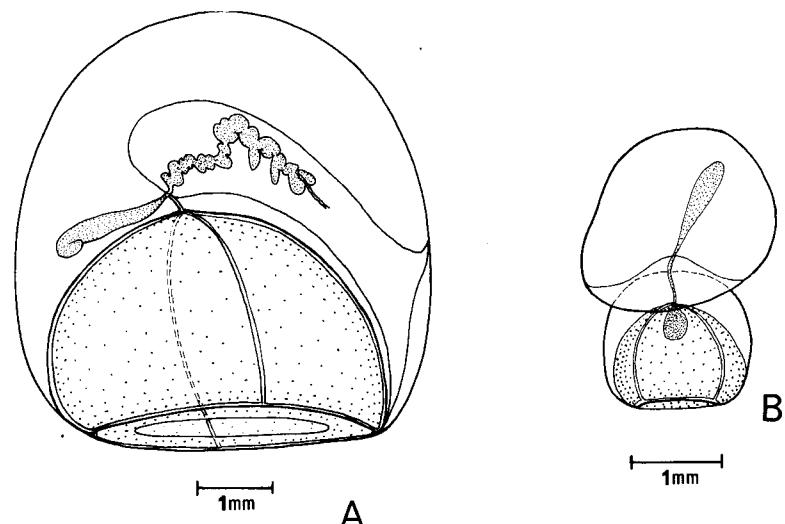


Fig. 56. *Sphaeronectes gracilis*. A, nectophore. B, eudoxid stage. (Both lateral view.)

Family ABYLIDAE

During development a temporary larval bract is formed before the larval nectophore. The latter is retained in the polygastric stage as the anterior nectophore. All but one species develop a second (definitive) nectophore, the posterior, which usually is considerably larger than the anterior and does not possess a somatocyst (cf. Clausophyidae). Nectophores are rigid and angular, the posterior one usually bearing serrated ridges and teeth. The hydroecium of the anterior nectophore is an enclosed tube opening basally.

The Abylididae is split into two subfamilies based on the presence (Abylinae) or absence (Abylopsinae) of a rectangular apical facet.

Key to the British Species of Abylididae

(based on characters of anterior nectophores)

1. Nectophore elongated and pointed at apex; nectosac extending to well above somatocyst (Fig. 57) *Ceratocymba sagittata* (p. 130)
- Nectophore pyramidal or polyhedral; nectosac not extending above somatocyst 2
2. Nectophore pyramidal, with a dorsal ridge (Fig. 60A)
- *Enneagonum hyalinum* (p. 136)
- Nectophore with a pentagonal dorsal facet; dorsal ridge absent 3
3. Somatocyst with apical diverticulum (Fig. 58)
- *Abylopsis tetragona* (p. 132)
- Somatocyst without apical diverticulum (Fig. 59)
- *Bassia bassensis* (p. 134)

Genus CERATOCYMBIA Chun, 1888

Abyline siphonophores with characteristically shaped bract, called a **cymba**. The ventro-lateral facet of the anterior nectophore is not divided by a horizontal ridge. The ridge arrangement on the posterior nectophore is diagnostic. There is a single British species.

Ceratocymba sagittata (Quoy and Gaimard, 1827)
(Fig. 57)

Anterior nectophore. (Fig. 57A) Roughly pyramidal, up to 40 mm in height. The long nectosac, reaching two thirds of the nectophoral height, is about twice the length of the hydroecium. The ovoid somatocyst does not extend above the hydroecium.

Posterior nectophore. (Fig. 57B) Oblong, up to 50 mm in height, pointed apically and bearing a characteristically elongated serrated ventral tooth. The hydroecium is bounded by two serrated ventral wings, one of which has a 'comb' of 6–7 large teeth.

Eudoxid. (Fig. 57D,E) Bract large, up to 20 mm in length, roughly triangular with a concave apical facet and prominent lateral horns. The cylindrical phyllocyst recurses basally and has two fine apical processes. The gonophore bears ventral ridges, serrated for most of their length and terminating in pronounced asymmetrical ventral teeth.

This is a common species in the shallow depths (0–300 m) of the warmer Atlantic waters. It is found rarely in temperate waters and consequently there is only a single British record from west of the Hebrides (Fraser, 1967).

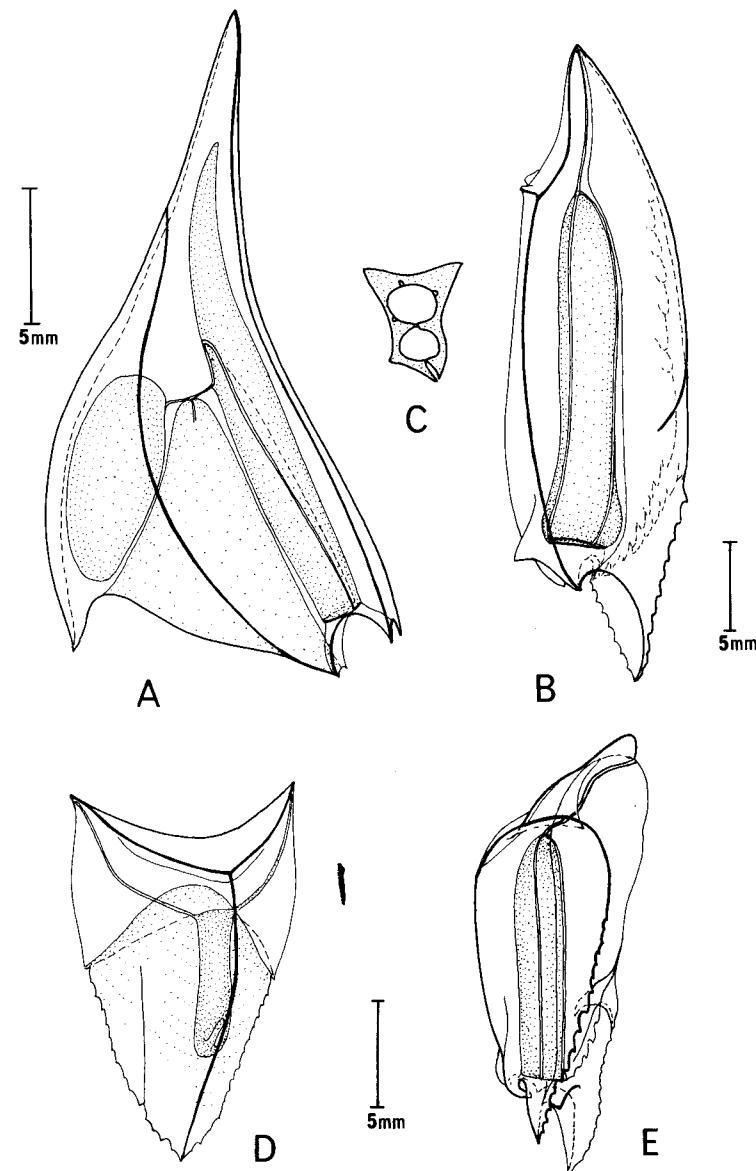


Fig. 57. *Ceratocymba sagittata*. A, anterior nectophore. B, posterior nectophore. C, cross section of B. D, eudoxid bract. E, gonophore. (A, B, E, lateral view; D, dorso-lateral view; C, E, after Sears, 1953.)

Genus ABYLOPSIS Chun, 1888

Anterior nectophore with a pentagonal dorsal facet without a median ridge. The somatocyst has an apical diverticulum. Posterior nectophore has prominent basal teeth. There is a single British species.

Abylopsis tetragona (Otto, 1823)
(Fig. 58)

Anterior nectophore. (Fig. 58B) Polyhedral, up to 10 mm in height. The nectosac extends above the main body of the somatocyst.

Posterior nectophore. (Fig. 58C) Up to 40 mm in length, with each longitudinal ridge ending basally in a stout tooth, one being more pronounced. One hydroecial wing bears a 'comb' of about nine teeth.

Eudoxid. (Fig. 58D,E) Bract up to 7 mm in height with a pentagonal dorsal facet whose lateral ridges run parallel to each other. The phyllocyst has two large, swollen lateral processes, an apical diverticulum and a long, thin basal branch. Gonophore oblong and slightly asymmetric.

A common species in the warmer water of the Atlantic Ocean and in the Mediterranean, usually in the top 100 m of water. The 'Discovery' collections in the North East Atlantic show only one record north of 30°N, while the single British record comes from the region off the Hebrides (Fraser, 1967).

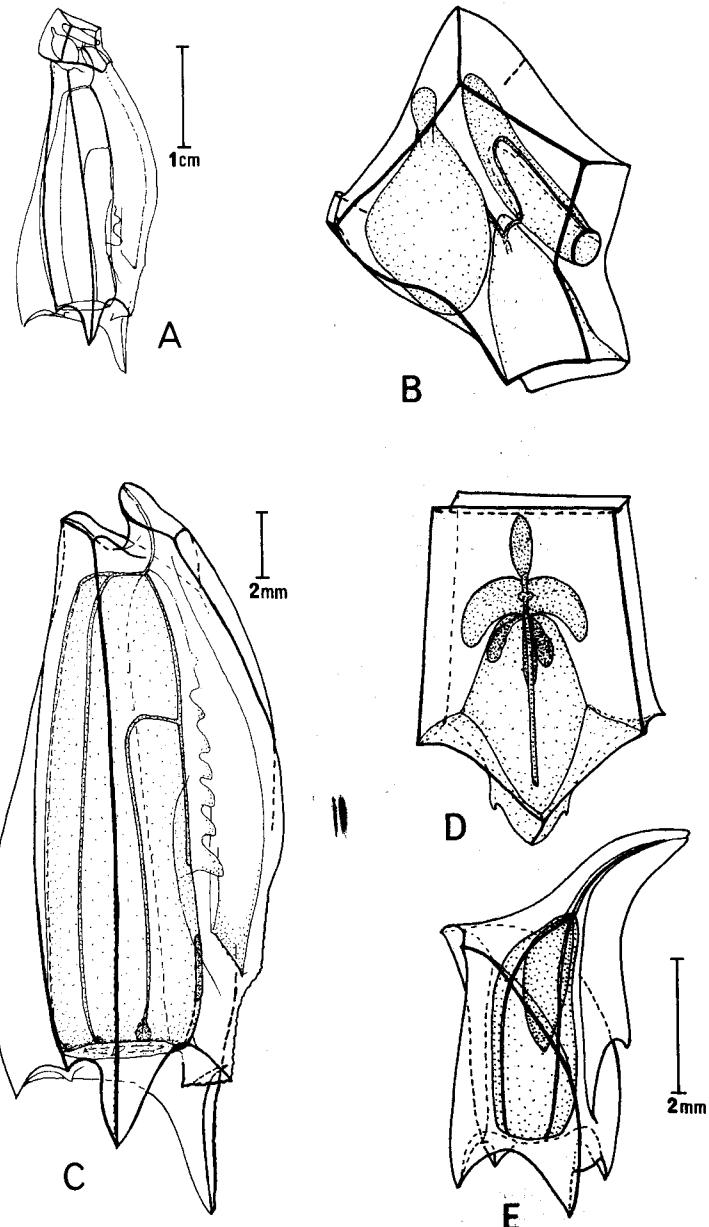


Fig. 58. *Abylopsis tetragona*. A, whole animal. B, anterior nectophore. C, posterior nectophore. D, eudoxid bract (dorsal view). E, gonophore. (All lateral view except D; E, after Sears, 1953.)

Genus BASSIA Agassiz, 1862
 Monotypic genus for *B. bassensis* (Quoy and Gaimard, (1833) 1834)

Bassia bassensis (Quoy and Gaimard, (1833) 1834)
 (Fig. 59)

There is a bluish tinge to the ridges of both the nectophores and the eudoxids.

Anterior nectophore. (Fig. 59) Similar in shape to that of *Abylopsis tetragona*, reaching 7 mm in height. The hydroecium does not extend up between the nectosac and somatocyst, this latter being large, globular and without an apical diverticulum.

Posterior nectophore. (Fig. 59B) Rectangular, up to 15 mm in length, with four main ridges which end in short basal teeth. A replacement posterior nectophore may be developed if the original is lost.

Eudoxid. (Fig. 59C) Bract, up to 8 mm in height, has a quadrilateral dorsal facet. The phyllocyst is a long tube, swollen apically and without lateral processes. Gonophore has four longitudinal ridges which end basally in minute teeth.

A very common species in the shallow (0–100 m) warmer waters of the Atlantic and other oceans. Numbers decline rapidly north of 42°–45°N. There are several records from off North and North West Scotland (Fraser, 1961, 1967), and one to the west of Ireland. It does not appear to have been found in shallower waters around Britain.

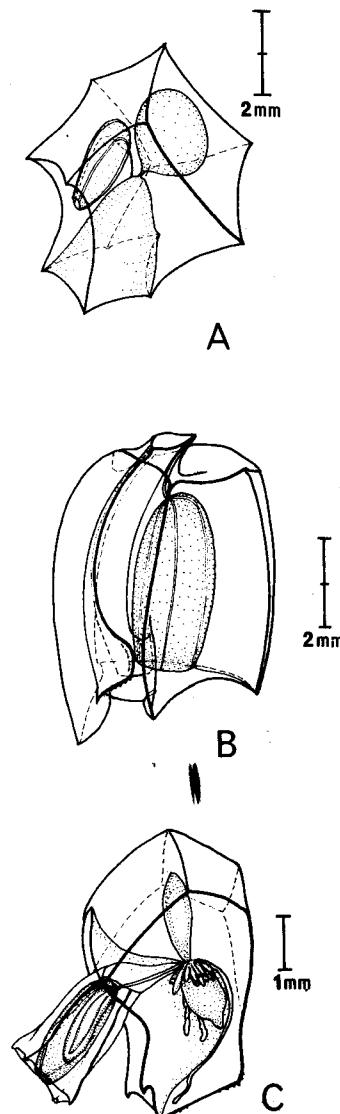


Fig. 59. *Bassia bassensis*. A, anterior nectophore. B, posterior nectophore. C, eudoxid
 (A after Quoy and Gaimard, 1833; B after Basson, 1952; C after Bigelow, 1911.)

Genus ENNEAGONUM Quoy and Gaimard, 1827
Monotypic genus for *E. hyalinum* Quoy and Gaimard, 1827

Enneagonum hyalinum Quoy and Gaimard, 1827
(Fig. 60)

Anterior nectophore. (Fig. 60A) The only nectophore to be developed is large, roughly pyramidal, and up to 15 mm wide. The conical somatocyst lies above the hydroecium, the latter reaching to only half the height of the nectosac.

Eudoxid. (Fig. 60B,C) Bract cuboidal, up to 12 mm in height, with slightly concave facets. The phyllocyst has two swollen lateral wings and a short apical process. Gonophore large with five serrated ridges terminating in pronounced teeth of varying sizes.

A well-known species from the warmer Atlantic waters. Pugh (1974) found a peak of abundance in the 415–450 m depth range, but specimens have occurred at all depths from 0 to 4040 m. The species is absent in the 'Discovery' collections north of 44°N, but there are two British records to the north west of the Hebrides (Fraser, 1967).

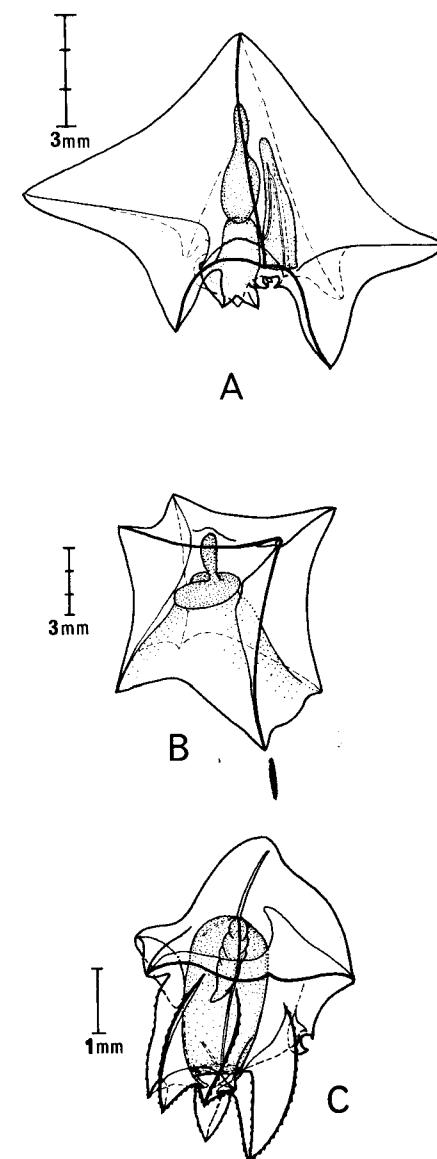


Fig. 60. *Enneagonum hyalinum*. A, anterior nectophore. B, eudoxid bract. C, gonophore. (All lateral view; after Sears, 1953.)

VELELLIDS:
ORDER ATHECATA.
FAMILY VELELLIDAE

Introduction

As mentioned in the introduction to the section on British Siphonophora (p. 3), the velellids were once thought to be closely related to that group. However, recent investigations (e.g. Mackie, 1959) have demonstrated that there is only a distant relationship between the two groups. Formerly the velellids were considered as a distinct order, the Chondrophorae, within the Class Hydrozoa, but now they are considered as a family, the Velellidae, within the suborder Capitata of the order Athecata (= Anthomedusae). The systematics within the velellid family also have undergone numerous alterations over the past century. Haeckel (1888), for instance, recognized 36 species distributed among nine genera. However, many of these 'species' have been shown to be merely growth stages of others, as summarized by Bigelow (1911) who reduced the number of species to seven, within three genera. Each of these genera contained a species which was found only either in the Pacific or in the Atlantic Ocean, and the seventh species inhabited only the Indian Ocean. Several subsequent authorities have concluded that there are no specific differences between these geographically separated forms and thus now only three species in monotypic genera are recognized. One of these, *Porpema prunella* (Haeckel, 1888) remains little known. Of the two others, *Velella velella* (Linné, 1758) and *Porpita porpita* (Linné, 1758) only the former occurs in British waters.

Velella velella (Linné, 1758)

General Structure

The Hydranth. The hydranth or hydroid stage is unmistakable (Fig. 61B). It is a pleustonic animal floating at the sea surface. The float, which is elliptical or nearly quadrangular in shape and measures up to 10 cm in length, has a deep-blue colour and a cartilaginous consistency. This raft-like structure bears a triangular fin that runs diagonally across its upper surface and is set to act as a 'sail'. This 'sail' gives the animal both its Latin name (i.e. from *velum*, a sail) and its colloquial name, Jack Sail-by-the-Wind. The animals exist in two (dimorphic) forms depending on the position of the sail on the float (Fig. 61C,D). The two types 'sail' either to the left or to the right of the wind direction, as happens with the dimorphic forms of the Portuguese Man O'War.

At first glance, the organization of the velelid hydranth appears to bear no relation to its presumed sessile hydroid ancestor. However, several authors, as reviewed by Field and Mackie (1971), have drawn attention to the homologous structures in each, but these similarities need not be considered here. Within the float of *Velella* there are a number of chitin-lined chambers which are arranged in concentric rings, while around its edge there is an outfolding which forms a skirt or **mantle** to the hydranth (Fig. 61E). This mantle is a flexible structure which normally lies along the surface film probably acting as a stabilizer. However, if the hydranth accidentally is capsized e.g. by wave action, then it can right itself by flexions of the mantle. The upper surface of the whole animal is water repellent.

Beneath the float are attached various organs, the most conspicuous of which is the central **siphon** (Fig. 61E), which is surrounded by numerous small actively moving siphons (Cheng, 1975) or **blastostyles** (Field and Mackie, 1971). These latter may ingest food but they also bear the gonophores (Fig. 61E). Finally, the float is fringed below by a large number of short, submarginal tentacles which bear numerous nematocysts. The cavities of the various siphons and tentacles connect into a widespread gastrovascular system which forms an anastomizing network mainly concentrated above the central siphon. Some researchers consider this area to be excretory in function and thus it has been termed a 'liver'.

Medusa or Chrysomitra Stage. (Fig. 61A) The medusa is released from a gonozooid on the hydranth before it is fully developed and initially measures approximately 1.5 mm in height. The mouth of the manubrium does not open for several days and later still two pairs of tentacles, bearing terminal

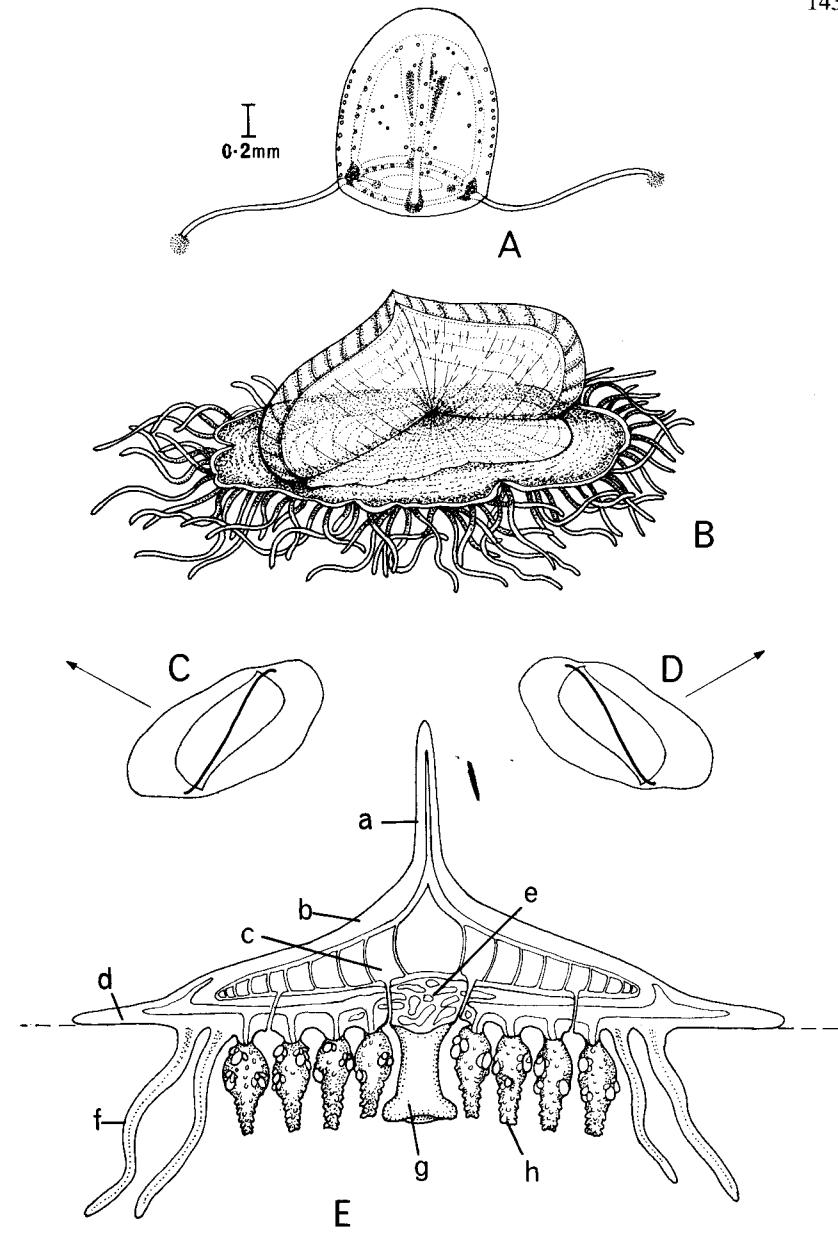


Fig. 61. *Velella velella*. A. Chrysomitra or medusa stage. B, adult hydranth (dorso-lateral view). C, D, dimorphism in sail position (top view). E, diagrammatic section through hydranth. (A, E, lateral view; A, after Brinckmann-Voss, 1970; B, after Haeckel, 1888; C, D, after Savilov, 1969.) (a, sail; b, float; c, chitin-lined chamber; d, mantle; e, 'liver'; f, tentacles; g, central siphon; h, blastostyles bearing gonophores.)

nematocyst bulbs, appear. Eventually the gonads become mature and the sexual products are released. The chrysomitra then dies.

Life History

During its extended development it is assumed that the free medusa sinks down through the water column to depths of 600–1000 m. Thus, after external fertilization of the eggs, the early developmental stages are presumed to take place at depth, although not all authorities agree on this point. Little is known of these early stages and the first larva identified is the **conaria**, which possesses a pair of short, aboral tentacles, a rudimentary float, and a conspicuous crimson cone which secrets oil droplets. This oil makes the larva positively buoyant and it ascends slowly through the water column to the sea surface. Further development meanwhile results in the loss of the larval tentacles and a transformation into a **rataria** larva. At the sea surface, the hollow, adult tentacles appear with a cruciform symmetry, the float becomes further enlarged and the sail appears. The hydranth then gradually increases in size.

The exact significance of the developmental period at depth is not clear, but Savilov (1969) demonstrates that it could aid either the dispersion of the species or, contrariwise, its retention within a certain geographical region, depending on the relative strengths and directions of the superficial and deep ocean currents.

Feeding

The peripheral tentacles of the hydranth are armed with numerous nematocysts to capture its prey which includes near-surface living crustaceans (mainly copepods), larval fish, and the eggs of various invertebrates. Both the hydranth and the chrysomitra also possess symbiotic zooxanthellae within their tissues, but whether these make any contribution to the energy budget of their hosts is uncertain. Although the tentacles can undergo concerted synchronous contractions, Garstang (1946) commented that they were poorly adapted for the capture of prey. Indeed he suggests that the mucous glands, which are densely packed around the margin of the hydranth, may produce an ensnaring web of threads. Nonetheless, as Savilov (1969) observes, the stomachs of velellids frequently are filled with large prey items and he comments on their importance as predators in the pleustonic/neustonic community. Further, the diet of many surface-dwelling animals, excluding the Portuguese Man O'War, is based largely on velellids. One particular example is the pelagic snail, *Ianthina*. This violet-blue shelled mollusc secretes a bubble raft to keep it afloat but when it encounters a velellid it attaches itself to the underside and browses on the various appendages.

General Ecology

Velella velella is most commonly found on the surface of the warmer waters of the World's oceans. The hydranths have no organs of propulsion but the presence of the sail enables them to be pushed over the water by the prevailing winds. Further, the fact that the sail is not aligned along the long axis of the float, but diagonally across it, means that the animals are not pushed directly downwind, but at an angle to it. The dimorphism in the positioning of the sail means that one form, the so-called North West one, sails to the left of the downwind direction, while the South West form sails to the right (Fig. 61C,D). The angle at which the animals sail varies according to the wind velocity, as Savilov (1969) discusses, and clearly a population initially containing both forms would soon be sorted into two pure shoals should a consistent wind blow. Savilov (1969) further discusses the geographical distribution of the two forms in the Pacific Ocean, with particular reference to the prevailing meteorological conditions. He noted that the right-sailing (South West) forms predominated in the central zone of the North Pacific, whilst the left-sailers (North West) occupied a peripheral zone; a result which would be consistent with the overall anticyclonic wind circulation.

Edwards (1966) found that both dimorphic forms were present in the North Atlantic Ocean with, from the available records, the left-sailing (North West) form predominant. Thus the majority of records for strandings of *Velella* around the British Isles are for left-sailing forms as would be expected because of the prevailing westerly winds. Further south, along the Iberian Peninsula, more right-sailing forms are found. Occasionally the right-sailing forms are stranded on British beaches and Edwards (1966) suggests that they may be young, recently surfaced animals which have not had time to be pushed further south. Also, because of the prevailing wind conditions, most of the records for the British Isles come from the west coast of Ireland, with others from the Scilly Isles, Cornwall and Pembrokeshire. Turk (1982) recently has reported sightings of exceptionally large numbers of *Velella* stranded on the coasts of Cornwall.

Collection and Preservation

Many of the British records are for specimens stranded on beaches, particularly in western regions, and so a search along the tide line may prove fruitful. Otherwise, since the hydranths are pleustonic animals, they may be collected by skimming a net along the surface of the sea or simply spotted from a boat and dip-netted. As with siphonophores, they can be preserved in 5% formalin.

Glossary

- abaxial** Opposite to, or situated away from, the stem or axis.
- aboral** Opposite to, or situated away from, the ostium.
- apical** Situated at the apex.
- apical wings** Apico-lateral processes of physonect nectophores, which extend around stem.
- athorybia stage** The stage in physonect development when the larva bears a pneumatophore, primary gastrozoid and tentacles and a ring of larval bracts.
- aurophore** Gas secreting structure in the pneumatophore of the Rhodaliidae.
- axial** Situated at, or close to, the stem or axis.
- basal facet of mouthplate** Ventral surface of mouthplate in calycophoran anterior nectophore, which may articulate with posterior nectophore.
- basal lamella** A thin extension of the nectophore below the ostium of the nectosac; one or more lamellae comprise the mouthplate.
- blastostyle** Siphosomal element which bears gonophores.
- bract** Siphosomal element, usually containing much mesogloea, with protective or buoyancy function.
- central organ** Swelling at junction of canal system and stem in some Prayidae.
- chrysomitra** Medusa stage in *Velella velella*.
- commissural canals** Transverse connections on the nectosac between lateral radial and ventral canals (*Sulculeolaria* spp. only).
- conaria** First known larval stage of *Velella velella*.
- corm** Contracted nectosome and siphosome of the Rhodaliidae forming a globular mass below the pneumatophore.
- Cormidum** An organized group of siphosomal elements, usually including a gastrozoid, tentacle, palpons (in physonects), blastostyle and bracts.
- cymba** Angular and flattened eudoxid bract, characteristic of *Ceratocymba* spp.
- ectoderm** Outer cell layers of Cnidaria.
- endoderm** Inner cell layer of Cnidaria.
- eudoxid** Reproductive stage of calycophorans, which usually becomes detached from polygastric stage.
- gas-gland** Area of secondary ectoderm which secretes gas to inflate pneumatophore.
- gastrovascular cavity** Central cavity with both digestive and circulatory functions; in the fully developed polygastric stage this becomes a gastrovascular canal system.
- gastrozoid** Feeding polyp, situated on the siphosome, bearing a tentacle usually with several tentilla.
- gonodendron** An organized group of gonopalpons, gonophores and occasionally asexual nectophores, developed from the siphosome.
- gonopalpon** A specialized palpon, budded from the gonodendron.
- gonophore** Medusa stage bearing sexual products.
- hydroecium** Ventral cavity of calycophoran nectophore into which the siphosome may be wholly or partly retracted.
- lateral ridges** Cross ridges, bordering the apical wings, present on some physonect nectophores.
- mantle** An outfolding along the float edge in *Velella velella*, probably with a stabilizing function.
- manubrium** Central structure inside gonophore on which the sexual products are developed.
- mesogloea** Non-cellular layer separating ectoderm and endoderm.
- mouthplate** See basal lamella.
- neck shield** Thin extension of eudoxid bract which partly surrounds gonophore.
- nectophore** Swimming bell.
- nectosac** Central cavity of nectophore, opening to exterior via the ostium and having muscular walls with propulsive function.
- nectosome** Section of stem which bears nectophores.
- nematocysts** Stinging cells, chiefly carried on tentilla and used to immobilize prey.
- neustonic** Found in surface layers of sea.
- ostium** Nectosac opening, through which water is expelled for propulsion.
- pallial canal** Section of gastrovascular system which joins radial canals on nectosac to somatocyst.
- paedophore** An asexual, larval nurse carrier of other polyps.
- palpacle** A small tentacle borne on a palpon.
- palpon** A cormidial element, probably a reduced gastrozoid, which may have sensory or excretory functions.
- phyllocyst** The reduced gastrovascular canal system in a eudoxid bract.
- pleustonic** Surface-drifting.
- pneumadenia** Synonym of gas-gland.
- pneumatophore** Apical, gas-filled float, present in Cystonectae and Physonectae; in the latter its function can be for orientation rather than buoyancy.
- polygastric stage** Complete animal bearing both asexual and reproductive elements.
- radial canals** Branches of the gastrovascular system, usually four in number, lying on the nectosac surface and linked to the pallial canal.
- rataria** Final larval stage of *Velella velella*.
- rête** A flattened, disc-shaped expansion on a canal; function unknown.
- siphon** A tubular structure in *Velella velella*, probably with a digestive function.
- siphosome** Section of stem below nectosome, generally long, bearing cormidia.
- somatocyst** Prominent extension of gastrovascular system in calycophoran nectophore.
- spur canals** Reduced longitudinal canals in gastrovascular system of prayid eudoxid bracts.
- tentacle** A hollow, highly contractile organ with sensory, feeding and occasionally anchoring functions.
- tentilla** Side branches of tentacle, bearing nematocysts.
- thrust block** Aboral section of a physonect nectophore, separating apical wings and abutting against nectosomal stem.
- transverse commissures** Synonym of commissural canals.
- velar ridge** Cross ridge, parallel to ostium, on nectophores of some *Lensia* spp.
- veronica** A spiral movement which spreads the tentacles into a characteristic pattern.
- zooxanthellae** Unicellular algae, living in symbiotic association in the tissues of many Cnidaria.

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