

# Siphonophorae

Phil R. Pugh

## Introduction

Siphonophores are complex, highly polymorphic hydrozoan cnidarians, whose "colonies" are formed by many medusoid and polypoid "individuals" that function physiologically as a single entity. They occur in a bewildering variety of shapes and sizes, from about 1 mm to several tens of metres in length. However, because of their fragility they are difficult to study both taxonomically and ecologically. The most famous, and first to be described, siphonophore is the Portuguese Man O'War, *Physalia physalis* (Linné, 1758), that floats at the surface of the ocean, with its stinging tentacles hanging down many metres into the water below. However, this species is exceptional, and almost all other siphonophore species are permanently planktonic, exclusively marine animals. The only other exception is a small group, of the family Rhodaliidae, that have become benthic attaching themselves to the sea-bed like tethered air-balloons.

There are 3 basic types (orders) of siphonophores that are classified according to whether an apical, gas-filled float is present (Cystonectae and Physonectae) or absent (Calycophorae). Those with a float are subdivided on the basis of the presence (Physonectae) or absence (Cystonectae) of a group of swimming bells immediately below the float. About two-thirds of the ca. 150-160 currently recognised species belong to the Order Calycophorae, and these predominate in samples collected by nets. However, from limited collections with submersibles, about two-thirds of the species and three-quarters of the specimens are physonects. This is probably because most calyco-phoran species are small and difficult to see, while many physonects are large and brightly coloured, and their spectacular appearance quickly draws one's attention to them. Many of the species collected by submersible have proved to be new to science. Thus, even though net collections have already demonstrated the importance of siphonophores in the marine ecosystem, the true significance of these animals can only be appreciated fully by combining the data from such collections with *in situ* observations.

Siphonophores are present throughout the World's oceans, and throughout the water column down to a depth of at least 4500 m, although individual species may have restricted latitudinal or depth ranges. The majority are truly oceanic, but a few species are neritic, occurring in shallow inshore waters where the salinity is not greatly reduced. In addition, in regions of high salinity, such as the Red Sea, species diversity can be greatly reduced.

Unlike most other hydrozoan coelenterates, siphonophores do not show an alternation of generations between an attached, asexual polyp stage and a free-swimming, sexual medusa. Instead, modified versions of both stages are found together, attached to the stem of the free-floating animal. Totton (1965) considered the fully grown siphonophore to be an enlarged, larval nurse carrier, which he called a paedophore. This does not itself become sexually mature, but buds off the adult sexual medusoids, which may be released, along with other stem components, to lead a separate life. Individual animals of most species appear to produce medusoids of both sexes, but not necessarily simultaneously. However, for a few species, such as the Portuguese Man O'War, each animal produces medusoids of only one sex. Fertilisation is external and development proceeds rapidly over a period of 2 to 3 weeks. A larval nectophore and/or bracts are usually developed first, and these can be morphologically different from those of the adult animal.

Little is known about the life span of an individual siphonophore, but it is presumed that some of the smaller species live for only a few months, while some of the larger ones may survive for 10 or more years. The abundance of the shorter-lived species thus varies seasonally, and the period of abundance varies from species to species. However, as Mackie *et al.* (1987) discuss, one cannot always assume that these variations in abundance are a true reflection of seasonal change, as temporal changes in their horizontal or vertical distribution may not have been observed.

Much of the biology of siphonophores has been reviewed by Mackie *et al.* (1987). They are important pre-

dators and often occur in such numbers that they form the dominant group of carnivores (Pugh, 1984). They feed primarily on small crustaceans that they ensnare by discharging their nematocysts. Some species, however, feed on soft-bodied animals, such as small fish, which they capture by injecting poison from penetrant nematocysts. Most of the nematocysts are grouped on the animal's tentacles, which can extend to considerable lengths, but other structures also may possess them.

Unlike many jellyfish, which actively pull or push their tentacles through the water, siphonophores are passive feeders, setting tentacular nets that often form complex patterns. Biggs (1977) discussed some of the methods that siphonophores use to capture their prey. He noted that the fishing cycle consisted of two phases: a fishing period, when the tentacles are spread out and the animal waits for a prey item to swim into its net; and a swimming phase, when the tentacles are retracted and at the end of which the fishing net is reset. The whole process is highly coordinated and the disposition of the tentacles is by no means a tangled mess. The exact fishing posture depends on several factors, including the animal's ability to remain neutrally buoyant, and the degree to which the stem can be extended. Some merely use an extended "long-line" posture, with the tentacles hanging down from the buoyant stem. Species using this posture tend to spend long periods fishing, and to capture larger prey items. Their "sit and wait" strategy, which expends little energy, relies on the greater swimming speed of the larger prey to increase the chances of an encounter. The active swimmers usually set complex nets, and some use a "veronica" movement that results in the tentacles being spread out from the stem to form a helix of 2 or 3 turns (Mackie and Boag, 1963).

The three-dimensional disposition of the tentacles allows a greater volume of water to be searched for prey. Madin (1988) has calculated that the encounter volume, within which the tentacles are disposed, may be  $0.5 \text{ m}^3$ , and probably is even greater for some of the large physonect species. Others "squid-jig", periodically contracting and relaxing an individual tentacle, or its side branches, to enhance prey capture. In addition, several species have evolved tentacular structures that appear to mimic other organisms in order to lure in their prey (Purcell, 1980; Pugh, 1989). Although many siphonophore species are generalist feeders, taking any

prey item, within a certain size range, that they encounter, some appear to be highly selective and feed only on certain taxa (Purcell, 1981). The siphonophore species that have adopted these various feeding strategies can have different patterns of geographical and vertical distribution. This has lead Pugh (1986, 1991) to speculate that these different distributions should reflect that of their preferred prey items.

The role of siphonophores in marine food chains is unclear, but they do not appear to be a dead end branch. Despite their gelatinous nature, they are preyed upon by a variety of other organisms, particularly other gelatinous carnivores such as medusae, ctenophores and pelagic molluscs. Several species of fish also feed on them, as do turtles. In addition, siphonophores have associations with a variety of organisms, of which hyperiid amphipods probably are the most important. The nature of the association can vary from simple phoresis, where the other animal simply is carried about, to total parasitism, as with some amphipods whose juvenile stages develop and gradually consume parts of the siphonophore (see Harbison *et al.*, 1977). Many of these amphipod associations are species specific, as is also that of the nudibranch, *Cephalopyge trematoides*, which feeds exclusively on *Nanomia bijuga* (Senz-Braconnot and Carré, 1966). Fish also are known to associate with siphonophores. The best known example is the association between the Man O'War fish, *Nameus gronovii*, and the Portuguese Man O'War (see Totton, 1960). *In situ* observations also have shown associations of fish with siphonophores, including *Caristius* sp. and a cystonect species (Janssen *et al.*, 1989). Various parasites have been observed on and within siphonophores (see Totton, 1965), but there is little detailed information.

## Methods

Most of our knowledge concerning the zoogeographical distribution of siphonophores has come from animals caught in a variety of nets, ranging from simple surface dip-nets to sophisticated deep-water trawls. However, the complexity and fragility of these animals mean that the whole structure can easily be broken apart, and typically this is what happens during net collection. This also means that many pieces can be lost through the meshes so that there can be problems in quantifying their abundance. This is particu-

larly the case for physonect siphonophores as many of their potentially myriad parts can be lost. The number of floats, or pneumatophores, can give some indication of the number of specimens collected but the physonect pneumatophore is relatively small and is rarely retained in net samples. This problem is further discussed by Pugh (1984).

The majority of siphonophore species belong to the Order Calycophorae and these are the ones that are most frequently caught by nets. These species do not possess a pneumatophore but, fortunately, most of them possess other unique "individual" parts that can enable a reasonably accurate estimate of their abundance to be made. This applies to both the polygastric (asexual) and eudoxid (sexual) stages. There are a few species, in the subfamily Prayinae, that develop two identical swimming bells or nectophores. In this case the numbers of nectophores need to be halved in order to quantify the number of specimens. Similarly, in the family Hippopodiidae multiple (up to ca. 15) nectophores are developed. In this case, the exact number per animal can vary, and some of the less well developed ones may be lost, and so quantification is more complicated. Again this is discussed further by Pugh (1984).

Since nets do not sample all species adequately then the importance of the total siphonophore population can be greatly underestimated. In general, net samples indicate that calycophoran siphonophores are more abundant in superficial waters and, in the open ocean, may reach densities of ca. 1 per m<sup>3</sup>, while in the top 1000 m of the water column they average about 10 per 1000 m<sup>3</sup>. However, in inshore waters concentrations of a single small species can exceed 500 per m<sup>3</sup> (e.g. Greve, 1994).

The best, and most exhilarating, way to study and collect siphonophores is to use an *in situ* technique such as SCUBA diving or submersibles. It is the only way by which the full beauty of these animals can be appreciated. In the case of SCUBA, the divers take down wide mouthed jars into which, with a lot of skill, the animals can be induced to swim. Shipboard experiments can then be carried out on the specimens, using large tanks. Nonetheless, siphonophores like their freedom of movement and so do not usually survive long under these conditions. "Blue water" SCUBA diving techniques have been described by Hamner (1975) and Madin and Swanberg (1984).

Many supposedly rare, but actually very fragile siphonophore species have been collected by this means, as well as several new species.

At deeper depths, submersibles with sophisticated collecting devices need to be used. Ones that have been used extensively in the recent past are the Johnson-Sea-Link I and II because of their ability to collect many delicate specimens intact (see Youngbluth, 1984), although they do have a depth limitation of ca. 1000 m. Even so, some gelatinous species still cannot be described because they simply disintegrate "before your very eyes", probably as a result of turbulence produced by the submersible. Such *in situ* studies have shown that even relatively large physonect species can be quite abundant; for instance *Nanomia cara*, which is about 20-40 cm in length, can occur at densities of 7-8 per m<sup>3</sup> (Rogers *et al.*, 1978).

Personal observations (Pugh, 1989) have shown that in contrast to nets, where calycophoran species predominate, over 60% of the siphonophore species and 70% of the specimens collected by submersible belonged to the order Physonectae. There is an obvious reason for this, in that the physonects are generally larger and more highly pigmented than the calycophoran species and, thus, much easier to observe. Nonetheless, it is also true that over half of the physonect, and a quarter of the calycophoran, species that have been collected have proved to be new to science. Again, species that had been thought to be rare are shown to be common. For instance, Pugh and Harbison (1986) found that *Lychnagalma utricularia* (Claus, 1879) was the commonest physonect species collected in the vicinity of the Bahamas, despite the fact that there have been no other substantiated records for this species since it was first described.

When siphonophores have been collected in nets it is best to fix and preserve the whole sample as early as possible in 5% formalin buffered by borax. After a few days, the formalin should be changed, but it is best otherwise not to disturb the sample so as to allow proper fixation of the animals. Further details can be found in the Ostracoda chapter (this volume). The siphonophores inevitably will shrink, and volume loss is rapid, with about a 50% reduction within the first 2 hours of preservation (Pugh, pers. obs.). However, most of this is due to a loss of turgor so that the interstitial water that previously was retained within the main cavity of

the nectophore, the nectosac, is lost. Nonetheless, and in contrast to a previous statement (Kirkpatrick and Pugh, 1984), it is best to leave the specimens to fix completely before sorting them from the remainder of the sample. As formalin is an unpleasant substance, during the sorting of our samples they are transferred into Steedman's preserving fluid, which contains only 1% formalin (Steedman, 1976). Nonetheless, some species are so delicate that they disintegrate when preserved in formalin. In such cases better success has been achieved using ca. 3% glutaraldehyde. Alcohol is not recommended for siphonophores.

It is very difficult to preserve siphonophore specimens intact. The suggested method is first to anaesthetise the specimen by the slow, dropwise, addition of an isotonic magnesium chloride solution to the sea water, followed by a further dropwise addition of 10-20% formalin.

Once preserved and sorted, the parts of the siphonophore specimens can be examined under a low magnification binocular microscope, preferably using dark background illumination. Many of the component parts of a siphonophore species have characteristic morphologies and, with a practised eye, can be readily identified. They can also be stained using a variety of stains, for instance Steedman's Triple Stain or Borax Carmine. Staining can be useful if dark background illumination is not available, or when there is a difficulty in identifying the specimen, as the stain will help to show up certain critical morphological features.

### Geographical and vertical distribution

There are very few, if any, wide ranging studies of the distribution of siphonophores in the South Atlantic Ocean. The data presented in Table 1 are, thus, based on the sparse records in the literature. Only the maximal latitudinal limits of distribution are given, although this may mask some of the finer details, such as the presence of certain species in certain water masses. The data on the main vertical range for each species is largely based on data in the Southampton Oceanography Center database.

Most siphonophore species are truly oceanic and rarely appear inshore. A few are mainly neritic, such as *Muggiae atlantica* and *M. kochi*, and there appears to

be a mutual exclusion between them, such that they almost never occur in the same area at the same time (Mackie *et al.*, 1987). The oceanic species can be roughly divided into boreal, tropical and equatorial species (Margulis, 1972), although such a scheme does not take account of the depth distribution of some. Thus, some species are clearly restricted to warm, superficial waters, while the deeper-living, bathypelagic species can occur at almost any latitude as the temperature at these depths does not vary greatly. The zoogeographic distribution of siphonophores in the North Atlantic Ocean has been addressed by Pugh (1977) and Mackie *et al.* (1987). These studies indicate that the species composition of a siphonophore population is influenced by the various water masses present. For instance, there was a clearly defined and very abundant population of siphonophores above the permanent thermocline present at lower latitudes. In addition, different populations were found in North and South Atlantic Central Waters. It is most likely that the same situation will pertain in the various water masses of the South Atlantic, but there are too few data to demonstrate this. Although there are clear correlations between hydrographical features and siphonophore populations, it is probable that this is an indication of other factors that have a more immediate impact on their distribution, such as dietary preferences (Mackie *et al.*, 1987).

In the North Atlantic maximal species diversity was reached at ca. 20°N (Mackie *et al.*, 1987) with a slow decrease in numbers toward the equator, and a more rapid one toward higher latitudes. The latter was mainly the result of the disappearance of epipelagic species living above the permanent thermocline. Nonetheless, there appear to be more species in Antarctic waters than there are in Arctic ones; and several of those species are indigenous to that region, for example *Pyrostephos vanhoeffeni* and *Diphyes antarctica*. There are also one or two bipolar species that have never been recorded at lower latitudes in the Atlantic, these being *Muggiae bargmannae* and possibly *Gilia reticulata*.

There is also a change in species diversity in the vertical plane, with fewer species being found in the colder, deeper waters. Individual species can occur over quite wide depth ranges but, in general, they can be classified as epipelagic (0-250 m), mesopelagic (250-1000 m) or bathypelagic (>1000 m). However, several species have a relatively restricted distribution with-

	Height of nectophore (mm)	Latitudinal range	Main depth range (m)
--	---------------------------------	----------------------	----------------------------

**Order Cystonectae**

<i>Physalia physalis</i>	-	55°N- 40°S	Pleuston
<i>Rhizophysa eysenhardtii</i>	-	SW Africa	?
<i>Rhizophysa filiformis</i>	-	SW Africa (1)	?

**Order Physonectae**

<i>Apolemia uvaria</i>	21	SW Africa (1)	?
<i>Agalma elegans</i>	10	57°N-38°S	0-400
<i>Agalma okeni</i>	12	50°N-44°S	0-200
<i>Athorybia rosacea</i>	-	18°N-36°S	0-300
<i>Bargmannia elongata</i>	25	38°N-59°S	500-1000
<i>Cordagalma cordiforme</i>	2	SW Africa (1)	0-200
<i>Erenna richardi</i>	32	35°N-31°S	700-1000
<i>Forskalia edwardsi</i>	10	SW Africa (1)	0-200
<i>Forskalia leuckarti</i>	10	SW Africa (1)	0-500
<i>Halistemma cupulifera</i>	?	58°S (1)	500-1000
<i>Halistemma rubrum</i>	8	60°N-42°S	0-500
<i>Halistemma striata</i>	20	53°N-33°S	300-600
<i>Marrus antarcticus</i>	17	?33°S-67°S	700-1400
<i>Melophysa melo</i>	9	42°N-10°S	0-200
<i>Moseria spp.</i>	?	37-65°S	>900
<i>Nanomia bijuga</i>	2.5	55°N-59°S	0-400*
<i>Physophora hydrostatica</i>	20	73°N-53°S	200-500
<i>Pyrostephos vanhoeffenii</i>	20	50-65°S	500-1000
<i>Stepanjantsia polymorpha</i>	1.5	52-54°S	?

**Order Calycophorae**

<i>Abyla bicarinata</i>	12	30°N-19°S	0-100
<i>Abyla haekeli</i>	8	18°N-18°S	0-100
<i>Abyla trigona</i>	9	46°N-38°S	0-100
<i>Abylopsis eschscholtzi</i>	10	40°N-40°S	0-200
<i>Abylopsis tetragona</i>	10	57°N- 45°S	0-200
<i>Amphicaryon acaule</i>	12	60°N-37°S	0-200*
<i>Amphicaryon ernesti</i>	8	35°N-35°S	0-100
<i>Amphicaryon peltifera</i>	9	55°N-38°S	0-100
<i>Bassia bassensis</i>	7	60°N-49°S	0-200
<i>Ceratocymba dentata</i>	13	39°N-18°S	0-100
<i>Ceratocymba leuckarti</i>	8	42°N-39°S	0-100
<i>Ceratocymba sagittata</i>	25	62°N-45°S	0-300
<i>Enneagonum hyalinum</i>	15	61°N-44°S	300-1000
<i>Chelophyses appendiculata</i>	20	55°N-56°S	0-300*
<i>Chelophyses contorta</i>	9	SW Africa (3)	0-200

	Height of nectophore (mm)	Latitudinal range	Main depth range (m)
<i>Chuniphyes moserae</i>	43	50°N-67°S	>1000
<i>Chuniphyes multidentata</i>	35	60°N-63°S	300-800+
<i>Clausophyes galeata</i>	21	47N-67°S	>1000
<i>Clausophyes laetmata</i>	10	59-62°S	1800
<i>Clausophyes moserae</i>	20	60°N-65°S	500-1000+
<i>Clausophyes tropica</i>	18	5-30°S	800-1500
<i>Crystallophyses amygdalina</i>	9	60°N-67°S	400-1000
<i>Dimophyes arctica</i>	15	74°N-67°S	0-600
<i>Diphyes antarctica</i>	30	50°S-67°S	0-600
<i>Diphyes bojani</i>	14	44°N- 40°S	0-100
<i>Diphyes chamissonis</i>	12	SW Africa	0-100
<i>Diphyes dispar</i>	36	47°N-45°S	0-200
<i>Eudoxoides mitra</i>	8	44°N-40°S	0-200*
<i>Eudoxoides spiralis</i>	12	60°N-60°S	0-250*
<i>Gilia reticulata</i>	4	60°N-62°S	700-1100
<i>Heteropyramis crystallina</i>	6	60°N-67°S	500-800
<i>Heteropyramis maculata</i>	5	60°N-63°S	300-700
<i>Hippopodius hippopus</i>	20	62°N-48°S	0-250*
<i>Lensia achilles</i>	15	60°N-65°S	500-900
<i>Lensia ajax</i>	8	44°N-33°S	200-1000
<i>Lensia campanella</i>	4	54°N-38°S	0-100
<i>Lensia conoidea</i>	20	69°N-59°S	0-300*
<i>Lensia cossack</i>	12	60°N-42°S	0-200
<i>Lensia exeter</i>	10	60°N-33°S	400-600
<i>Lensia fowleri</i>	20	61°N-45°S	0-300
<i>Lensia grimaldi</i>	8	53°N-34°S	400-600
<i>Lensia hardy</i>	15	18°N-57°S	0-200
<i>Lensia havock</i>	16	60°N-67°S	1200-1600
<i>Lensia hostile</i>	15	60°N-66°S	500-1500
<i>Lensia hotspur</i>	10	47°N-43°S	0-200
<i>Lensia hunter</i>	11	18°N-39°S	0-200
<i>Lensia leloupi</i>	5	44°N-2°S	0-200
<i>Lensia lelouveteau</i>	7	60°N-33°S	600-1000
<i>Lensia meteori</i>	7	55°N-39°S	200-500
<i>Lensia multicristata</i>	15	60°N-57°S	100-500*
<i>Lensia subtilis</i>	10	55°N-39°S	0-200
<i>Lensia subtiloides</i>	5	SW Africa	0-200
<i>Lilyopsis rosea</i>	10	35-40°S	?
<i>Maresearsia praeclera</i>	20	55°N-8°S	400-700
<i>Muggiae a atlantica</i>	7	55°N-37°S	0-100
<i>Muggiae a bargmannae</i>	8	42-67°S (2)	200-500

	Height of nectophore (mm)	Latitudinal range	Main depth (m)
<i>Muggiae kochi</i>	7	48°N-36°S	0-100
<i>Nectadamas diomedeeae</i>	60	60°N-62°S	500-1000
<i>Nectopyramis natans</i>	40	44°N-65°S	400-800
<i>Nectopyramis thetis</i>	20	63°N-34°S	300-600
<i>Praya dubia</i>	100	60°N-44°S	100-600
<i>Praya reticulata</i>	60	SW Africa (1)	100-200
<i>Rosacea cymbiformis</i>	30	SW Africa (1)	100-200
<i>Rosacea plicata</i>	30	60°N-65°S	200-500
<i>Sphaeronectes gracilis</i>	8	SW Africa (1)	0-100
<i>Sulculeolaria biloba</i>	26	50°N-41°S	0-100
<i>Sulculeolaria chuni</i>	8	42°N-32°S	0-100
<i>Sulculeolaria monoica</i>	18	40°N-29°S	0-100
<i>Sulculeolaria quadrivalvis</i>	20	40°N-31°S	0-100
<i>Sulculeolaria turgida</i>	16	43°N-39°S	0-200
<i>Vogtia glabra</i>	30	62°N-56°S	100-500*
<i>Vogtia pentacantha</i>	40	SW Africa (1)	300-500
<i>Vogtia serrata</i>	40	66°N-65°S	400-800
<i>Vogtia spinosa</i>	30	69°N-59°S	100-300

**Table 1.** Distribution of siphonophore species found in the South Atlantic. Height refers to the anterior nectophore in the calyphoran families Diphyidae, Clausophyidae and Abylidiae. Remarks: (1) Also uncommon in North Atlantic and/or Mediterranean; (2) Bipolar species also found at similar latitudes in North Atlantic; (3) Other records treated as doubtful as this is an Indo-Pacific neritic species; \* Species known to undergo small-scale diel vertical migrations.

in the mesopelagic zone. In the North Atlantic there was a marked discontinuity, at ca. 42°N, between the more southerly and more northerly siphonophore populations in the top 1000 m of the water column. Although the number of species present on either side of this discontinuity was very similar, there was a change over in the specific population and a dramatic increase in biovolume to the north, with just a few species predominating. To the south the siphonophore population consisted mainly of small epipelagic species (chiefly in the families Diphyidae and Abylidiae). To the north the deeper living but larger species of the families Prayidae, Hippopodiidae and Clausophyidae became predominant. It is probable that similar changes will occur across the various major fronts, for instance the Subtropical Convergence and the Polar Front (=Antarctic Convergence), in the South Atlantic; but again there are no detailed studies.

Several epipelagic siphonophore species undergo diel vertical migrations over a depth range of up to 200-250 m (Table 1). However, such migrations may not always be apparent because, in some species the rate of depth change is relatively slow so that there is a sinusoidal wave of depth change throughout the day and night (Mackie *et al.*, 1987). In addition, it may be that the depth range of sampling is too coarse to establish any small-scale diel vertical migrations (Pugh, 1984). The factors that might initiate these migrations, and the processes involved in them are discussed by Pugh (1977, 1984). It is presumed that siphonophores undertake such migrations in order to remain in the vicinity of their prey, which often migrate to superficial waters at night. Physonect species, with a gas-filled float, are known to be important contributors to deep-scattering layers, and some have a pore to allow release of gas from their float that may facilitate a diel vertical migration.

## Taxonomy

## Morphology

As siphonophores are comprised of many types of structures ("individuals"), each with a different function and some found only in these animals, a unique terminology for these structures has been developed. This can appear somewhat daunting to the non-specialist and necessitates a detailed introduction to it as it is critical to the identification of the species. In the following section the important terms and features are emboldened.

Siphonophores are cnidarians, and so basically consist of two cell layers, the outer **ectoderm** and the inner **endoderm**, with the latter forming the lining to the **gastro-vascular cavity**. These two layers are separated by a more or less thickened, amorphous **mesogloea**.

As noted above, the species in the 3 basic divisions (orders) are primarily distinguished on the basis of the presence or absence of either an apical, gas-filled float, the **pneumatophore**, or of swimming bells, **nectophores**. The latter, numbering from one to fifty or more, usually are grouped together at or toward the apex of the animal to form the **nectosome**. The pneumatophore (Fig. 1A) is produced, during development, by an invagination at the aboral end of the larva, which results in its cavity being lined by ectodermal cells. At the base of the cavity, there is a specialised area of cells, the **gas-gland** or **pneumadenia**, that secretes the gas to inflate the cavity. In some cystonect siphonophores this gland may bear processes, **hypocystic villi**, while in the benthic rhodaliids it is greatly expanded to form an **aurophore**.

Most siphonophores possess a long stem to which are attached the various "individuals". The latter usually are organised into two zones, the **nectosome** and **siphosome**, although only the latter is present in the Cystonectae.

**Nectosome.** The nectosome, which lies immediately below the pneumatophore (Physonectae) (Fig. 1A) or is apical (Calycophorae) (Fig. 2), bears, with the exception of one family, only asexual, medusoid nectophores. These act in a co-ordinated way to propel the animal through the water. Within the Calyco-

phorae, they may also contain large amounts of mesogloea, which contributes to the buoyancy of the animal. New or replacement nectophores are developed at the apex of the nectosome.

The morphology of the nectophores is important for specific identification. The nectophores of physonect siphonophores generally conform to a basic design (Fig. 1D, E). They do not possess a somatocyst (see below) and, with a practised eye, easily can be distinguished from calycophoran nectophores. The important taxonomic features of the physonect nectophores are:

- (a) their general shape;
- (b) whether the **apico-lateral ridges** have a notch or divide toward the abaxial (furthest from the stem) end of the nectophore;
- (c) the course of the 4 (dorsal, ventral and 2 laterals) **radial canals** on the **nectosac**. The nectosac is equivalent to the sub-umbrella cavity of a medusa and, by means of contractions of its muscular walls, water is expelled through the narrowed, basal opening, or **ostium**, so that the animal is propelled by jet propulsion;
- (d) the shape of the apico-lateral processes, or **axial wings**, which extend around the stem;
- (e) the structure of the **thrust block**, which abuts the stem and through which passes the gastro-vascular canal; and
- (f) the presence or absence of ridges on the sides of the nectophore. In this paper two types of these ridges will be referred to, in continuation of the scheme adopted by Pugh and Youngbluth (1988). Firstly, there are **vertical lateral ridges**, which are closer to the axis than any others, and run from the apico-laterals to or toward the **infra-laterals**. The course of this pair of ridges is not always vertical, and in two species, at least, more than one pair is present. Secondly, **lateral ridges** that usually run from the apico-laterals to the ostium. There are specific variations in their arrangement.

The nectophores of calycophoran siphonophores generally are more specialised, but there is a great deal of variability amongst the various families and it is difficult to give an overall picture. Six different types are illustrated in Fig. 2. The first type (Fig. 2A, 3.31-3.43) is basically a smooth, rounded structure containing large volumes of mesogloea, giving buoy-

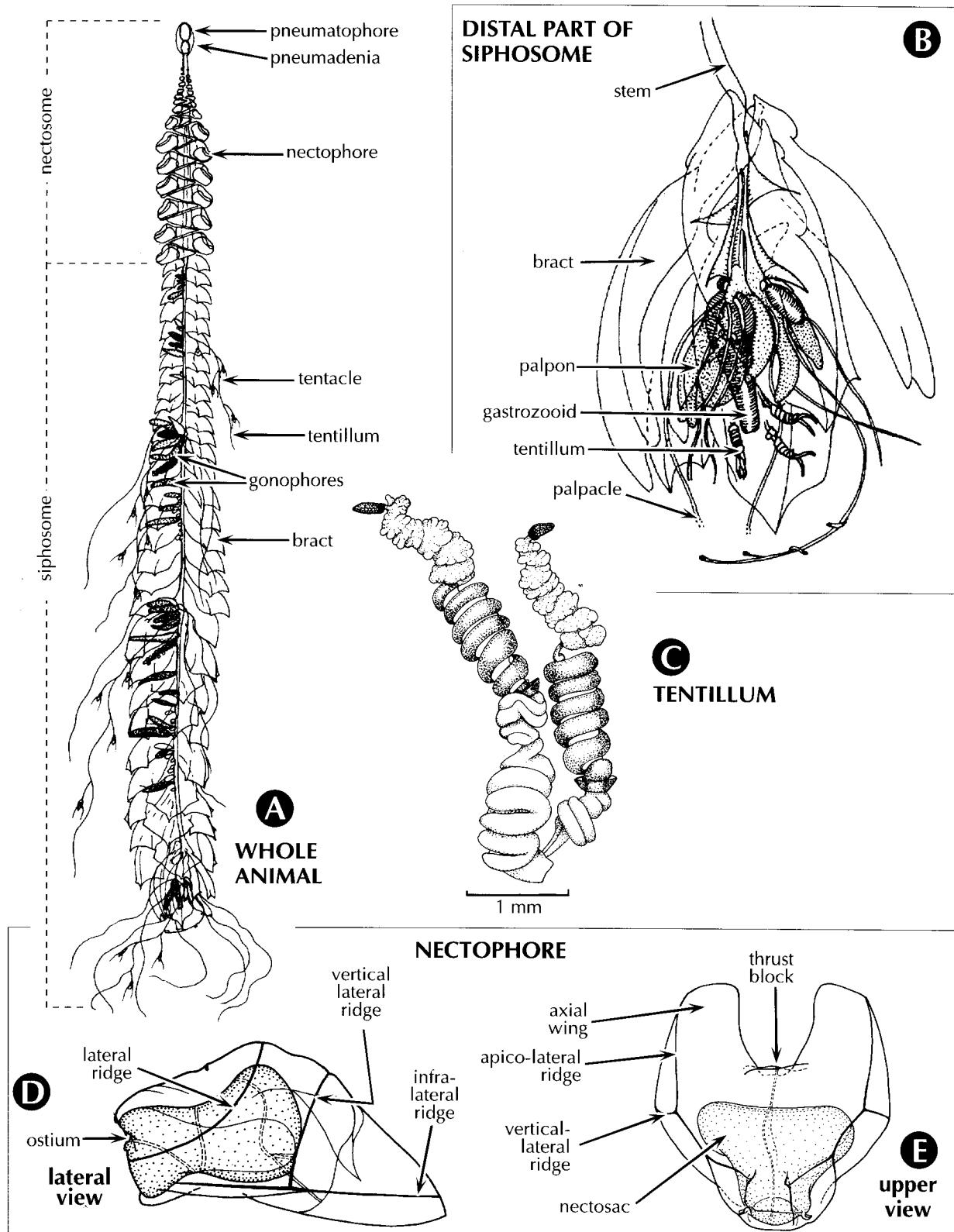


Fig. 1. General structure of a physonect siphonophore. A, B, D, E after Totton (1965).

ancy to the animal. The extent of the nectosac can vary considerably between species. This type of nectophore is found in species of the families **Prayidae** and **Sphaeronectidae**. In the latter family only a single nectophore, the **larval** one, is developed and is retained by the adult animal. In the former the larval nectophore may be retained in the adult, and a second, greatly reduced nectophore developed in addition; or the larval nectophore can be autotomised and replaced by one or, more usually, two adult or **definitive** nectophores. Further definitive nectophores may be developed in some species. When two definitive nectophores are present, they are identical in design and form an apposed pair.

The second type of nectophore (Fig. 2B, 3.55-3.59), found in the family **Hippopodiidae**, is flattened in the axial-abaxial direction and usually bears spines or protuberances. The nectosac is widely open, but shallow, giving the impression that the animals must be weak swimmers. On the ventral radial canal of the nectosac there is a **rete mirabile**, a dilation of the ventral canal, which is particularly obvious in younger nectophores. Up to fifteen nectophores may be developed, which have a tight, biserial arrangement.

In the remaining calycophoran families the nectophores are more streamlined, and the animals themselves usually are active and rapid swimmers. Generally a larval nectophore is developed, which is then replaced by one or, more commonly, two definitive nectophores. However, it is believed that the larval one may be retained in certain species. When two nectophores are present, they differ in structure and do not form an apposed pair, rather one is wholly (**Diphyidae** and **Abylidae**, Fig. 2C, D, F) or partially (**Clausophyidae**, Fig. 2E) superimposed above the other. The upper, **anterior nectophore**, often has a pointed apex, while the lower, **posterior nectophore** often is truncated apically so as to fit snugly with the other. These nectophores frequently bear patterns of **external ridges** and **teeth**, which are useful diagnostic features. Most of the ridges run longitudinally, from the apex to the base of the nectophore, but are not necessarily complete. In some species a transverse **velar** ridge, lying close to the ostium, is present. In addition, many species have a **basal lamella** or **mouth plate** that extends below the ostium, the opening of the nectosac, on its ventral side. The angle at which the mouth plate is joined to the

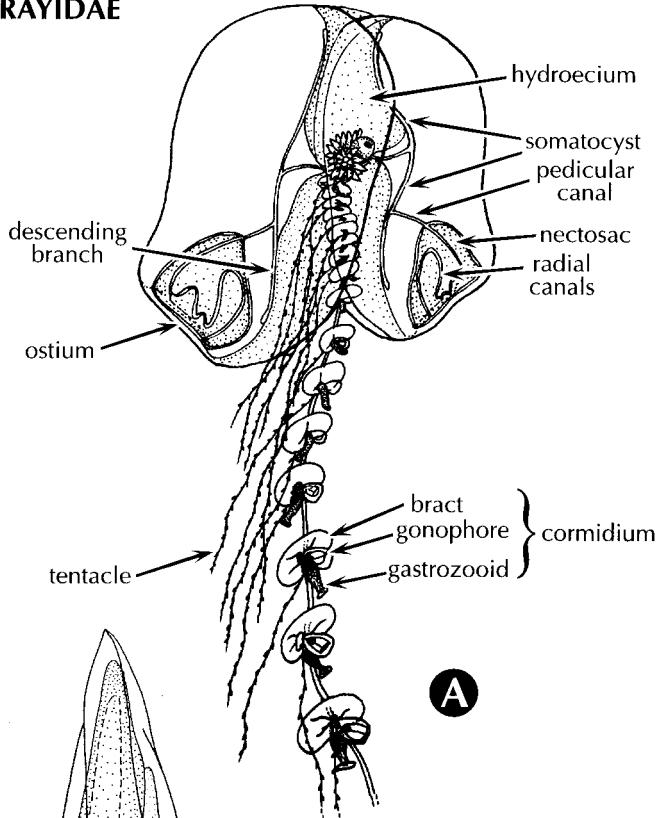
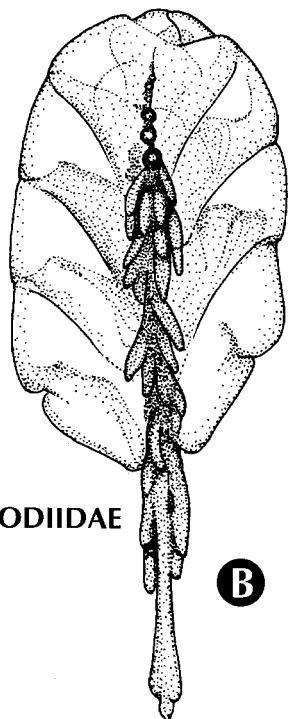
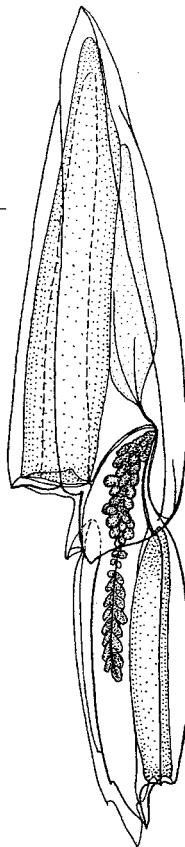
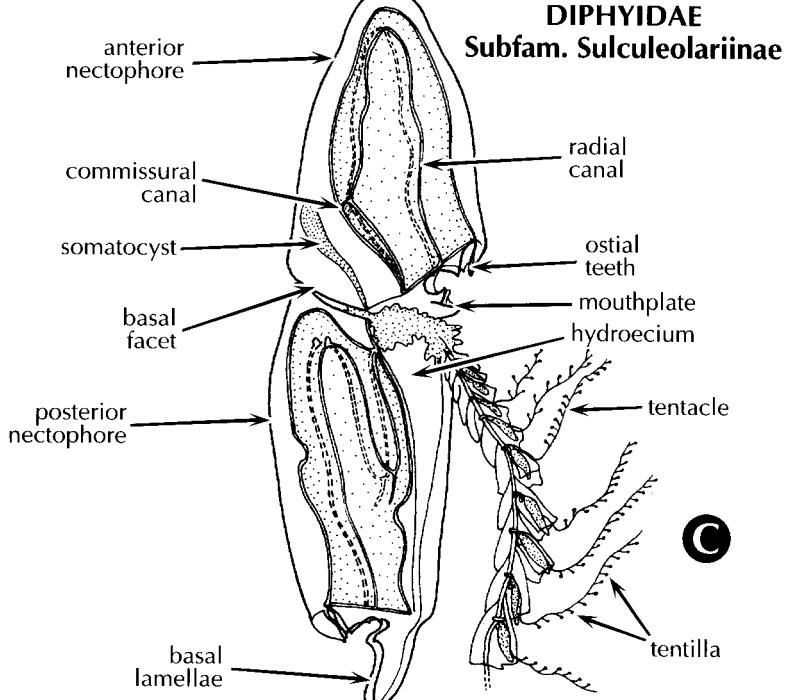
ventral surface of the nectophore, where it forms the **basal facet**, also can be of taxonomic importance.

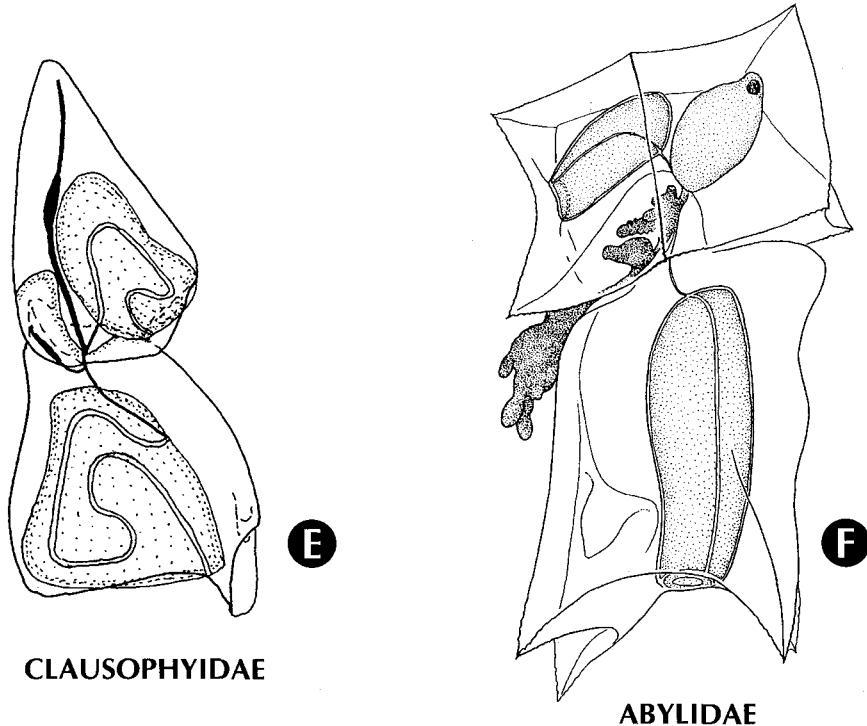
The structure of the **hydroecium** is only of taxonomic importance in calycophoran siphonophores (Fig. 2A, C). In species with stream-lined nectophores, the hydroecium of the anterior nectophore may be greatly reduced or absent. However, in the posterior nectophore it usually extends the full length of the nectophore and the siphosomal stem may be partially or wholly retracted into it for protection and to reduce drag during locomotion. In the genus *Sulculeolaria* the nectosac of the anterior nectophore may have additional **commissural** canals connecting the laterals to the dorsal radial canal (Fig. 2C).

In calycophoran siphonophores a **somatocyst** lies above the apical wall of the hydroecium. This may be a relatively simple tube, as in certain species of the family Prayidae, forming part of the gastro-vascular canal system, and connecting with the radial canals on the nectosac via a **pedicular canal** (Fig. 2A). It may have **basal** (descending) or **apical** (ascending) extensions, or **branches**. In the other calycophoran families, the somatocyst tends to form a caecal extension to the gastro-vascular canal, of taxonomically variable shape and design (Fig. 2C). In those species with nectophores designated anterior and posterior the somatocyst is present only in the anterior one, except for the family Clausophyidae where it is present in both. The morphological features of importance for the taxonomy of calycophoran nectophores are:

- (a) their basic shape and design;
- (b) the presence and pattern of ridges; and
- (c) the structure of the somatocyst.

**Siphosome.** The siphosome generally is much longer than the nectosome, and in some physonect species can extend to several tens of metres. Its zone of proliferation lies immediately below the nectosome. The siphosome bears a succession of different polypoid and medusoid structures, with different functions, arranged into a succession of groups or **cormidia** (Fig. 2A). Each cormidium consists of a single **gastrozoid**, the digestive organ or stomach, to the base of which is attached a **tentacle**. The tentacle bears numerous **nematocysts**, usually on side branches called **tentilla** (Fig. 1C), that are discharged on contact with a prey item and either paralyse or ensnare it. Many

**PRAYIDAE****HIPPOPODIIDAE****B****DIPHYIDAE**  
Subfam. Diphyinae**C**



**Fig. 2.** General structure of calycophoran siphonophores from various families. A: after Totton (1965); C: after Carré (1979).

large nematocysts are often arranged into a **cnido-band** that may be covered by an **involuterum**. Frequently a **terminal filament** is present. The structure of the tentillum can be useful in identifying some species, particularly physonect ones.

The cormidia of physonects usually include a number of **palpons**, which are reduced gastrozooids and bear a small tentacle or **palpacle** (Fig. 1B). The palpacle probably has a sensory function, while the palpon aids in digestion, and accumulates and disposes of waste products. Palpons usually are attached directly to the stem, but a specialised type, the **gonopalpon**, may be budded from a **gonodendron**. The latter itself may be a specialised palpon (Totton, 1965). The gonodendron bears the developing sexual medusoids, the **gono-phores**, and in some species asexual nectophores.

Another cormidal structure is the **bract** (Fig. 1A, 2A), whose medusoid or polypoid origin is uncertain. These structures have a protective function, overlying

the other cormidal elements. Often they contain large amounts of mesogloea and play an important role in flotation. They are absent in cystonects, while in physonects each cormidium usually contains several bracts, which are leaf-like with a simple bracteal canal. In calycophores each cormidium has a single bract, except in the family Hippopodiidae where it is absent. The bract may have a complex structure, with a divided canal system or a **phyllocyst** (equivalent to the somatocyst of the nectophore), whose arrangement is of taxonomic importance. The bracts of some species are rounded, while others are angular, conical or helmet-shaped. The latter types usually possess a basal process called the **neck shield**. Those calycophores with stream-lined nectophores usually release individual cormidia, which are then known as **eudoxids**. Each eudoxid, thereby, comprises a bract, a gastrozooid and tentacle, a succession of sexual gono-phores and, possibly, an asexual nectophore. The specific identification of this stage often is difficult, and depends largely on the structure of the bract.

## Outline classification

The classification adopted here is basically that used by Totton (1965). That taxonomy is well established, although a few more recent authors (e.g. Alvariño, 1981) still use a few outmoded names. Other useful references include Bigelow (1911), Kirkpatrick and Pugh (1984) and Totton (1954). The only change that has been adopted here is the re-establishment of the Siphonophorae as a subclass of the class Hydrozoa (see Bouillon *et al.*, 1992), and the consequent raising of the 3 old suborders to order status. Totton (1965) recognised approximately 130 species and since then about 70 other species and subspecies either have been described or resurrected. However, it is certain that several of Totton's "doubtful" species, and many of the subsequent new ones, are not valid. This is because many aberrant forms have been described as new species, or the reasons given for distinguishing the new material from extant species are insufficient. Nonetheless, it is clear from submersible collections that there are still many species yet to be described.

### Phylum Cnidaria Verril, 1865

#### Class Hydrozoa Owen, 1843

##### Subclass Siphonophorae Eschscholtz, 1829

###### Order Cystonectae Haeckel, 1887

###### Family Physaliidae Brandt, 1835

###### Family Rhizophysidae Brandt, 1825

###### Order Physonectae Haeckel 1888

###### Family Apolemidae Huxley, 1859

###### Family Agalmatidae Brandt, 1835

###### Family Pyrostephidae Moser, 1925

###### Family Physophoridae Eschscholtz, 1829

###### Family Athorybiidae Huxley, 1859

###### Family Rhodaliidae Haeckel, 1888

###### Family Forskaliidae Haeckel, 1888

###### Order Calycocephorae Leuckart, 1854

###### Family Prayinae Kölleker, 1853

###### Subfamily Amphicaryoninae Chun, 1888

###### Subfamily Prayinae Haeckel, 1888

###### Subfamily Nectopyramidinae Bigelow,

1911

###### Family Hippopodiidae Kölleker, 1853

###### Family Diphyidae Quoy and Gaimard, 1827

###### Subfamily Sulculeolariinae Totton, 1954

###### Subfamily Diphyniae Moser, 1925

###### Subfamily Giliinae Pugh and Pagès, 1995

###### Family Clausophyidae Totton, 1954

###### Family Sphaeronectidae Huxley, 1859

## Family Abylidae L. Agassiz, 1862

### Subfamily Abylinae L. Agassiz, 1862

### Subfamily Abylopsinae Totton, 1954

The only family not dealt with herein is the Rhodaliidae whose species are benthic.

## Identification of the taxa

Because of their fragility, the identification of species of siphonophores is based largely on the morphology of one or more of the "individuals" that comprise the whole animal. The structure of the nectophores and bracts is of particular importance, although neither of these, with the exception of asexual nectophores on the gonodendra, are present in cystonect species. The following diagnoses refer almost exclusively to the adult stage of the various siphonophore species. The larval nectophore and bracts often have a different morphology, but there is insufficient space to deal with these in the present text. The species included here are those that have been recorded from the South Atlantic Ocean. Because of the dearth of sampling, particularly at deeper depth, it is possible that other species may be found, although the list is quite comprehensive.

## Order Cystonectae

Siphonophores with a relatively large, and for the Portuguese Man O'War enormous, pneumatophore, whose gas gland may bear hypocystic villi. The pneumatophore has an apical pore. No nectosome or bracts are present, and the cormidia are relatively simple comprising only a gastrozooid and tentacle, and a gonodendron. The tentacles, which in some species are unbranched, bear only one type of penetrant nematocyst. The gonodendron bears gonopalpons, gonophores and asexual swimming bells. Each animal probably bears gonophores of only one sex. Only 5 recognised species within two families.

## Family Physaliidae

This family is monotypic for *Physalia physalis*, the Portuguese Man O'War.

- ***Physalia physalis*** Linné 1758. (Fig. 3.1). This is the only pleustonic siphonophore. It has a huge, asymmetric pneumatophore, purplish blue in colour and up to 30 cm in length. The top of the pneumatophore is formed into an erectile "sail" that runs diagonally across it either from the right-

hand or left-hand side. The cormidia are attached to one side of the float and their tentacles can stretch down many metres.

#### Family Rhizophysidae

Only 4 species, in 2 genera, are recognised here. Totton (1965) also included 3 "species inquirendae" within this family, of which 2 belonged to the genus *Epibulium* Eschscholtz, 1829. In these species there is supposed to be a ring of palpons surrounding the base of the pneumatophore: but palpons are absent in other cystonect species. Totton (1965) suggested that these alleged palpons might be young gastrozooids and personal observations have shown this to be the case. The whole specimen is highly contracted and the young gastrozooids bear no sign of a tentacular bud. The genus and its species are, therefore, considered to be invalid. However, Alvariño (1981) has recorded *Epibulium ritteriana* Haeckel, 1888 from the western South Atlantic. Judging from her illustration, showing a pneumatophore with large hypocystic villi, it is concluded that her specimens most likely belong to *Rhizophysa filiformis*.

Genus *Rhizophysa* Périon and Lesueuer, 1807 (Fig. 3.2) Pneumatophore with hypocystic villi; no wing-like processes on gastrozooids.

- *Rhizophysa eysenhardtii* Gegenbaur, 1859 (Fig. 3.3). Mature specimens pale pink in colour. Hypocystic villi at base of pneumatophore. Tentacles with filiform tentilla.
- *Rhizophysa filiformis* (Forskal, 1775) (Fig. 3.4). Mature specimens pale green in colour. Well-developed hypocystic villi. Tentacles with side branches (tentilla) of 3 types. Ref.: Totton (1965).

#### Order Physonectae

Siphonophores with a relatively small apical pneumatophore. A nectosome with an array of identical nectophores is, with two exceptions, present. The number of nectophores is specifically variable, but they are usually arranged biserially, except in the family Forskaliidae. The cormidia, arranged linearly down the stem, are comprised of a gastrozooid and tentacle, and a specifically variable number of bracts and gonodendra, the last not bearing asexual swimming bells. As is always the case there is an exception in that one species does not have bracts. In addition to these cormidial elements palpons with palpacles usually are present, but they are absent in some species. About 50

species presently distributed amongst 7 families, although it is clear that some revision is necessary. Species from all 7 families occur in the South Atlantic, but as those of the family Rhodaliidae are benthic, using their tentacles to tether themselves to the substrate (Pugh, 1983; Hissmann *et al.*, 1995), they will not be considered here. Riemann-Zürneck (1991) gives details of the distribution of *Rhodalia miranda* Haeckel, 1888. The other 6 families can be distinguished according to the arrangement of the nectosome and siphosome:

- |  |   |
|--|---|
| 1 Nectophores present .....  | 2 |
| 1a Nectophores absent .....  | 6 |
| 2 Nectophores deeply hollowed axially and with tentacles between them; small delicate bracts:                              |   |
| Family Apolemiidae   |   |
| 2a Nectophores not hollowed axially; nectosomal tentacles absent .....   | 3 |
| 3 Nectosome and siphosome elongate, with a narrow stem .....   | 4 |
| 3a Nectosome and/or siphosome contracted or reduced .....  | 6 |
| 4 Nectophores bilaterally symmetrical, arranged biserially .....   | 5 |
| 4a Nectophores dorso-ventrally flattened, usually asymmetric in shape, arranged in a spiral: Family Forskaliidae           |   |
| 5 Nectophores with straight dorsal radial canal: Family Agalmatidae  |   |
| 5a Nectophores with sinuous dorsal radial canal: Family Pyrostephidae  |   |
| 6 Nectosome reduced or absent; siphosome reduced to solid body or corm: Family Athorybiidae                                |   |
| 6a Nectosome normal; siphosome shortened into laterally expanded spiral sac bearing enlarged palpons: Family Physophoridae |   |

The following diagnoses will mainly concentrate on the distinguishing features of the nectophores or bracts, as these are the parts most frequently found in net samples.

#### Family Apolemiidae

Nectophore with a very characteristic shape being deeply hollowed axially, forming a pair of large axial wings. The nectosac is extensive and its lateral radial canals follow an S-shaped course of varying complexity. Uniquely, amongst the physonects, there is a tentacle, or clump of tentacles (? larval) between each pair of nectophores. Small delicate bracts that preserve poorly. Three species in separate genera have been

described, 2 since Totton (1965). Material collected from submersibles indicates that there might be up to another ten species (Pugh, pers. obs). However, the 4 nectophores in the single record for the area (Pagès and Gili, 1992) belong to *Apolemia uvaria*.

#### Genus *Apolemia* Eschscholtz, 1829

Monotypic genus for *Apolemia uvaria*.

- ***Apolemia uvaria*** (Lesueuer, ?1811) (Fig. 3.5, 3.21). 5-6 tentacles between each pair of nectophores. Nectophores having lateral radial canals on nectosac with numerous, short, blind-ending diverticula on the axial half. Flimsy bracts covered in opaque spots.

#### Family Agalmatidae

Nectosome without tentacles between the biserially arranged nectophores. Dorsal radial canal on nectosac straight. Siphosome straight, not coiled up to form a sac or corm. This is rather a catch all family, and Totton (1965) included in it most of the physonect species. At present about 25 species are included in the family, although the status of some remains uncertain. As better material is collected for some of the "rarer" species, and many new ones, it is probable that certain species will be removed into new families.

#### Genus *Agalma* Eschscholtz, 1825

Tricornuate tentilla consisting of a coiled cnidoband enveloped in an involucrum, plus a terminal vesicle and 2 lateral processes. When the lateral processes of the tentillum are relaxed, the whole structure has the semblance of a copepod. Purcell (1980) has suggested that this is a form of aggressive mimicry.

- ***Agalma elegans*** (Sars, 1846) (Fig. 3.6, 3.22). Apico-lateral ridges on nectophores with distinct notch toward the ostium. Lateral and vertical lateral ridges only present in larger nectophores, and even then the former can be indistinct. Nectosac T-shaped. Lateral radial canals distinctly looped. Foliate bracts, usually tridentate at the distal end, but some small bracts do not show this feature. The convex dorsal side bears 3 ridges, often indistinct in smaller ones, on the distal half. Bracteal canal extends to about four-fifths the length of the bract, occasionally continuing as a very fine canal to the distal tip.
- ***Agalma okeni*** Eschscholtz, 1825 (Fig. 3.7, 3.23). Apico-lateral ridges on nectophores without distinct notch. One (young nectophores) or 2 (adult) vertical lateral ridges. Lateral ridges absent.

Nectosac becoming Y-shaped in larger nectophores. Lateral radial canals distinctly looped. Bract with 4 (only 2 in youngest) very characteristic distal facets. Bracteal canal usually ends before reaching the distal extremity, but a vestigial canal may extend towards it.

#### Genus *Bargmannia* Totton, 1954

Presently a monotypic genus for *Bargmannia elongata*.

- ***Bargmannia elongata*** Totton, 1954 (Fig. 3.8) [=? *Mica micula* Margulis, 1982]. Very characteristically shaped, elongate nectophores with large triangular thrust block and axial wings virtually absent. Apico-lateral ridges each divide above the ostium. Highly oblique vertical lateral ridges join infra-laterals close to the ostium. Long, narrow nectosac with straight radial canals. Bract broad and rounded with many patches of cells on its dorsal surface. Totton (1965) included this genus in the family Pyrostephidae. Although there are some similarities with the single species in that family, for the present we follow Stepanjants (1967) and include the genus in the family Agalmatidae. Nevertheless, it is certain that its status will need further review. Margulis (1982) described a new species *Mica micula* that appears to be the post-larval stage of a physonect siphonophore and, from the shape of the nectophores, it is suggested that the species to which it belongs is *B. elongata*.

#### Genus *Cordagalma* Totton, 1932

Physonects with heart-shaped nectophores devoid of lateral or vertical lateral ridges.

- ***Cordagalma cordiforme*** Totton, 1932 (Fig. 3.9, 3.24). Small delicate physonect reaching 30 cm in length. Small characteristically heart-shaped nectophores. Lateral radial canals with one ascending loop but without sigmoid curves. All radial canals arise from pedicular canal. Characteristic bracts shaped like a truncated pyramid, with 4 lateral facets. Short bracteal canal terminating in the middle of the bract. Very characteristic tentilla. Totton's (1932) description of this species was based only on the nectophores with their very characteristic shape. However, Carré (1968a) was able to give a full description when the entire animal was collected. From this description it is apparent that the bracts and, particularly, the tentilla of this species resemble very closely those of *Anthemodes ordinata* described by Haeckel (1888). However,

the nectophores of the two species appear entirely different. Nonetheless, there may be sufficient reason to adopt the name *Cordagalma ordinata* (Haeckel, 1888), but for the present Totton's specific name is retained, with a modified ending to agree with the gender of the genus. Ref.: Carré, 1968a.

#### Genus *Erenna* Bedot, 1904

Monotypic genus for *Erenna richardi*. A second species, *Erenna bedoti*, was described by Lens and van Riemsdijk (1908), but was synonymised with *E. richardi* by Bigelow (1911); a procedure followed by Totton (1965). Margulies (1977a, 1990) believed that there were sufficient reasons to resurrect *E. bedoti*, but here the synonymy is retained and only a single species recognised.

- ***Erenna richardi*** Bedot, 1904 (Fig. 3.10, 3.25)  
[=*Erenna bedoti* Lens and van Riemsdijk, 1908]. Large, but thin, nectophores with a relatively large thrust block bearing 2 digitate processes at its base, on the ventral side. Apico-lateral ridges divide very close to the ostium. Distinct vertical lateral ridges define triangular facets on the outer sides of the large axial wings. Nectosac has muscle free region axially. All radial canals have a straight course and bear black pigmentation. Long, narrow foliaceous bracts, up to 25 mm in length, with one or 2 pairs of lateral teeth. Bracteal canal runs the entire length of the bract and terminates below an aggregation of cells (? nematocysts). Distinctive tentilla with uncoiled, powerfully armoured cnidoband, black in colour; a secondary, diverticular canal; and a pair of spots on the broad terminal filament.

#### Genus *Halistemma* Huxley, 1859

Agalmatids whose tentilla have a single terminal filament (unicornuate) and only a vestigial involucrum. Characteristic sigmoidal courses for radial canals on the nectosac of the nectophore, that begins with a downward sweep. The post-larval stage of a *Halistemma* spp. was described by Haeckel (1888) as a separate species, *Nectalia loligo*. Pugh (1974) correctly surmised its true status, but Alvariño (e.g. 1981) continued to refer to it as a separate species.

- ***Halistemma cupulifera*** Lens and van Riemsdijk, 1908 (cf. Fig. 1C). The only described feature that could distinguish this species from others of the genus *Halistemma* is the terminal filament of the tentillum that ends in a cupulate process. With the description of *Halistemma transliratum* Pugh and

Youngbluth, 1988 it has become apparent that *H. cupulifera* is not the only species whose tentillum ends in a cupulate process. The two processes are distinguishable, but with care. It is thus uncertain as to what species the records given by Alvariño *et al.* (1990) belong. Ref.: Pugh and Youngbluth (1988).

- ***Halistemma rubrum*** (Vogt, 1852) (Fig. 3.11, 3.26). Nectophores with large axial wings and extensive thrust block. Vertical lateral ridges run obliquely down from apico-laterals, but do not reach infra-laterals. Similarly, lateral ridges run obliquely up from ostium but do not reach the apico-laterals. Bracts foliaceous, elongate, thin, distally pointed, with 2 latero-terminal teeth. Bracteal canal runs almost the entire length of the bract, but is absent from a proximal process. Distally it runs beneath an indistinct dorsal ridge in which are imbedded 2 rows of cells, probably nematocysts. Tentillum with vestigial involucrum at base of cnidoband, and a terminal filament, often tightly coiled when contracted, that has no terminal process. It is probable that the nectophores and bracts of other *Halistemma* species have been confused with those of *H. rubrum*. Recent material collected by submersible has allowed the distinction of at least one other new species (Pugh and Youngbluth, 1988).
- ***Halistemma striata*** Totton, 1965 (Fig. 3.12). Presently identified only by its very distinctive nectophores. These are large, robust structures, with prominent thrust block and deep axial wings. There are 3, slightly oblique but complete, pairs of vertical lateral ridges. Ostial to these there is a pair of lateral ridges, each of which bifurcates shortly after leaving the apico-laterals, with the upper branch running down to the ostium, while the basal branch heads toward the infra-lateral but peters out before reaching it.

#### Genus *Marrus* Totton, 1954

Nectophores with straight radial canals; unicornuate tentilla on tentacles. The exact status of this genus, and the 3 species contained within, appears uncertain.

- ***Marrus antarcticus*** Totton, 1954 (Fig. 3.13, 3.27). Nectophores without a vertical lateral ridge. In 1954 Totton stated that the apico-lateral ridges bifurcated distally; while in 1965 he mentioned pairs of *Vk'*(apico-lateral) and *Vk''* (lateral) ridges. It is, therefore, not clear what affinities the latter ridges have. The bracts were described to be

flattened, cone-shaped, and truncated distally. The bracteal canal runs the entire length of the bract and ends on a small papilla on the distal facet. New material of this species, in excellent condition, needs to be examined in order that a more detailed description can be given.

#### Genus *Moseria* Totton, 1965

Very thin, flimsy nectophores with straight radial canals. Involucrum covers cnidoband of unicornuate tentilla. Very little is known about the species of this genus. The first species to be described was *Moseria convoluta* (Moser, 1925) based on some young material, with a pneumatophore of peculiar construction. Totton (1965) enhanced the earlier description, including a new description of the tentillum, as he believed that that described by Moser (1925) belonged to another species. Margulis (1977b) described a new species, *M. similis*, based mainly on a difference in the number of cavities in the pneumatophore. However, as this gas-filled structure usually explodes when the specimen is brought to the surface, and the gas forced down the stem, the number of cavities may be totally misleading. It is not clear, therefore, whether *M. similis* is a distinct species. There also appears to be another *Moseria* species in the Southern Ocean (see Pagès *et al.*, 1994; Pugh *et al.*, in press) but it has yet to be described. In the area under consideration there are records only for *M. similis* and *M. sp. nov.* and these will be considered together as *Moseria* spp.

#### Genus *Nanomia* A. Agassiz, 1865

Agalmatids whose unicornuate tentillum has a basal involucrum. Characteristic arrangement of the gonodendra in that male and female ones, attached at the bases of palpons, alternate on either side.

- *Nanomia bijuga* (Chiaje, 1841) (Fig. 3.14, 3.28). Nectophores are flattened in the abaxial-adaxial plane and, in that view, square in shape. L-shaped when viewed laterally. Ridges indistinct. Axial wings twisted. Looped lateral radial canals on extensive nectosac. Leaf-like bracts, variable in design. Often with 3 processes at distal end, occasionally with a cross ridge.

#### Genus *Stepanjantsia* Margulis, 1982

Monotypic genus for *Stepanjantsia polymorpha*.

- *Stepanjantsia polymorpha* Margulis, 1982. Minute nectophores, very variable in shape. Nectosac occupying most of nectophore, with looped lateral

radial canals. Tentacles filiform (?). There is some doubt as to the validity of this species, particularly as Margulis's (1982) description is rather vague and it is difficult to pin-point any clear distinguishing characters. For this reason the nectophores are not illustrated.

#### Family Pyrostephidae

Monotypic family for the species *Pyrostethos vanhoeffeni*.

- *Pyrostethos vanhoeffeni* Moser, 1925 (Fig. 3.15, 3.29). Nectophores with large thrust block and axial wings that are extensive laterally but not axially. Highly looped lateral radial canals on nectosac, whose adaxial wall lacks musculature. Dorsal radial canal with several pronounced bends; ventral canal straight. Thickened, dorsally convex bracts, somewhat triangular in shape, with irregular teeth on the broad distal end. Canal ends some distance from distal extremity. Tentilla with diverticular canal. Ref.: Totton (1965).

#### Family Physophoridae

Monotypic family for the species *Physophora hydrostatica*.

- *Physophora hydrostatica* Forskal, 1775 (Fig. 3.16). Flimsy, apparently ridgeless nectophores each with an extensive nectosac, which has characteristically looped lateral radial canals. Both dorsal and ventral canals are sinuous. Siphosome compact sac on which the simple, bractless cormidia are borne in a spiral. Each cormidium has a single, greatly enlarged palpon, pinkish blue in colour. Ref.: Totton (1965).

#### Family Athorybiidae

Relatively large pneumatophore. Nectosome greatly reduced (genus *Melophysa*) or absent (genus *Athorybia*). Siphosome reduced to a dense corm on which the cormidia are arranged in a spiral. Only 3 known species, of which 2 occur in the region under consideration.

- *Athorybia rosacea* (Forskal, 1775) (Fig. 3.17, 3.30). Large, red pigmented pneumatophore, with cormidia arranged in a spiral around it. No nectosome. Elongate, flimsy bracts with 7 inconspicuous rows of nematocysts running down the convex dorsal side. A very distinctive species. The bracts can be moved in a rhythmic manner, probably enabling the animal to swim about.

- ***Melophysa melo*** (Quoy and Gaimard, 1827) (Fig. 3.18). Nectosome reduced bearing a maximum of 5 nectophores. The nectophores are boot-shaped, with the nectosac occupying most of the foot, and a long, thick pedicular canal running from its apex up through the heel. The flattened base has two facets separated by a central protuberance. The dorsal radial canal is straight, while the ventral one makes several curves. The lateral canals are looped. The large, gelatinous bracts bear a proximal keel for attachment. The dorsal surface of the mature bracts bears several rows of prominent papillae. A very distinctive species. Only the most distorted nectophores in any way resemble those illustrated by Totton (1954).

#### Family **Forskaliidae**

Genus ***Forskalia*** Kölliker, 1853

Cylindrical or cone-shaped nectosome, whose numerous nectophores have a multiserial, spiral arrangement. Nectophores flattened dorso-ventrally and often asymmetrical in shape. Nectosac restricted to basal half; with straight radial canals. The siphosome also is coiled, particularly in its contracted state, with the gastrozooids borne on long stalks. Bracts usually gelatinous and of variable shape. There is no known way to distinguish the various species on the basis of their bracts alone.

- ***Forskalia edwardsi*** Kölliker, 1853 (Fig. 3.19). Slightly asymmetrical nectophores with two distinct facets on either side of ostium. Bracts variable in shape.
- ***Forskalia leuckarti*** Bedot, 1893 (Fig. 3.20). Asymmetric nectophores with only one pronounced axial wing, and 2 patches of epidermal cells on their sides. There is a vertical, disc-like expansion of the pedicular canal of the adult nectophores, which is usually red in colour. Bracts variable in shape.

#### Order **Calycophorae**

Siphonophores without an apical pneumatophore. The nectosome usually consists of one or two, often dissimilar, nectophores, although up to ca. 15 are present in the family Hippopodiidae. The cormidial elements consist of a bract, a gastrozooid, with tentacle, and a succession of gonophores. Again the Hippopodiidae are exceptional in that they do not possess bracts. There are no palpons, with the possible exception of one species. Asexual swimming bells have also been

reported in some species, but these may be the first (spent) gonophore retained. In many species the mature cormidial units are set free from the stem to lead a separate existence, known as the eudoxid or sexual stage.

About 100 species distributed amongst 6 families. The families usually can be distinguished by the basic shape of the nectophores and bracts, but the following key cannot take account of every specific variation, or all the larval stages.

- 1 Up to 15+ similar, closely applied, dorso-ventrally flattened nectophores bearing protuberances or spines; large, but shallow nectosac; bracts absent: **Family Hippopodiidae**
  - 1a Small, flattened nectophores, with vestigial nectosac and reduced somatocyst: **Family Prayidae**, Subfamily **Amphicaryoninae**
  - 1b Nectophores not dorso-ventrally flattened; bracts present .....
- 2 Nectophores and bracts rounded, smooth-walled, with thick mesogloea.....3
- 2a Nectophores and bracts pointed, toothed or of irregular shape.....4
- 3 Usually 2 nectophores of approximately equal size, forming an apposed pair; somatocyst simple or branched. Bracts with 5 or 6 branches to the canal system: **Family Prayidae**, Subfamily **Prayinae**
  - 3a Two nectophores of unequal size, with reduced somatocysts; nectosac of smaller nectophore usually reduced or obsolescent. Bracts with 2 branches to canal system: **Family Prayidae**, Subfamily **Amphicaryoninae**
  - 3b Single, fragile, larval nectophore, with a simple somatocyst and narrow hydroecium. Small, fragile bract with a single canal: **Family Sphaeronectidae**
- 4 Two, morphologically different nectophores; one (anterior) superimposed over the other (posterior) .....
- 4a Single, usually large, nectophore bearing simple or toothed ridges; somatocyst usually branched. Large bract without neck shield and extensively branched canal system: **Family Prayidae**, Subfamily **Nectopyramidinae**
  - 4b Single, usually small, apically pointed nectophore, with simple caecal somatocyst. Bract conical or angular.....6
- 5 Posterior nectophore with a somatocyst; anterior nectophore with extensive opening of hydroecium onto ventral surface. Small bract with phyllocyst

and 2 canals extending into neck shield: Family **Clausophyidae**

- 5a Posterior nectophore without somatocyst; hydroecium of anterior nectophore usually opens basally. Bracts conical or angular, with phyllocyst and, at most, one canal.....6
- 6 Conical stream-lined anterior nectophore, usually with shallow hydroecium; posterior nectophore, when present, usually apically truncated and of similar size or smaller than anterior one. Conical bracts: Family **Diphyidae**
- 6a Anterior nectophore angular, with inflated somatocyst and deep hydroecium; posterior nectophore, when present, larger than anterior one. Rigid, angular bracts: Family **Abylidiae**

### Family Prayidae

#### Subfamily **Amphicaryoninae**

Two nectophores differing in size. The larger, rounded one is believed to be the retained larval nectophore. The first definitive one is smaller (genus *Maresearsia*) or vestigial (genus *Amphicaryon*). The bracteal canals are reduced to 2 long hydroecials. The bracts of the 3 species of the genus *Amphicaryon* cannot be distinguished at present.

- ***Amphicaryon acaule*** Chun, 1888 (Fig. 3.31, 3.44). Nectosac of larval nectophore occupies about half the height, dorsal canal longer than ventral, and laterals slightly, and irregularly, expanded in region where they bend through 90°. The vestigial nectophore is embraced by the larval one. Its reduced nectosac has no ostial opening and the radial canals are simple, but distinct.
- ***Amphicaryon ernesti*** Totton, 1954 (Fig. 3.32). Larval nectophore similar to that of *A. acaule*, but lateral radial canals are more convoluted where they bend. Flattened vestigial nectophore not embraced by larval one. Nectosac greatly reduced and of characteristic shape. It's ventral canal forms a network on the ventral wall, while the dorsal canal is simple. No lateral canals.
- ***Amphicaryon peltifera*** (Haeckel, 1888) (Fig. 3.33). Larval nectophore similar to those of other species, but lateral radial canals are simple and usually straight. The flattened, plate-like vestigial nectophore is not embraced by the larval one. Its nectosac has disappeared leaving 3, characteristically arranged, finger-like radial canals.
- ***Maresearsia praeclarra*** Totton, 1954 (Fig. 3.34, 3.45) [=*Maresearsia sphaera* Stepanjants, 1967;

*Amphicaryon intermedia* Daniel, 1970]. The two nectophores, both with a functional flask-shaped nectosac, fit together to form a ball-like structure. The larval nectophore has a large, often swollen somatocyst, while that of the definitive one is minute. The radial canals on the nectosac of the larval nectophore are highly branched near their bases, and those of the definitive one also show some branching. Small, spherical bract with 2 recurved hydroecial canals.

#### Subfamily **Prayinae**

Two, occasionally up to 4, rounded, smooth-walled nectophores of similar size. Bracts with 6, occasionally reduced to 5, canals. Currently there are 8 genera encompassing 16 species, of which 5 have been recorded in the area under consideration.

#### Genus **Lilyopsis** Chun, 1885

Monotypic genus for *Lilyopsis rosea*.

• ***Lilyopsis rosea*** Chun, 1885 (Fig. 3.35, 3.46). Two, possibly more, very delicate nectophores with large nectosacs. Larval nectophore has a simple somatocyst, slightly swollen at its tip, and straight radial canals on the nectosac. Definitive nectophore has a bifurcated somatocyst and sinuous lateral radial canals on the nectosac. Bract like a cushion, with characteristically arranged canals. This is a very fragile species and is rarely seen; having not, to my knowledge, been collected by SCUBA divers. There is thus some doubt, in my mind, as to the records in the area under consideration here. Ref.: Carré (1969).

Genus **Praya** Quoy and Gaimard in Blainville, 1834 Two large, rounded nectophores (often with additional reserve bells) whose somatocysts can be complexly branched. Multibranched radial canals on nectosac. Bract laterally flattened with dorsal canal arising from end of spur-like right longitudinal canal. Gonophores with characteristically three-pronged mantle canal. Ref.: Pugh (1992b).

• ***Praya dubia*** (Quoy and Gaimard, 1833) (Fig. 3.36, 3.47). Cylindrical definitive nectophores with a baso-ventral extension below the ostium of the nectosac. Bifurcating canals on nectosac. Somatocyst simple in larval nectophore, but with an ascending (dorsal) and two long, branching lateral canals in the mature definitive one. Bract with relatively short dorsal canal, which may bifurcate subterminally. Left hydroecial canal not recurved distally.

- *Praya reticulata* (Bigelow, 1911) (Fig. 3.37, 3.48). Nectophores similar to previous species in basic design. Highly branched canals on nectosac form a reticulated pattern. Somatocyst, in mature nectophore, with several short lateral and ascending branches. Bract usually with relatively long, recurved dorsal and left hydroecial canals.

Genus **Rosacea** Quoy and Gaimard, 1827

Nectophores with simple somatocyst without side branches. Sinuous lateral radial canals on nectosac. Bracts kidney-shaped, but with characteristic arrangement of canals. The status of the generic name *Rosacea* was briefly discussed by Totton (1965), who noted that the name presently may not be being applied in the way the original authors intended. However, so as not to further complicate the involved nomenclature he proposed to retain the use of the name *Rosacea* in the way that Bigelow (1911) applied it, and he designated *R. plicata* Quoy and Gaimard *sensu* Bigelow as its type species. Unfortunately, Margulis (1994) decided to destabilise the nomenclature, which is contrary to its very purpose, and erected a new genus *Neorosacea*. The issue is too complicated to be dealt with here, but the destabilisation of the nomenclature is rejected and the generic name *Rosacea* is used in the sense that it has been used for the past 85 years, that is *sensu* Bigelow (1911). Ultimately, a submission to the ICZN may be required; although it is possible that the description of the original type species *R. ceutensis* Quoy and Gaimard, 1827 could be interpreted as that of a larval nectophore of a *Rosacea sensu* Bigelow species.

- *Rosacea cymbiformis* (Chiaje, 1822) (Fig. 3.38, 3.49). Nectophores relatively flimsy, slightly flattened. Hydroecium extends to base of nectophore. Nectosac opens dorso-basally. Bract with dorsal canal arising from left longitudinal canal, prior to origin of left hydroecial.
- *Rosacea plicata sensu* Bigelow, 1911 (Fig. 3.39, 3.50). Cylindrical nectophores with solid mesogloea. The simple somatocyst extends beyond the point of origin of the pedicular canal. Extensive hydroecium, not reaching the base of the nectophore. Nectosac opens basally. Bract similar to *R. cymbiformis*, but dorsal canal arises from left hydroecial canal distal to the short longitudinal canal. The nectophores of these two *Rosacea* species can be difficult to tell apart. Generally *R. cymbiformis* lives at shallower depths than *R. plicata*.

#### Subfamily **Nectopyramidinae**

Only a single, asymmetrical large definitive nectophore, which bears a vague pattern of ridges. Eudoxid stage resembles nectophore, and a special nectophore may be present. Smaller larval nectophore also bears ridges, which are spinose in the genus *Nectopyramis*. Ref.: Pugh (1992a).

#### Genus **Nectadamas** Pugh, 1992

Definitive nectophore with hydroecium restricted to a pocket-like structure; branched somatocyst with no lateral bend at base; radial canals on nectosac arise from a single pedicular canal. Ridges of larval nectophore not spinose; same arrangement of radial canals. No special nectophore present on eudoxid.

- *Nectadamas diomedae* (Bigelow, 1911) (Fig. 3.40, 3.51). Large rhomboidal definitive nectophore bearing a faint pattern of surface ridges. Small nectosac offset laterally; obliquely slanted, deep hydroecium with narrow opening. Complexly divided somatocyst. Large, roughly triangular bract with a vague ridge pattern and a small hydroecium. Phyllocyst complexly divided.

#### Genus **Nectopyramis** Bigelow, 1911

Definitive nectophore with extensive hydroecium; somatocyst with lateral bend at base; radial canals arise separately and directly from somatocyst. Larval nectophore with spinose ridges. Eudoxid bears a special nectophore.

- *Nectopyramis natans* (Bigelow, 1911) (Fig. 3.41, 3.52). Elongate, bow-shaped definitive nectophore with a pointed apex and truncated base. Seven longitudinal ridges arranged characteristically. Simple somatocyst without branches. Larval nectophore with functional nectosac and 4 radial canals arising separately from the simple somatocyst. Bow-shaped eudoxid bract with 5 longitudinal ridges. Distinctive lateral branch to dorsal canal.
- *Nectopyramis thetis* Bigelow, 1911 (Fig. 3.42, 3.53). Pyramidal definitive nectophore with indistinct ridges. Somatocyst with lateral branches. Larval nectophore with vestigial nectosac, usually with only 2 radial canals. Pyramidal eudoxid bract with 6 canals; dorsal canal with lateral branch.

#### Family **Hippopodiidae**

Diagnosis as briefly summarised in above key. There are 2 genera, but as Totton (1965) pointed out they are not really distinct. However, in order to maintain the stability of the nomenclature he retained both. The

genus *Hippopodius* is monotypic for *H. hippopus*. Poorly preserved material of certain species can be difficult to specifically identify. It appears that hippopodiids may feed almost exclusively on ostracods (Purcell, 1981), and Pugh (1991) found a very significant correlation between the latitudinal and depth distributions of the two groups.

- ***Hippopodius hippopus*** (Forskal, 1776) (Fig. 3.55). Horse-shoe shaped definitive nectophores with 4 rounded dorsal protuberances of variable size. The nectophores, which can luminesce brightly, generally turn a milky colour when preserved.
- ***Vogtia glabra*** Bigelow, 1918 (Fig. 3.56). More broadly horse-shoe shaped than *H. hippopus* with 2 dorso-lateral protuberances.
- ***Vogtia pentacantha*** Kölliker, 1853 (Fig. 3.57). Roughly quadrangular nectophores. Some ridges bear small protuberances, but these are generally absent from the facets between them.
- ***Vogtia serrata*** (Moser, 1925) (Fig. 3.59) [=*Vogtia kuruae* Alvariño, 1967]. Roughly triangular nectophore with distinctive ridges and no spines or protuberances.
- ***Vogtia spinosa*** Keferstein and Ehlers, 1861 (Fig. 3.58). Roughly quadrangular nectophore bearing numerous gelatinous teeth on the ridges and the dorsal and lateral facets.

#### Family Diphyidae

Usually two, occasionally only one, dissimilar streamlined nectophores. One, the anterior, usually is pointed apically and is positioned directly above the other, the posterior, which usually is apically truncated. The nectosac occupies the bulk of both nectophores. The hydroecium of the anterior one usually, but not always, is small or virtually absent. Bracts generally helmet shaped with a variably shaped phyllocyst. Except for one or species, no bracteal canals are present. It is difficult to give an all embracing diagnosis for the ca. 50 species in this family as there is so much specific variability. The family is divided into 3 subfamilies. The third subfamily has been erected recently (Pugh and Pagès, 1995) to encompass a single species, *Gilia reticulata*.

#### Subfamily Sulculeolariinae

Monotypic subfamily for genus *Sulculeolaria*.

#### Genus *Sulculeolaria* Blainville, 1834

Anterior nectophore with rounded apex, and without ridges; posterior nectophore of similar size with

extensively looped lateral radial canals. Replacement nectophores of both types are frequently produced, and these may have different characters. Small leaf-like bracts that may not be released as eudoxids. Anterior nectophores of a few species of the diphyine genus *Lensia* may be confused with this genus. Bracts of various species are not distinguishable. Ref.: Carré (1979).

- ***Sulculeolaria biloba*** (Sars, 1846) (Fig. 3.60). Anterior nectophore with obliquely angled somatocyst and without ostial teeth. Commissural canals present; mouth-plate divided into two elongated lobes. Posterior nectophore without ostial teeth; best characterised by the mouth plate with its two lateral lobes and a central protuberance.
- ***Sulculeolaria chuni*** (Lens and van Riemsdijk, 1908) (Fig. 3.61) [=? *Lensia campanella elongata* Margulies, 1984]. Anterior nectophore without ostial teeth. Long, filiform somatocyst reaching to two to three fifths the height of the nectophore. Commissural canals may or may not be present. Mouth plate formed by two lateral, non-overlapping lobes, without a central protuberance. Posterior nectophore without ostial teeth with slightly emarginated mouth plate.
- ***Sulculeolaria monoica*** (Chun, 1888) (Fig. 3.62). Anterior nectophore with 5 ostial teeth, 3 dorsal and 2 (smaller) lateral. Commissural canals present; minute somatocyst. Mouth plate divided with pair of dorsal teeth. Posterior nectophore with similar ostial teeth; mouth plate variably divided, but with 2 dorsal teeth.
- ***Sulculeolaria quadrivalvis*** Blainville, 1834 (Fig. 3.63). Anterior nectophore with 2 dorsal and 2 lateral ostial teeth, although both may be reduced or, very occasionally, absent. Commissural canals present; bilobed mouth plate without protuberances. Long, sinuous somatocyst reaching one third to two fifths the height of the nectophore. Posterior nectophore with similar arrangement of ostial teeth. Deeply divided mouth plate with 2 protuberances, although these can be reduced or absent. The nectosac has two characteristic constrictions.
- ***Sulculeolaria turgida*** (Gegenbaur, 1853) (Fig. 3.64). Anterior nectophore without ostial teeth. Commissural canals may or may not be present. Minute ovoid or filiform somatocyst. Bilobed mouth plate without protuberances. Posterior nectophore without ostial teeth and rounded, undivided mouth plate without protuberances.

Subfamily **Diphyinae**

Only a single anterior and posterior nectophore produced, although the latter may be reduced or suppressed entirely. Anterior nectophore usually apically pointed and usually larger than posterior one. The bracts of the free-swimming eudoxids usually are helmet-shaped. The bulk of the diphyid species is contained in this subfamily divided amongst about 7 genera, with most being included in the catch-all genus *Lensia*. In several species the posterior nectophore is either not developed or has not been described. Some, particularly within the genus *Lensia*, are very difficult to distinguish specifically. Similarly many eudoxid stages remain unknown. It is, therefore, impossible to give a comprehensive description for every part of every species.

Genus ***Chelophyes*** Totton, 1932

Rigid anterior nectophores with 5 ridges, although dorsal one extends only a short distance up from the ostium. Divided mouth-plate; hydroecium claw-shaped in lateral view extending to about one sixth the height of the nectophore and not opening ventrally. Posterior nectophore apically pointed and the divided mouth plate forms 2 strong, asymmetric teeth. Strong serrations on basal parts of ridges, particularly the ventral ones. Conical eudoxid bracts with small, rounded neck shield, and relatively deep hydroecium. The phyllocyst is cylindrical and almost stretches to the apex. The two species are very similar in form and the eudoxid stages have not been distinguished.

- ***Chelophyes appendiculata*** (Eschscholtz, 1829) (Fig. 3.65, 3.78). Only the right lateral and the 2 ventral ridges reach the apex of the anterior nectophore, the former having twisted so as to lie dorsally. Long, spindle-shaped straight somatocyst. Ventral ridges of posterior nectophore bear an obvious notched tooth on a level with the ostium.
- ***Chelophyes contorta*** (Lens and van Riemsdijk, 1908) (Fig. 3.66). Anterior nectophore very similar to that of *C. appendiculata*. The main difference is that the ventral facet is strongly twisted to the right. In this case the right ventral ridge does not reach the apex, and it may merge with the left ventral close to the apex. The somatocyst is similarly affected by the torsion and is twisted to the right. The posterior nectophore does not have a distinct notched tooth on the ventral ridges. The anterior nectophores of the two *Chelophyes* species are easily confused, particularly if the somatocyst of that of *C. appendiculata* becomes distorted during preservation.

Genus ***Dimophyes*** Moser, 1925

Monotypic genus for *Dimophyes arctica*.

- ***Dimophyes arctica*** (Chun, 1897) (Fig. 3.67, 3.79). Anterior nectophore without lateral ridges. The mouth plate is undivided and the prominent hydroecium is largely open on its ventral side. Carrot-shaped somatocyst reaching to about two-thirds the height of the nectophore. Posterior nectophore reduced and seldom found; with the opening of the nectosac lying dorso-basally. Very characteristic conical bract, with extensive neck shield that is penetrated by a median canal from the phyllocyst. The latter has both apical and lateral horns.

Genus ***Diphyes*** Cuvier, 1817

Anterior nectophores with 5 complete longitudinal ridges. There are 3 prominent ostial teeth, although in one species the dorsal one is obscured. Deep hydroecium, only a small basal portion of which may open ventrally. Posterior nectophore, when developed, also with 3 ostial teeth, but again the dorsal may be obscured. Long apical process (apophysis) that is inserted into hydroecium of anterior nectophore. Bracts generally helmet-shaped, although flattened in one species. There are 4 recognised species, all of which have been found in the area under investigation.

- ***Diphyes antarctica*** Moser, 1925 (Fig. 3.68, 3.80). Apex of nectosac of anterior nectophore not constricted, lying close to apex of nectophore. Hydroecium to about half the height of the nectophore; relatively short spindle-shaped somatocyst. Dorsal ostial tooth obscured, and smaller than laterals. Very broad, divided mouth plate. Dorsal ostial tooth of posterior nectophore similarly obscured. Head piece and neck shield of bract of similar height; spindle-shaped phyllocyst tapering toward its top.
- ***Diphyes bojani*** (Eschscholtz, 1829) (Fig. 3.79, 3.81). Anterior nectophores with variably serrated ridges. The nectosac gradually narrows toward its apex, which lies close to that of the nectophore itself. Hydroecium extends to about one-third the height of the nectophore, with the spindle-shaped somatocyst extending up from it to close to the apex of the nectophore. The dorsal ostial tooth is of equal size to or smaller than the lateral ones. Mouth plate not divided. Posterior nectophore with similar arrangement of 3 ostial teeth. Lateral teeth, and the baso-lateral margins are serrated.

- Eudoxid bract shield-like, lying on the ventral side of the gonophore.
- ***Diphyes chamissonis*** Huxley, 1859 (Fig. 3.70). Anterior nectophore is blunt apically. Nectosac with rounded apex lying a short distance from that of the nectophore. Hydroecium extends to mid-height of nectophore; with relatively short spindle-shaped somatocyst extending above it. Ostial teeth of equal size. Mouth plate not divided. Posterior nectophore not developed; eudoxid not found in area. Like *Chelophyses contorta*, this is largely a neritic Indo-Pacific species and has only been found off South Africa due to the intrusions of water from the Agulhas Current.
  - ***Diphyes dispar*** Chamisso and Eysenhardt, 1821 (Fig. 3.71, 3.82). Very similar to *D. bojani*. Nectosac of anterior nectophore cylindrical basally but with narrow caecal extension ending close to the apex of the nectophore. Hydroecium extends to about one-half the height of the nectophore, with the spindle-shaped somatocyst extending up to just above the beginning of the nectosacal caecum. The dorsal ostial tooth is considerably larger than the lateral ones. Mouth plate not divided. Posterior nectophore with similar arrangement of ostial teeth. Lateral teeth and baso-lateral margins not serrated. Bract somewhat similar to that of *Chelophyses appendiculata*, but the phyllocyst is narrower and tapers towards its apex, which lies further from the apex of the bract.

#### Genus *Eudoxoides* Huxley, 1859

Small, rigid anterior nectophores with 5 ridges; the dorsal one being complete. Mouth plate divided; no conspicuous ostial teeth.

- ***Eudoxoides mitra*** Huxley, 1859 (Fig. 3.72, 3.83). Anterior nectophore not spirally twisted. All ridges complete and serrated basally. Dorsal ridge extended to form basal tooth. Large mouth plate with serrated wings, the left one being larger than the right. Hydroecium truncated apically; somatocyst relatively short and pear-shaped. Posterior nectophore with distinct notch between apex and apical apophysis. Hydroecium open except near apex where 2 hydroecial flaps overlap each other. Large undivided, asymmetric mouth plate with 2 large teeth. Large teeth on ventral ridges about the level of the ostium, also asymmetrically disposed. Bract with serrated ridges and a deep hydroecium. Phyllocyst pear-shaped.

- ***Eudoxoides spiralis*** (Bigelow, 1911) (Fig. 3.73, 3.84). Anterior nectophore with characteristically twisted, serrated ridges. The ventral ridges unite close to the apex. Large, divided and claw-shaped hydroecium. Carrot-shaped somatocyst extending to about half the height of the nectophore. No posterior nectophore is developed. Conical bract with lightly serrated ridges. Large neck shield; shallow hydroecium; thick phyllocyst reaching almost to apex. The gonophore is also characteristically twisted.

#### Genus *Lensia* Totton, 1932

Small pyramidal anterior nectophores, generally ridged, the number and disposition of the ridges being variable. Small, divided mouth plate, with shallow hydroecium, rarely extending above ostial level. No ostial teeth. Posterior nectophore, when developed, truncated apically with a rounded mouth plate. Bracts helmet-shaped. Shape of phyllocyst generally resembling that of somatocyst of anterior nectophore. This is a catch-all genus, containing over thirty species that do not show the distinctive characters of the other genera. The species are here grouped according to whether they have 7 or less ridges (1 dorsal, 2 ventral and 0, 2 or 4 laterals), all running longitudinally, or they are multi-ridged.

#### Species with 7 or less ridges

- ***Lensia achilles*** Totton, 1941 (Fig. 3.87) [=*Lensia eltanin* Alvariño and Wojtan, 1984]. Anterior nectophore with 5 complete ridges. The basal parts of the lateral ridges bend sharply dorsad. Small, broad mouth plate, with hydroecium extending to ostial level. Elongate somatocyst, somewhat variable in shape, extending to a quarter to a half the height of the nectophore. Posterior nectophore and eudoxid stage have not been described.
- ***Lensia campanella*** (Moser, 1925) (Fig. 3.88, 3.106) [=*Lensia eugenioi* Alvariño and Wojtan, 1984]. Anterior nectophore with indistinct ridges that have been subjected to a torsion towards the right. This results in a twisting of the apex of the preserved specimens. Oblique baso-ventral facet with mouth plate and hydroecium being virtually non-existent. Short, oblique, club-shaped somatocyst. Bract conical with rounded apex, with minute hydroecium. Club-shaped phyllocyst. Ref.: Carré (1968b).

- ***Lensia conoidea*** (Keferstein and Ehlers, 1860) (Fig. 3.89, 3.107). Anterior nectophores with 5 complete straight ridges. Mouth plate shallow but broad; hydroecium minute. Spindle-shaped somatocyst extending to over half the height of the nectophore. Posterior nectophore with 5 ridges, with a large, asymmetric, notched mouth plate. Bract conical with long spindle-shaped phyllocyst.
- ***Lensia cossack*** Totton, 1941 (Fig. 3.90). Anterior nectophore with very vague ridges, but obvious folds. Minute mouth plate with oblique basal facet, and virtually no hydroecium. Ovoid, obliquely inclined somatocyst reaching up to about one third the height of the nectophore. This species may not develop a posterior nectophore and the eudoxid has not been described. Alekseev (1984) suggested that this species should be relegated to a subspecies of *Lensia campanella*, but for the present it is retained as a separate one.
- ***Lensia fowleri*** (Bigelow, 1911) (Fig. 3.91, 3.108). Anterior nectophore with 5 complete, straight ridges. Mouth plate relatively extensive and contains the globular somatocyst; hydroecium virtually absent. Hydroecium of posterior nectophore delimited by triangular wings; mouth plate rounded and undivided. Elongate bract, rounded apically, with a wide notched neck shield. Phyllocyst globular.
- ***Lensia hardy*** Totton, 1941 (Fig. 3.92). Anterior nectophore with 5 complete, straight longitudinal ridges. Mouth plate broad but shallow, largely occupied by hydroecium, which lies below ostial level. Globular somatocyst with short stalk. Posterior nectophore and eudoxid stage have not been described. This species closely resembles *L. fowleri*.
- ***Lensia havock*** Totton, 1941 (Fig. 3.93). Anterior nectophore with 7 complete longitudinal ridges. A characteristic feature is that the ventro-lateral ridges bend ventrad, slightly above the ostial level, and run down onto the mouth plate. Extensive hydroecium extending to well above ostial level, and largely open ventrally. Short somatocyst, usually club-shaped, but its outline is often difficult to discern. Posterior nectophore and eudoxid stage have not been described.
- ***Lensia hotspur*** Totton, 1941 (Fig. 3.94). Anterior nectophore with 5, complete, straight longitudinal ridges. Small mouth plate, with basal facet obliquely inclined, and minute hydroecium. Short, obliquely inclined, ovate somatocyst with short stalk. Posterior nectophore difficult to distinguish from that of other *Lensia* species; eudoxid stage not described.
- ***Lensia hunter*** Totton, 1941 (Fig. 3.95). Anterior nectophore with 7 straight longitudinal ridges. The dorso-lateral ridges do not reach the ostium, while the ventro-laterals, which basally form the margins of the mouth plate, do not reach the apex. Oblique mouth plate, occupied by hydroecium, which lies below the ostium and is open ventrally. Short, usually bilobed somatocyst borne on short stalk. Posterior nectophore and eudoxid stage have not been described.
- ***Lensia leloupi*** Totton, 1954 (Fig. 3.96). Anterior nectophore with 5 straight longitudinal ridges, the laterals not reaching the ostium. Oblique mouth plate with hydroecium reaching slightly above ostial level. Narrow somatocyst stretching to about one third the height of the nectophore. Posterior nectophore and eudoxid stage have not been described. This species closely resembles *L. subtiloides* (see below) and further studies on the relationship of these two species are warranted.
- ***Lensia meteori*** (Leloup, 1934) (Fig. 3.97). Fragile anterior nectophore without any obvious ridges. Narrow, almost vertical mouth plate with shallow hydroecium, extending above ostial level and open ventrally. Somatocyst expanded laterally with short stalk. Posterior nectophore and eudoxid stage have not been described.
- ***Lensia multicristata*** (Moser, 1925) (Fig. 3.98). Anterior nectophore with 7 straight longitudinal ridges. Neither of the pairs of laterals reach the ostium, and the ventro-lateral pair also do not reach the apex. Small mouth plate with shallow hydroecium not extending above ostial level. Somatocyst long and thin, extending to one third to a half the height of the nectophore. The posterior nectophore is hard to distinguish. The bract has not positively been identified, but probably is that of *Eudoxia tenuis* Patriti, 1965 (see Kirkpatrick and Pugh, 1984).
- ***Lensia subtilis*** (Chun, 1886) (Fig. 3.99, 3.109). Fragile anterior nectophore, up to 10 mm in height, apparently ridgeless, but with folds. Small mouth plate with oblique basal facet and shallow hydroecium. Somatocyst spherical borne on a long stalk. Small, rounded bract with small phyllocyst. The posterior nectophore is hard to distinguish. In general form the anterior nectophore resembles

that of *Lensia meteori*, but the shape of the somatocyst clearly distinguishes them.

- ***Lensia subtiloides*** (Lens and van Riemsdijk, 1908) (Fig. 3.100, 3.110). Anterior nectophore with 5 straight, complete ridges. Small mouth plate and hydroecium with an ovoid somatocyst borne on an oblique stalk. Rounded bract with club-shaped phyllocyst. The posterior nectophore is hard to distinguish. Like *Chelophyses contorta* and *Diphyes chamissonis* this is largely an Indo-Pacific neritic species that can be carried into the Atlantic via the Agulhas Current. Other Atlantic records should be treated with caution, particularly in the light of Totton's (1954) description of a very similar species *Lensia leloupi*.

#### Species with more than 7 ridges

- ***Lensia ajax*** Totton, 1941 (Fig. 3.101). Anterior nectophore with 5 sets of from 2 to 4, usually 3, often incomplete longitudinal ridges. Hydroecium extends to ostial level and is open ventrally. Small, club-shaped somatocyst. Mouth plate squarely truncated basally. Posterior nectophore and eudoxid stage have not been described.
- ***Lensia exeter*** Totton, 1941 (Fig. 3.102). Anterior nectophore with several ridges, only 5 of which reach the apex. The dorso-lateral ridges connect with a transverse velar ridge. Large mouth plate with hydroecium extending up to ostial level and open ventrally. Long, slender somatocyst extending to one third the height of the nectophore. Posterior nectophore and eudoxid stage have not been described.
- ***Lensia grimaldi*** (Leloup, 1933) (3.103). Anterior nectophore with a variable number of ridges. Only the 2 ventral ridges are complete, and only 5 ridges reach the apex. The dorso-lateral ridges turn dorsal near their bases and bifurcate. Large mouth plate and hydroecium, which is open ventrally, extends to slightly above ostial level. Short, club-shaped somatocyst. Posterior nectophore and eudoxid stage have not been described.
- ***Lensia hostile*** Totton, 1941 (3.104). Anterior nectophore with multiple ridges; several of the laterals being complete. Extensive mouth plate, and deep hydroecium, which is open ventrally. Inverted, heart-shaped somatocyst whose true outline may be difficult to discern. Posterior nectophore and eudoxid stage have not been described.
- ***Lensia lelouvetteau*** Totton, 1941 (Fig. 3.105). Anterior nectophore with numerous, mainly com-

plete, straight ridges that are linked by a velar ridge. Mouth plate rounded ventrally and hydroecium, which extends above ostial level, is open ventrally. Short, laterally expanded, mushroom-like somatocyst. Posterior nectophore and eudoxid stage have not been described. The eudoxid stage described by Alvariño and Wojtan (1984) belongs to *Dimophyes arctica*.

#### Genus *Muggiaeae* Busch, 1851

Anterior nectophore with complete dorsal ridge Deep hydroecium not open ventrally, although the divided mouth plate may be oblique. Somatocyst arises very close to wall of nectosac. A posterior nectophore is not developed. Three of the 4 known species are largely neritic.

- ***Muggiaeae atlantica*** Cunningham, 1892 (Fig. 3.74, 3.85). Anterior nectophore with 5 complete, relatively straight longitudinal ridges. Relatively deep hydroecium, extending to one third the height of the nectophore. Long, thin somatocyst reaching to apex of nectosac. Small conical bract with an asymmetrical neck shield and a very shallow hydroecium. The phyllocyst is club-shaped.
- ***Muggiaeae bargmannae*** Totton, 1954 (Fig. 3.75). Anterior nectophore with lateral folds in place of ridges. Nectosac reaches to almost the apex of the nectophore. Oblique mouth plate, with relatively shallow hydroecium. Somatocyst sausage-shaped extending to over half the height of the nectophore. The eudoxid stage has not been described. This species can be confused with *Dimophyes arctica*, but the divided mouth plate clearly distinguishes it.
- ***Muggiaeae kochi*** (Will, 1844) (Fig. 3.76). Anterior nectophore with 5 complete longitudinal ridges, the laterals bending dorsad toward their bases. Relatively shallow hydroecium, with somatocyst extending to only half the height of the nectophore. The eudoxid stage is not distinguished from that of *Muggiaeae atlantica*.

#### Subfamily *Giliinae*

Monotypic subfamily for *Gilia reticulata*.

- ***Gilia reticulata*** (Totton, 1954) (Figs 9.13, 10.9). Anterior nectophore with a reticulated pattern of ridges and a velar ridge. Mouth plate divided with hydroecium extending above ostial level. Small ovoid somatocyst. Posterior nectophore and bract also with reticulated pattern of ridges. Phyllocyst of bract with swollen centre and a tapering irregular apico-dorsal process. Two canals run down into

the neck shield. This very distinctive species previously had been included in the diphyine genus *Lensia*, but recently its status has become uncertain. This is because of the presence of 2 canals in the neck shield of the bract (see Pugh and Pagès, 1995), which is a characteristic of the bracts of species of the family Clausophyidae. The nectophores, however, show typical diphyine characters and so Pugh and Pagès (1995) chose to erect a new diphyid subfamily to encompass the species.

#### Family **Clausophyidae** Totton, 1965

Both anterior and posterior nectophores possess a somatocyst. The phyllocyst of the eudoxid bract, when known, has 2 fine branch canals that run down into the neck shield. This is a small group of ten, mainly deep living, species divided amongst 4 genera. Nine of the species have been found within the area under consideration.

Genus ***Chuniphyes*** Lens and van Riemsdijk, 1908  
Nectophores with ridges that end in distinct teeth. Anterior nectophores with 4 ridges (dorsal, ventral and a pair of laterals) at the pointed apex. Each of these ridges bifurcates below the apex, the ventrals forming the margins to the hydroecium, so that there are 8 ridges at the base. Posterior nectophore with 3 ridges (dorsal and pair of laterals) reaching apex, all of which bifurcate further down. Hydroecium extends for virtually the whole length of the nectophore and has 2 large, asymmetrical flaps in its upper half. Bract flattened; phyllocyst asymmetrical with an apical and 2 lateral horns in addition to the canals running down into the neck shield. The two known species are very similar in design, and the eudoxid stages are, at present, indistinguishable. The anterior nectophore is usually smaller than the posterior one.

- ***Chuniphyes moserae*** Totton, 1954 (Fig. 3.111). The lateral ridges bifurcate relatively close to the apex of the anterior nectophore, and the resulting dorso-laterals do not end, basally, in pronounced teeth. The hydroecium stretches up almost to the same level as the apex of the nectosac. Main body of the somatocyst globular with a narrow canal, that may bear side branches, running up to the apex of the nectophore. In the posterior nectophore the mouth plate bears 2, only slightly asymmetric teeth.
- ***Chuniphyes multidentata*** Lens and van Riemsdijk, 1908 (Fig. 3.112, 3.120). Lateral ridges bifurcate relatively further away from the apex of the anterior nectophore, and dorso-laterals end, basally, in

distinct teeth. Hydroecium reaches to only a little over half the height of the nectosac. Main body of somatocyst consists of 2 broad wings, of variable extent, with simple canal running up from it to apex of nectophore. Mouth plate of posterior nectophore bearing 2, distinctly asymmetrical teeth.

#### Genus ***Clausophyes*** Lens and van Riemsdijk, 1908

Smooth-walled, ridgeless, laterally flattened, rounded nectophores. Anterior nectophore with deep hydroecium in basal half. Lateral radial canals of both nectophores are looped. Somatocyst long tube of varying thickness, part of which is swollen. For most species the eudoxid stage is unknown. The genus currently includes 5 species, 2 of which have been described only recently. The anterior nectophores of 3 of the species are very similar in basic form. The first species to be described was *Clausophyes ovata* (Keferstein and Ehlers, 1860), but Margulies (1988) pointed out that since Moser (1925) this name had been wrongly applied to another species. The name *C. moserae* has been established for this other species. Although this destabilises the nomenclature, the species in question have not been recorded very often, particularly *C. ovata*, and so this change is accepted here. A table comparing the characters of the 4 species found in the area under consideration is given by Pugh (1995).

- ***Clausophyes galeata*** Lens and van Riemsdijk, 1908 (Fig. 3.113). Large, robust anterior nectophore whose mouth plate is partially divided. Deep hydroecium extending to over half the height of the nectophore, with thickened walls, and a large, central protuberance, where the posterior nectophore attaches. Thick somatocyst, irregularly expanded. Large, robust posterior nectophore, with relatively complicated arrangement of lateral radial canals on nectosac. The most characteristic feature is the presence of a pair of finger-like projections from the walls of the hydroecium, close to its apex. Ref.: Pugh and Pagès (1993).
- ***Clausophyes laetmata*** Pugh and Pagès, 1993 (Fig. 3.114). Anterior nectophore with undivided mouth plate. Deep hydroecium extending to two-thirds the height of the nectophore, and having characteristic flaps. Somatocyst expanded only in its apical half. The posterior nectophore and eudoxid stage have not been described.
- ***Clausophyes moserae*** Margulies, 1988 (Fig. 3.115). Anterior nectophore up to 20 mm in height, but usually much smaller (7-8 mm). Mouth plate almost

completely divided; hydroecium usually extending to half the height of the nectophore, and without flaps. The central third of the somatocyst is regularly, but variably, expanded. Posterior nectophore with simple somatocyst; no finger-like processes in hydroecium, whose left lateral wing is entire.

- *Clausophyes tropica* Pugh, 1995 (Fig. 3.116). Nectosac of anterior nectophore relatively small occupying less than half the height of the nectophore. Hydroecium without flaps, but with extensive central process. Somatocyst expanded, to a variable degree for the quarter below its middle. Posterior nectophore with relatively small nectosac. Somatocyst expanded in an irregular fashion. Extensive flap in the middle of the left hydroecial wing.

#### Genus *Crystallophyses* Moser, 1925

Monotypic genus for *Crystallophyses amygdalina*.

- *Crystallophyses amygdalina* Moser, 1925 (Fig. 3.117) [=*Thalassophyes ferrarii* Alvariño and Frankwick, 1983]. Anterior nectophore with 5 complete ridges; the pair of laterals being sharply recurved ventrad at their bases. Nectosac extends to three quarters the height of the nectophore, and the shallow hydroecium almost reaches the apex. The somatocyst is swollen in its basal two thirds, and the canal above may have short side branches. Posterior nectophore also with 5 ridges, but on each side the laterals and ventrals unite close to the apex. Basally the laterals end in distinct teeth. The hydroecium extends the entire height of the nectophore, and has small, pointed flaps. The long somatocyst is a simple canal. The eudoxid stage has not been described. Margulis (1988) transferred this species into the genus *Chuniphyes*, possibly based on Totton's (1954) statement that there was an obvious relationship between the two genera. However, Totton (1954) then noted the clear differences between the genera and retained, as is followed here, the genus *Crystallophyses*.

#### Genus *Heteropyramis* Moser, 1925

Anterior nectophore with 5 straight, complete longitudinal ridges; small nectosac and hydroecium restricted to central half. Somatocyst thick and slanting basally, with a narrow apical canal extending to close to the apex of the nectophore. Posterior nectophore not described and possibly not developed. Pyramidal bract whose phyllocyst resembles the somatocyst of the anterior nectophore. The two species in this genus are

very similar in basic form. However, Moser (1925) initially separated the species into separate genera, the other being *Thalassophyes* Moser, 1925. Totton (1965) pointed out that they were probably congeneric but retained the two genera, while Margulis (1988) went as far as synonymising them as a single species. The latter is clearly not the case, but the two species are here treated as congeneric.

- *Heteropyramis crystallina* (Moser, 1925) (Fig. 3.118, 3.121). No opaque spots present on ridges of anterior nectophore or eudoxid stage. Eudoxid bract with relatively large neck shield.
- *Heteropyramis maculata* Moser, 1925 (Fig. 3.119, 3.122) [=*Heteropyramis alcala* Alvariño and Frankwick, 1983]. Opaque spots present on some of the ridges and at the apex of the anterior nectophore and eudoxid bract, and on the gonophore. Neck shield of bract relatively small.

#### Family Sphaeronectidae

The small, delicate, rounded larval nectophore is the only one developed. The bract also is small and rounded. This is a small group of species, rarely found in net material, all of which are here treated as belonging to the genus *Sphaeronectes* Huxley, 1859. Only one species has been found in the area under consideration.

- *Sphaeronectes gracilis* (Claus, 1873) (Fig. 3.43, 3.54). Larval nectophore whose nectosac occupies the basal half and has 4 straight radial canals. The long, narrow hydroecium bends over one side of the nectosac. The narrow, curved somatocyst may have a slight terminal swelling. Small hemispherical bract, with minute neck shield and shallow hydroecium. The long, club-shaped phyllocyst is obliquely angled.

#### Family Abylidiae

Rigid, angular nectophores, the posterior one, without a somatocyst, usually being much larger, and bearing serrated ridges and teeth. In all but one species the somatocyst of the anterior nectophore has curved over to occupy a ventral position. There are two subfamilies that are distinguished by the presence (Abylinae) or absence (Abylopsinae) of a rectangular apical facet on the anterior nectophore. However, there is an exception in the former subfamily. Sears (1953) made a detailed study of this family using material from the "Dana" collections, and described several new species. However, Totton (1965) pointed out that many of the descriptions were based on deformed specimens. Nonetheless he

retained some of the new species, whilst noting that it was not clear whether they were truly distinct. Here we go further and reject all of Sears' (1953) new species and synonymise them with previously described ones. Several other, more recent descriptions of new species also appear to be based on deformed specimens and are also treated as junior synonyms.

#### Subfamily Abylinae

##### Genus *Abyla* Quoy and Gaimard, 1827

Anterior nectophores with 10 or 11 facets. The apical facet is divided by a transverse ridge, and many ridges are serrated, particularly basally. Dorsal nectosac and median hydroecium are long tubes extending almost to apex of nectophore. The large oval somatocyst lies ventrally. Posterior nectophore with long, tapering apical apophysis, has only 4 ridges. The ventral ridges define the hydrocial wings and are heavily serrated basally. The left hydrocial wing bears a toothed comb or flap. Five, usually serrated, ostial teeth. Prismatic bracts with 6 facets, the dorsal one being rectangular. Very large phyllocyst, with 2 canals running down toward the ventro-lateral corners of the apical facet. The bracts (Fig. 3.133) cannot, at present, be identified specifically.

- *Abyla bicarinata* Moser, 1925 (Fig. 3.123) [=*Abyla brownia* Sears, 1953]. Wide anterior nectophore with lateral ridges defining wing-like processes, and edges of facets rounded. No transverse ridge between ventral and apico-ventral facets. Posterior nectophore as wide as it is long. Comb with 4 to 7 teeth; strong ostial teeth.
- *Abyla haeckeli* Lens and van Riemsdijk, 1908 (Fig. 3.124) [=*Abyla ingeborgae* Sears, 1953]. Anterior nectophore as wide as it is long, without wing-like processes. Transverse ridge separates ventral facet from apico-ventral one. Posterior nectophore with up to 5 teeth on comb. Lateral ostial teeth closer to dorsal tooth than to ventral ones.
- *Abyla trigona* Quoy and Gaimard, 1827 (Fig. 3.125) [=*Abyla carina* Haeckel, 1888, *Abyla peruviana* Sears, 1953, *Abyla schmidti* Sears, 1953, ? *Abyla tottoni* Sears, 1953]. Anterior nectophore as broad as it is wide, with most ridges heavily, but irregularly, serrated. Ventral facet not separated, by a transverse ridge, from apico-ventral one. Posterior nectophore with from 4 to 11 teeth on comb. Two rows of teeth on basal margin of right ventral wing. Ostial teeth heavily serrated.

##### Genus *Ceratocymba* Chun, 1888

Anterior nectophore with 7 facets. Apical facet not

divided by a transverse ridge. Posterior nectophore long and narrow, without wing-like expansions. Short dorsal ridge ends on the dorsal tooth. Bracts with a median dorsal ridge. Left lateral facet divided by another ridge with a characteristic disposition. Phyllocyst with 2 thin ventro-lateral branches. Its distal end bends dorsad to form a blind sac.

- *Ceratocymba dentata* (Bigelow, 1918) (Fig. 3.126, 3.134) Anterior nectophore with triangular dorsal facet. Its lateral margins are deeply bowed and serrated. This facet continues over the top of the nectophore and extends into a short peak into which the nectosac is extended. Posterior nectophore has a relatively large dorsal tooth and numerous small teeth on the comb. The left lateral ridge on the bract joins the apico-lateral ridge, but not the posterior margin.
- *Ceratocymba leuckarti* (Huxley, 1859) (Fig. 3.127, 3.135). Anterior nectophore rectangular in shape with flat apical facet and narrow ventral one. Apices of hydroecium, nectosac and somatocyst all on the same level. Posterior nectophore with only 5 or 6 teeth on the comb. Left lateral ridge on bract complete.
- *Ceratocymba sagittata* (Quoy and Gaimard, 1827) (Fig. 3.128, 3.136) [=*Ceratocymba intermedia* Sears, 1953, *C. indica* Daniel, 1970]. Very characteristic anterior nectophore with a long pyramidal apical extension that masks the apical facet. Long, tubular nectosac about twice as long as hydroecium. Posterior nectophore with characteristically long right ventral tooth. The left lateral ridge on bract joins the posterior margin but not the apico-lateral one.

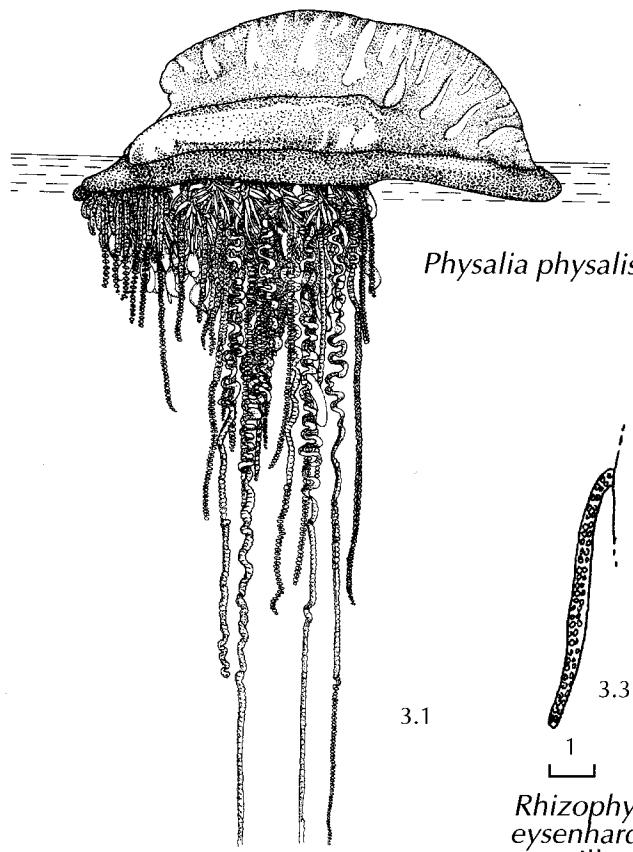
#### Subfamily Abylopsinae

There are 3 genera and 4 species.

##### Genus *Abylopsis* Chun, 1888

Seven-faceted anterior nectophore, but without an apical facet, and pentagonal dorsal and ventral facets. Hydroecium only partially interposed between somatocyst and nectosac. Somatocyst with apical diverticulum. Posterior nectophore with 5 ridges and a short curved apical apophysis. The left lateral ridge bifurcates close to the apex. Flaps on both wings of hydroecium. Bracts with 7 facets. Phyllocyst with swollen apico-lateral branches and apical diverticulum, while distally it is a narrow tube. The anterior nectophores of the two species are very similar in design.

# Cystonectae

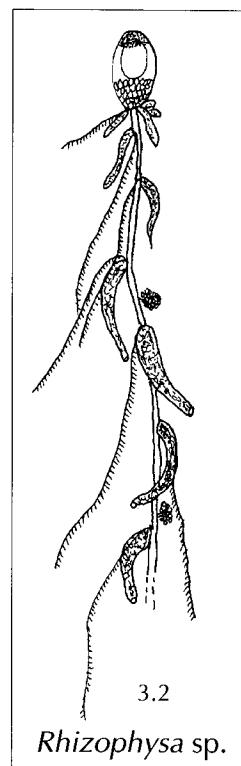
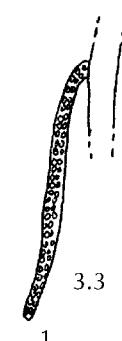


3.1

*Rhizophysa eysenhardtii*,  
tentillum

1

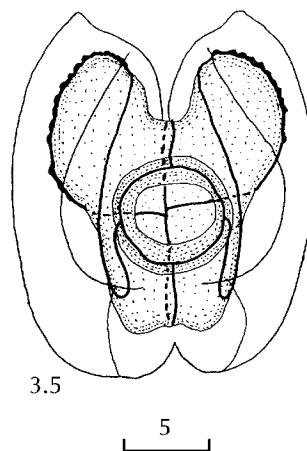
3.3



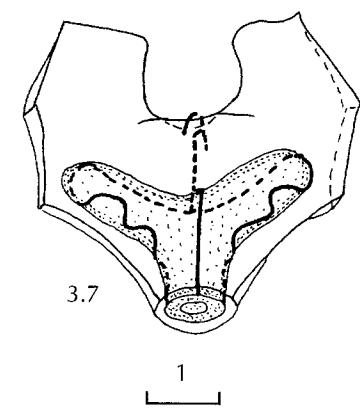
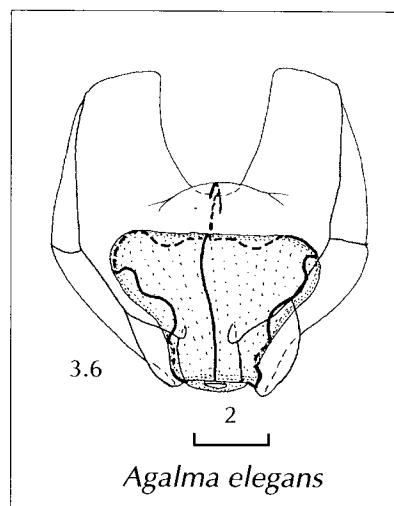
3.2



## Upper view of nectophores or whole specimens of Physonectae



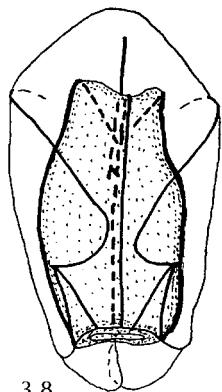
*Apolemia uvaria*



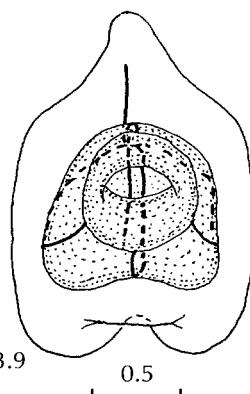
*Agalma okeni*



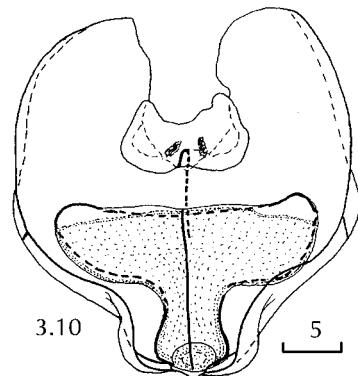
**Upper view of nectophores  
or whole specimens of Physonectae**



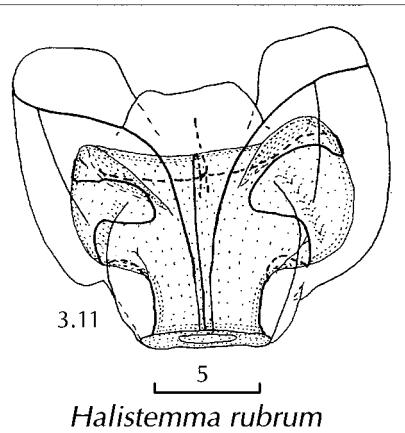
*Bargmannia  
elongata*



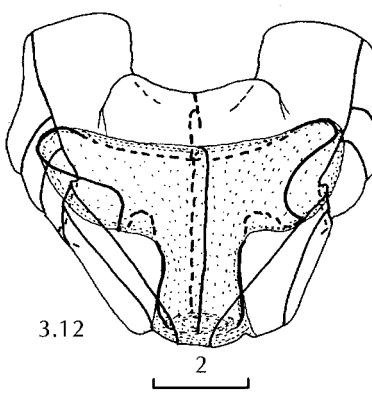
*Cordagalma cordiforme*



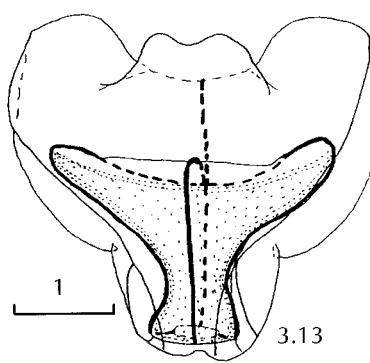
*Erenna richardi*



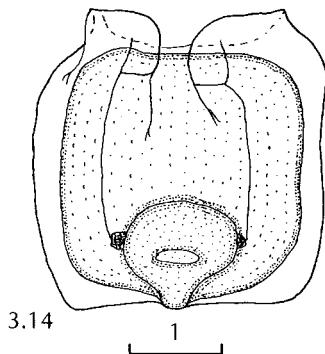
*Halistemma rubrum*



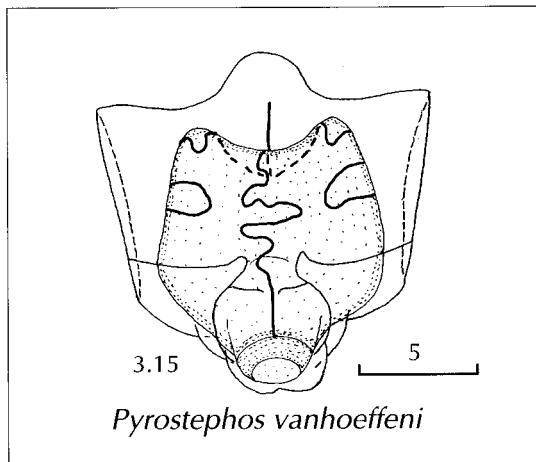
*Halistemma striata*



*Marrus antarcticus*



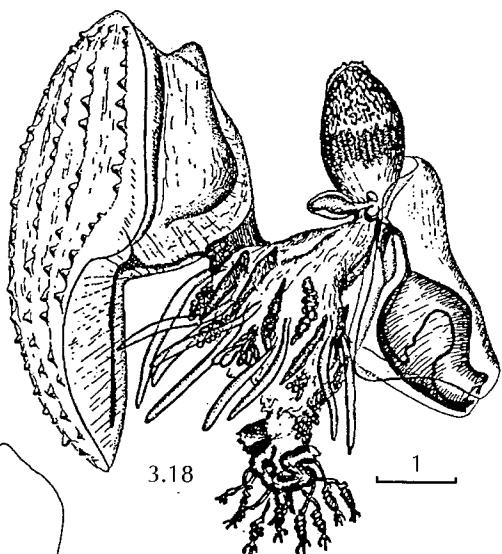
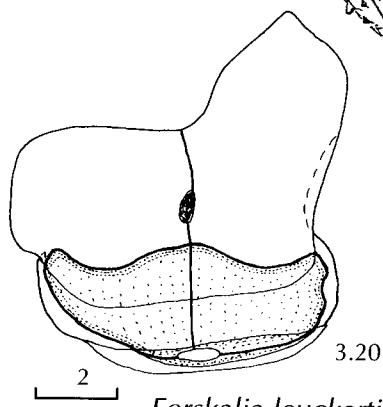
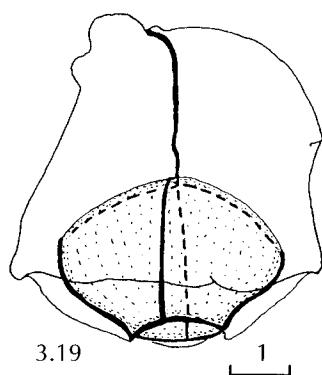
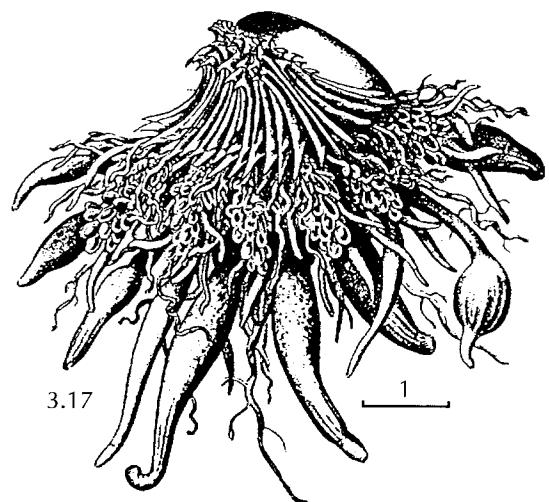
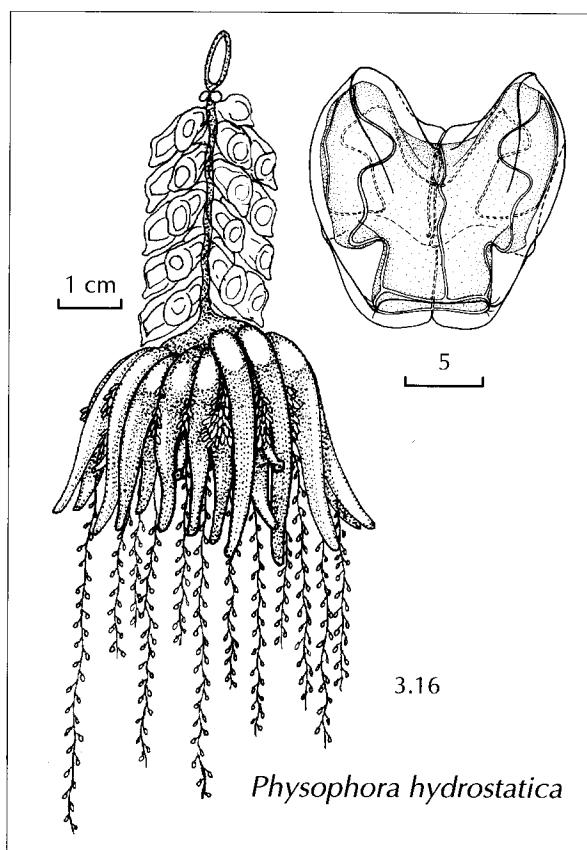
*Nanomia bijuga*



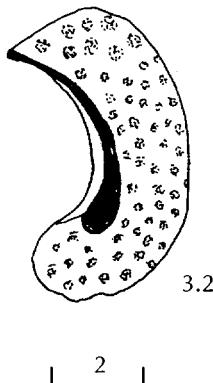
*Pyrostephos vanhoeffeni*



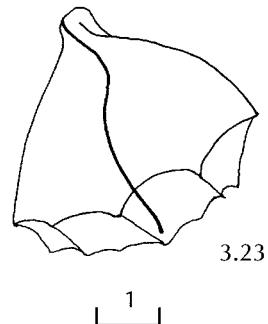
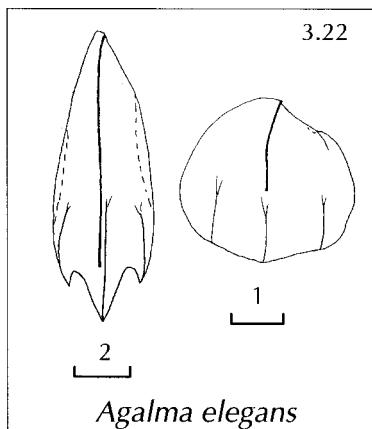
Upper view of nectophores  
or whole specimens of Physonectae



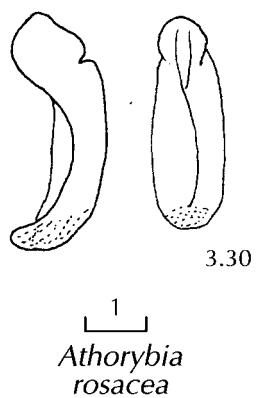
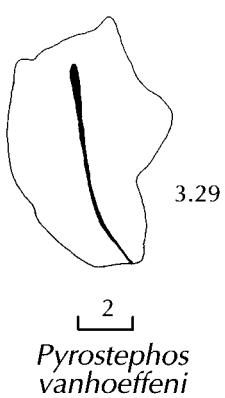
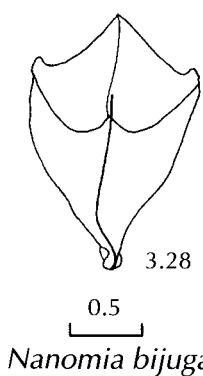
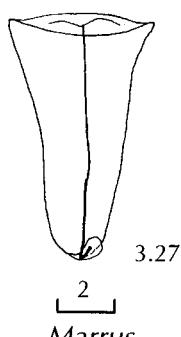
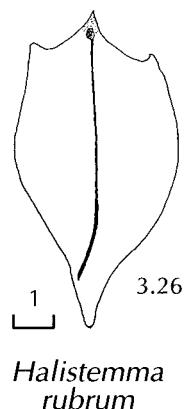
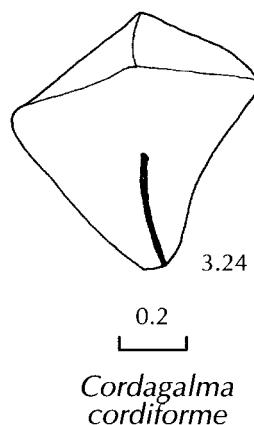
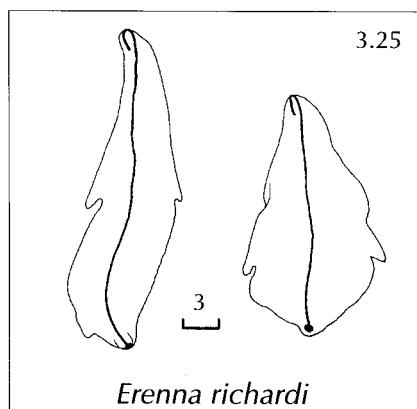
## Bracts of physonect siphonophores



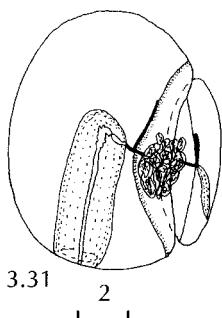
*Apolemia  
uvaria*



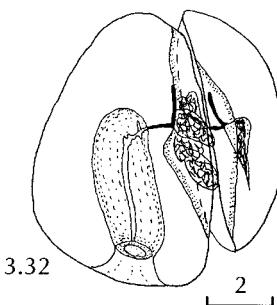
*Agalma okeni*



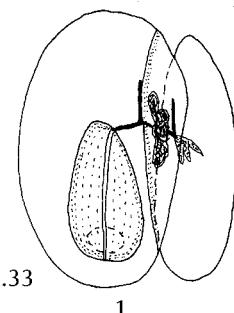
**Lateral views of calycophoran nectophores  
of the families Prayidae and Sphaeronectidae**



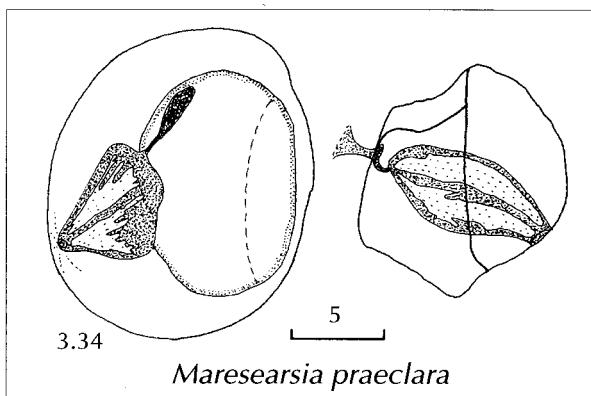
*Amphicaryon acaule*



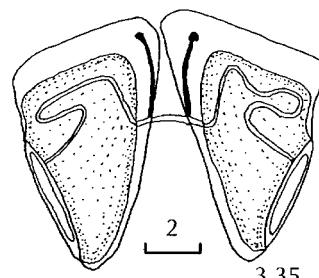
*Amphicaryon ernesti*



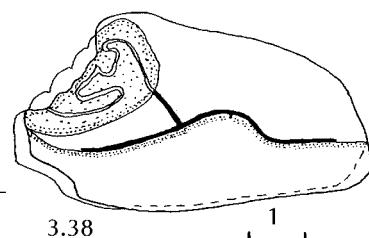
*Amphicaryon peltifera*



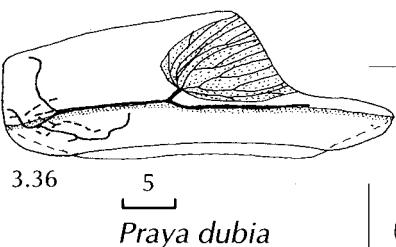
*Maresearsia praecleara*



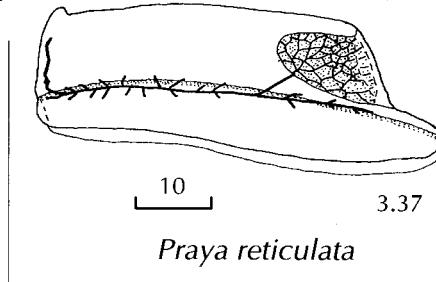
*Lilyopsis rosea*



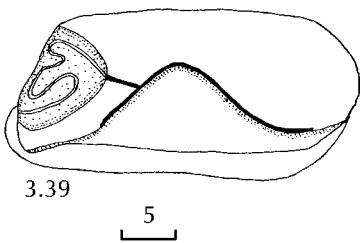
*Rosacea cymbiformis*



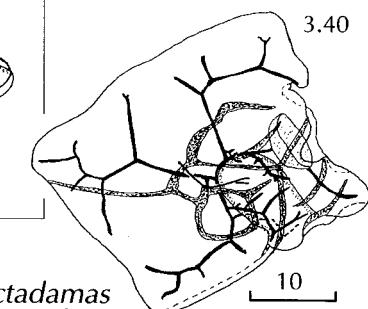
*Praya dubia*



*Praya reticulata*



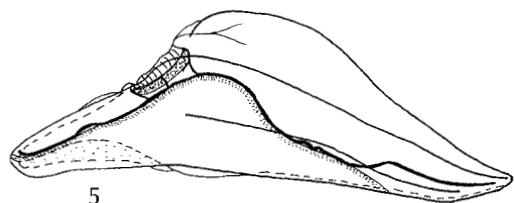
*Rosacea plicata*



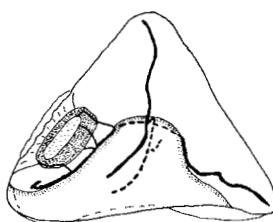
*Nectadamas diomedaeae*



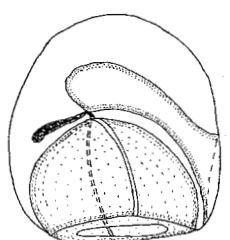
**Lateral views of calycophoran nectophores  
of the families Prayidae and Sphaeronectidae**



*Nectopyramis natans*

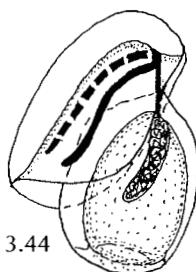


*Nectopyramis thetis*

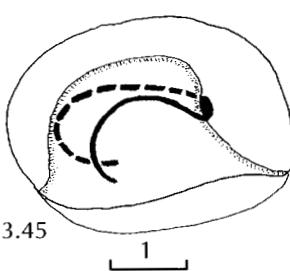


*Sphaeronectes  
gracilis*

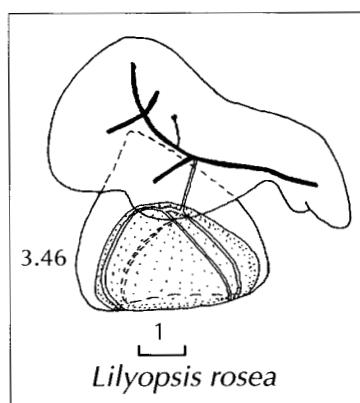
**Bracts, some with gonophores or special nectophores,  
of Calycophorae of the families Prayidae and Sphaeronectidae**



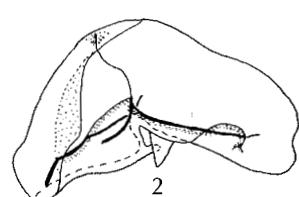
3.44  
*Amphicaryon  
acaule*



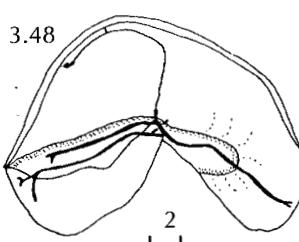
3.45  
*Maresearsia  
praecleara*



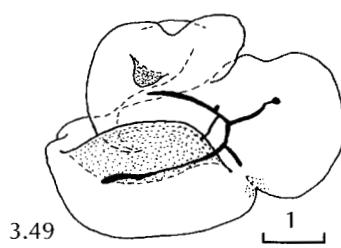
3.46  
*Lilyopsis rosea*



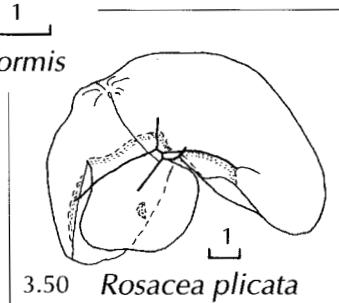
3.47  
*Praya dubia*



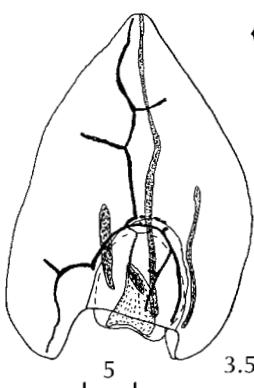
3.48  
*Praya reticulata*



3.49  
*Rosacea cymbiformis*



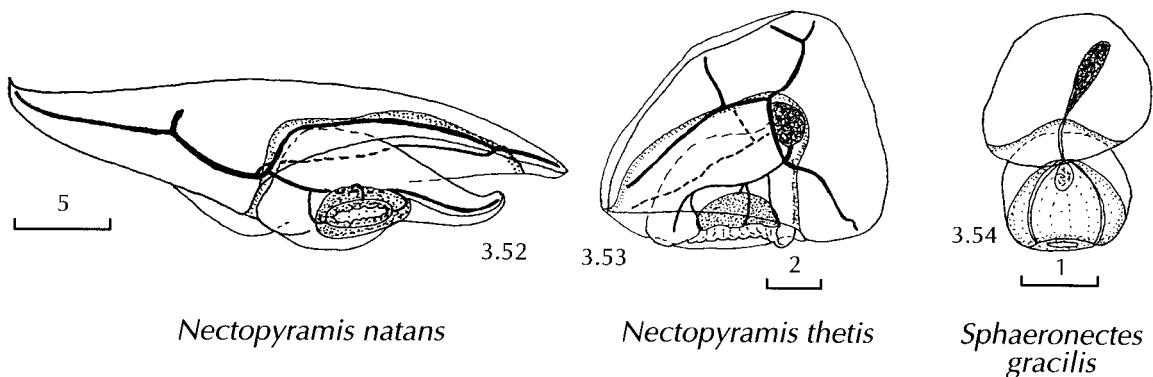
3.50  
*Rosacea plicata*



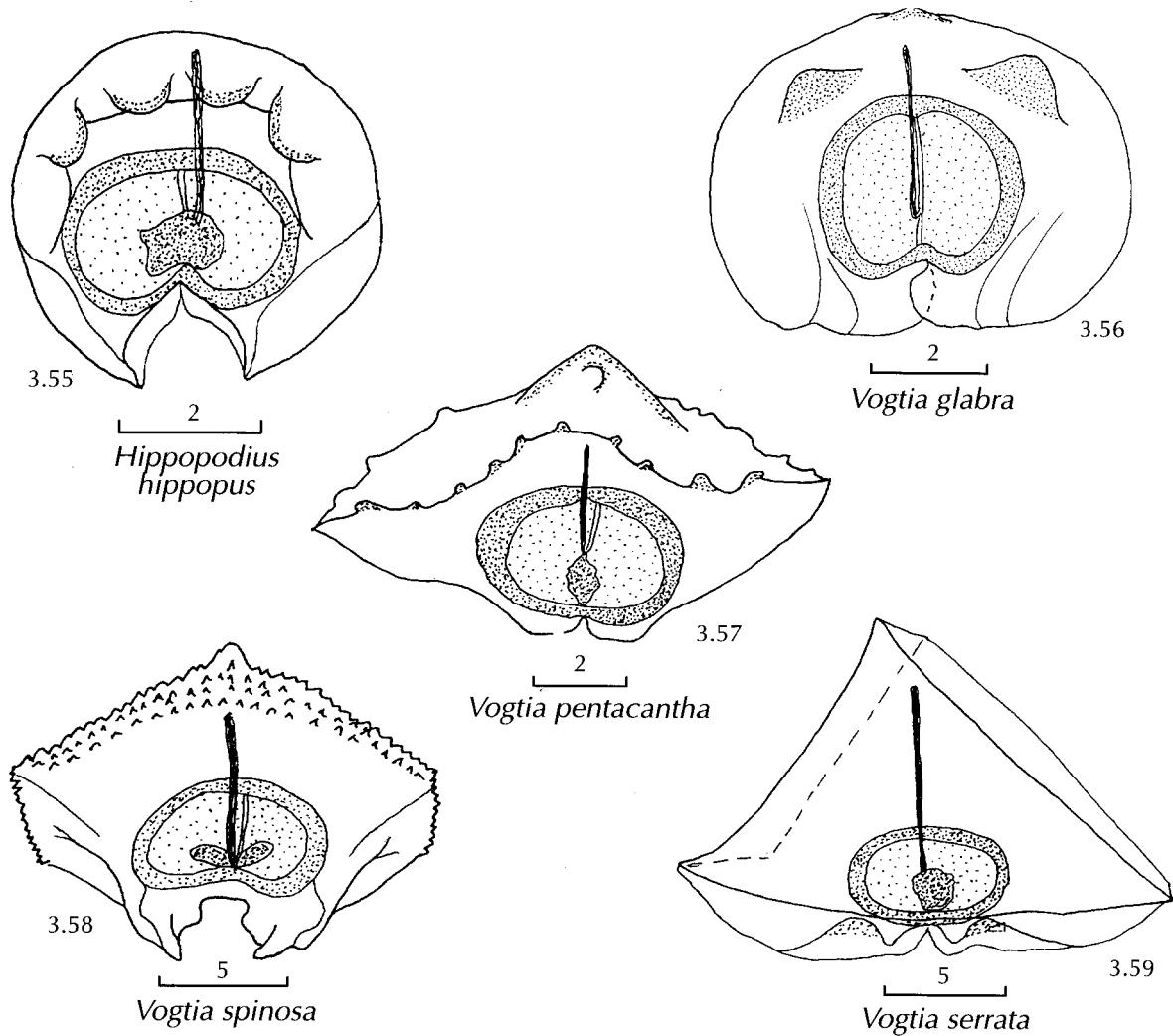
3.51  
*Nectadamas diomedeeae*



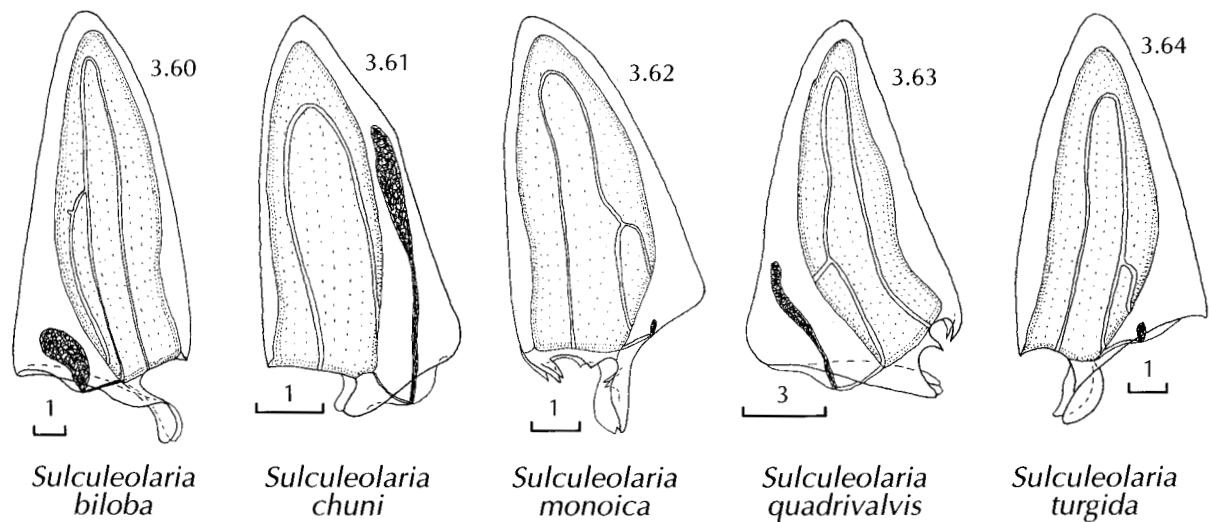
**Bracts, some with gonophores or special nectophores,  
of Calycophorae of the families Prayidae and Sphaeronectidae**



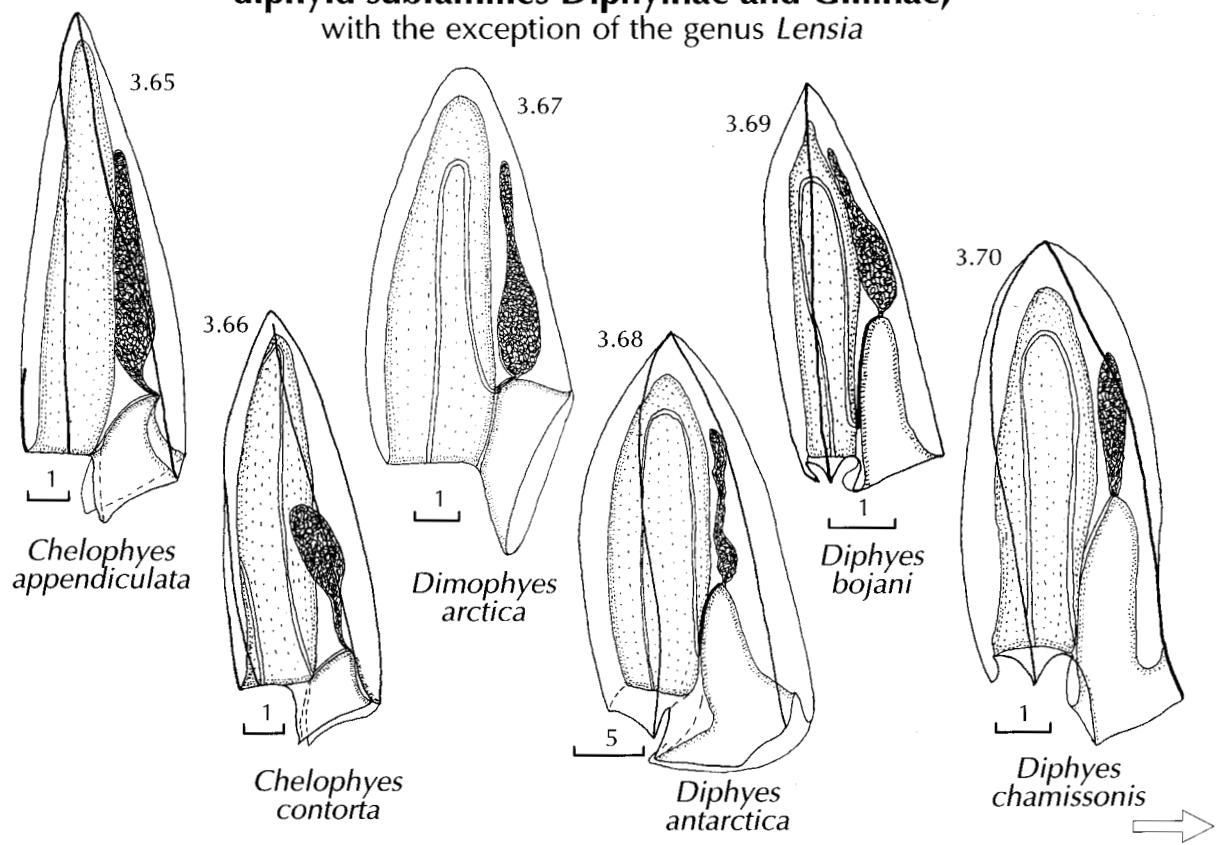
**Nectophores of Calycophorae of the family Hippopodiidae**



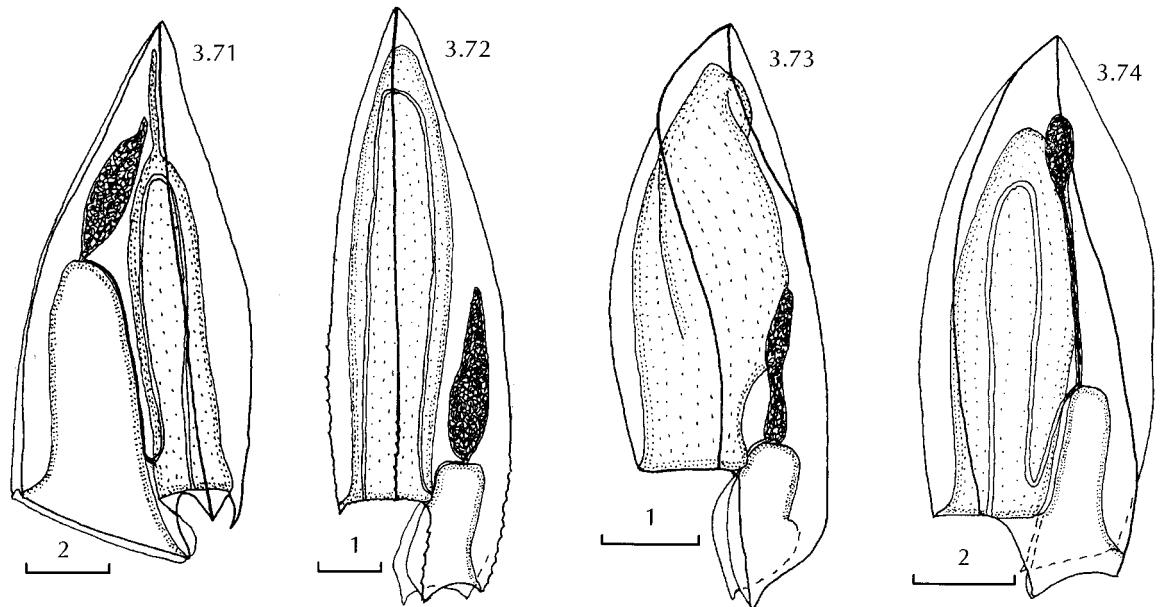
**Lateral views of anterior nectophores of Calycophorae of the diphyid subfamily Sulculeolariinae**



**Lateral views of anterior nectophores of Calycophorae of the diphyid subfamilies Diphyinae and Giliinae,  
with the exception of the genus *Lensia***



**Lateral views of anterior nectophores of Calycophorae of the diphyid subfamilies Diphyinae and Giliinae,  
with the exception of the genus *Lensia***

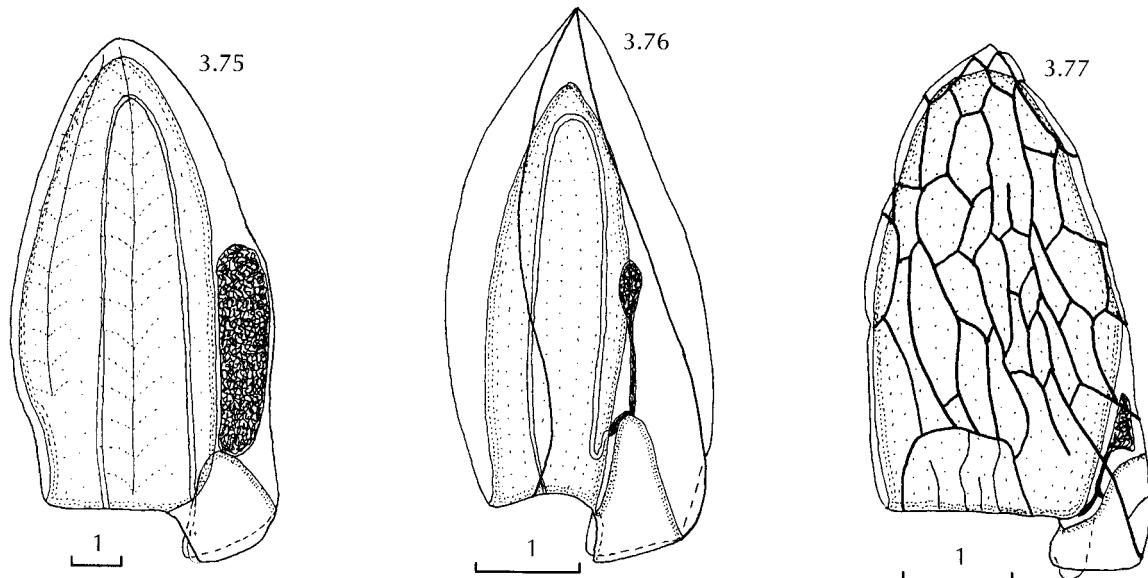


*Diphyes  
dispar*

*Eudoxoides  
mitra*

*Eudoxoides  
spiralis*

*Muggiaeа  
atlantica*

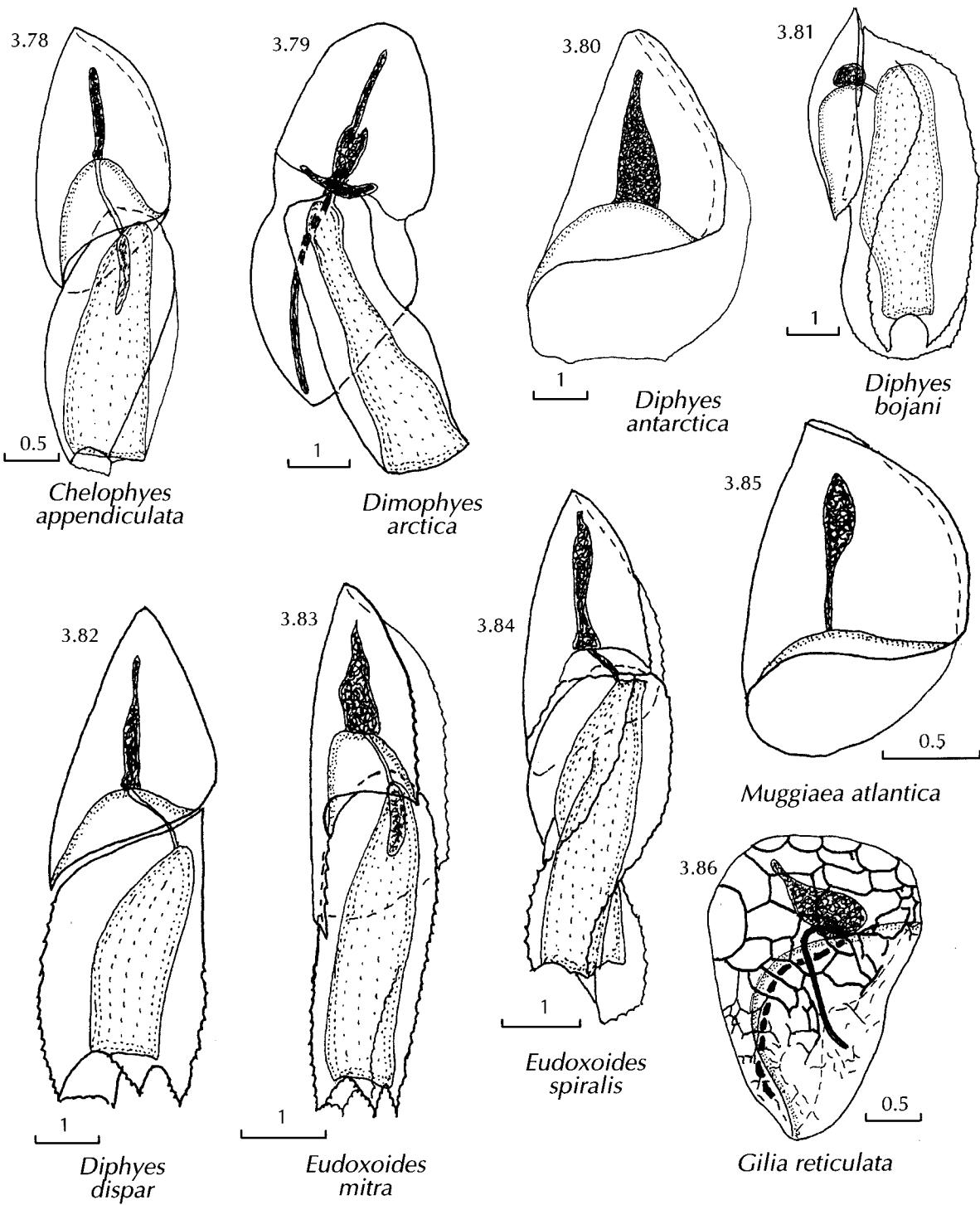


*Muggiaeа  
bargmannae*

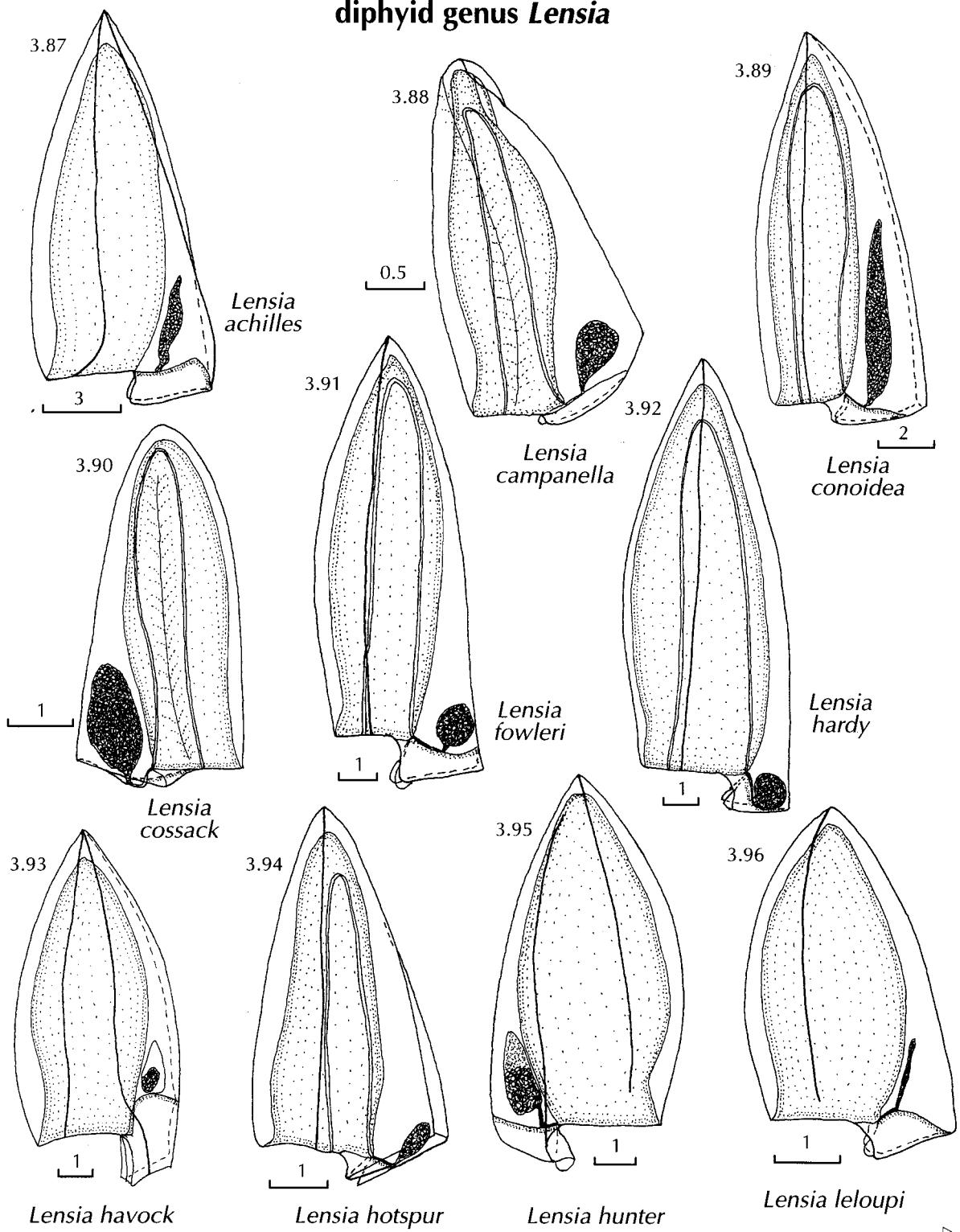
*Muggiaeа  
kochi*

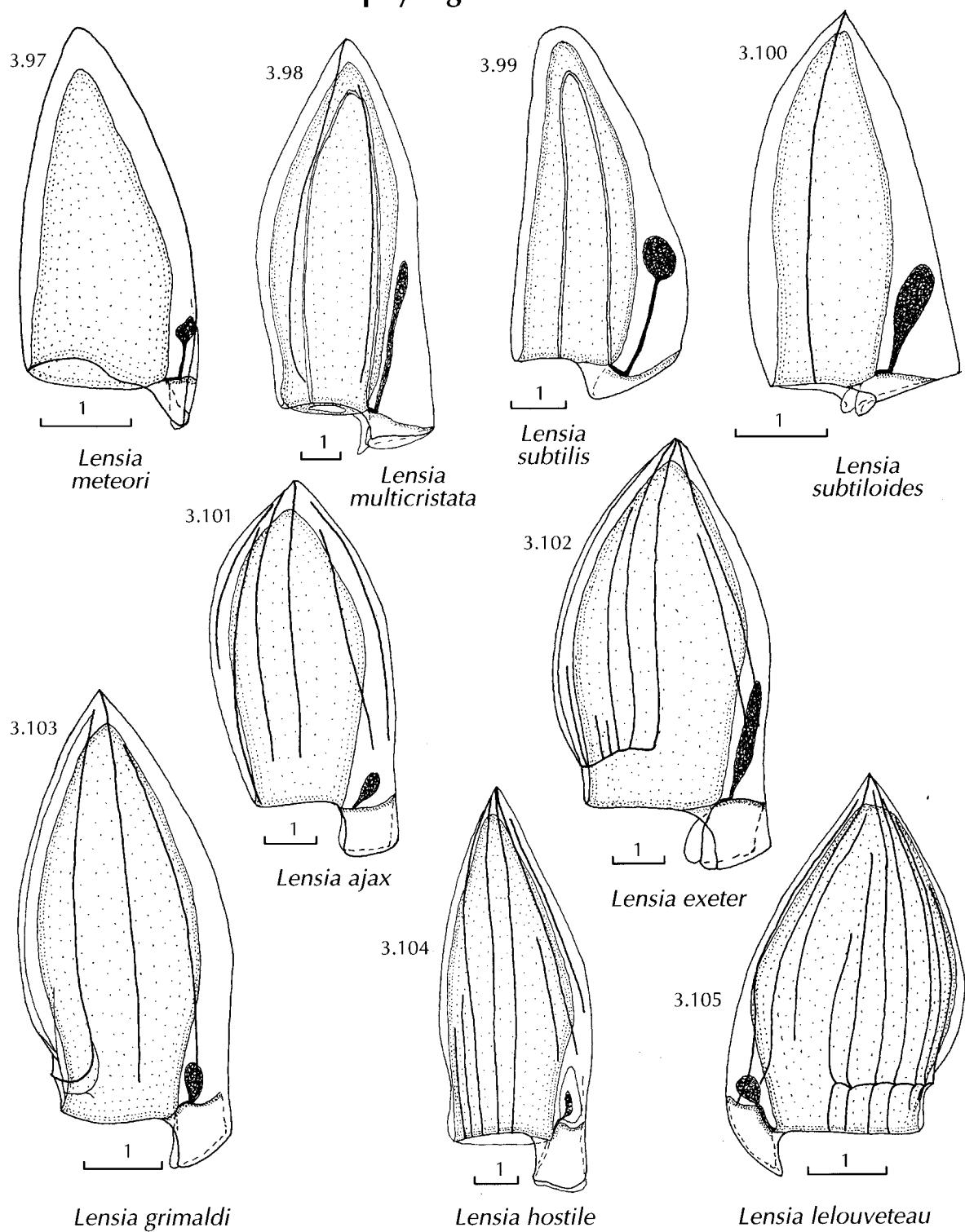
*Gilia  
reticulata*

**Bracts, some with gonophores, of Calycophorae of the diphyid subfamilies Diphyinae and Giliinae,  
with the exception of the genus *Lensia***

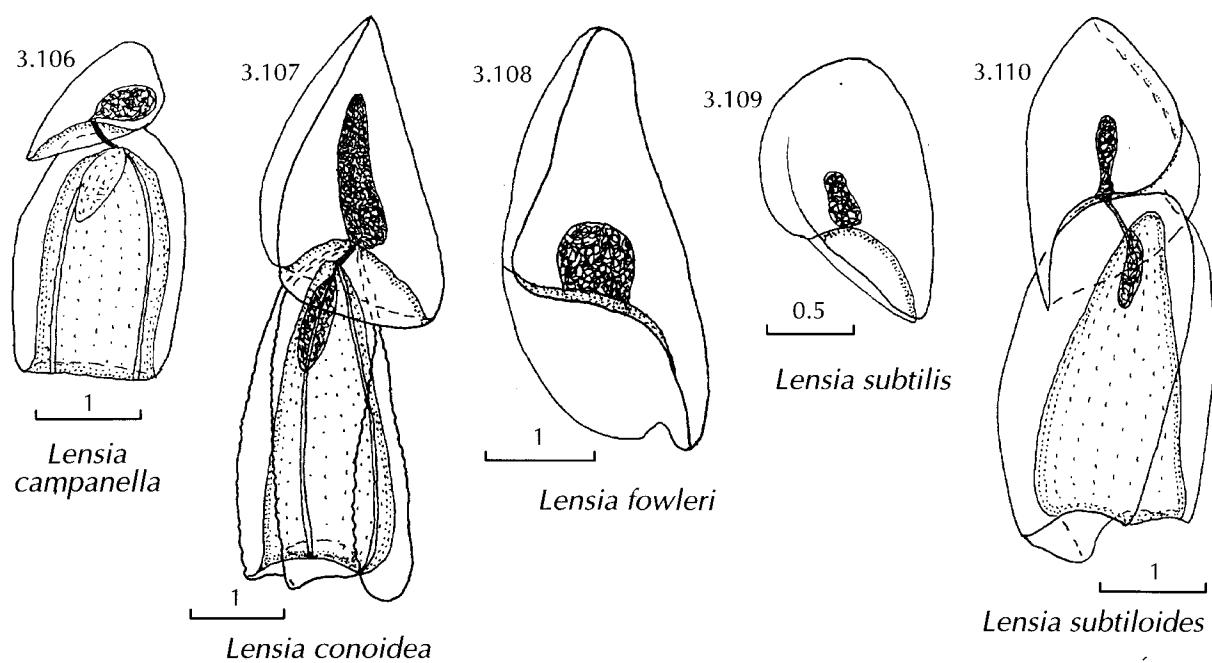


**Lateral views of anterior nectophores of the diphyid genus *Lensia***

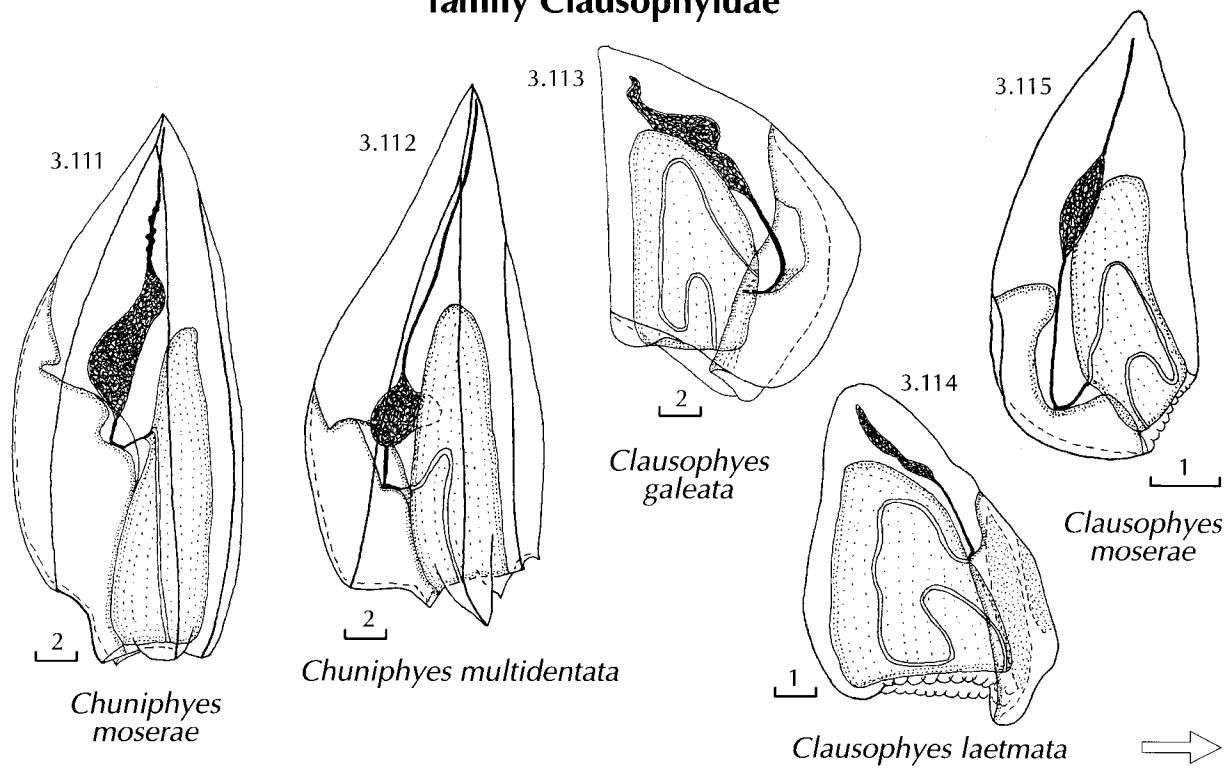


**Lateral views of anterior nectophores of the diphyid genus *Lensia***

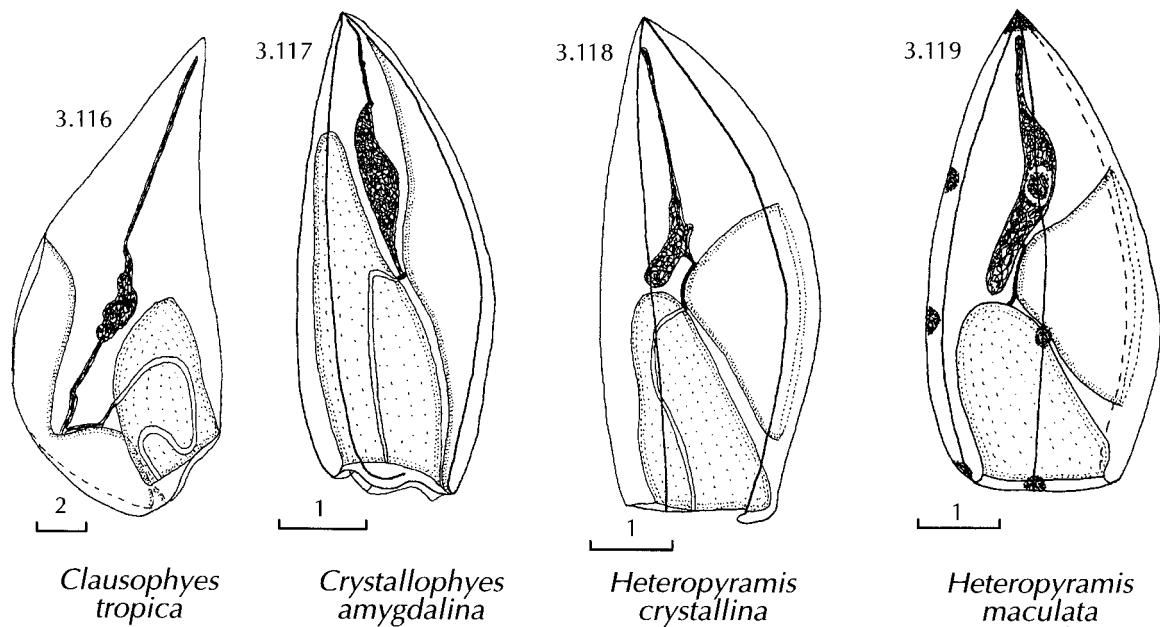
**Bracts, some with gonophores, of the diphyid genus *Lensia***



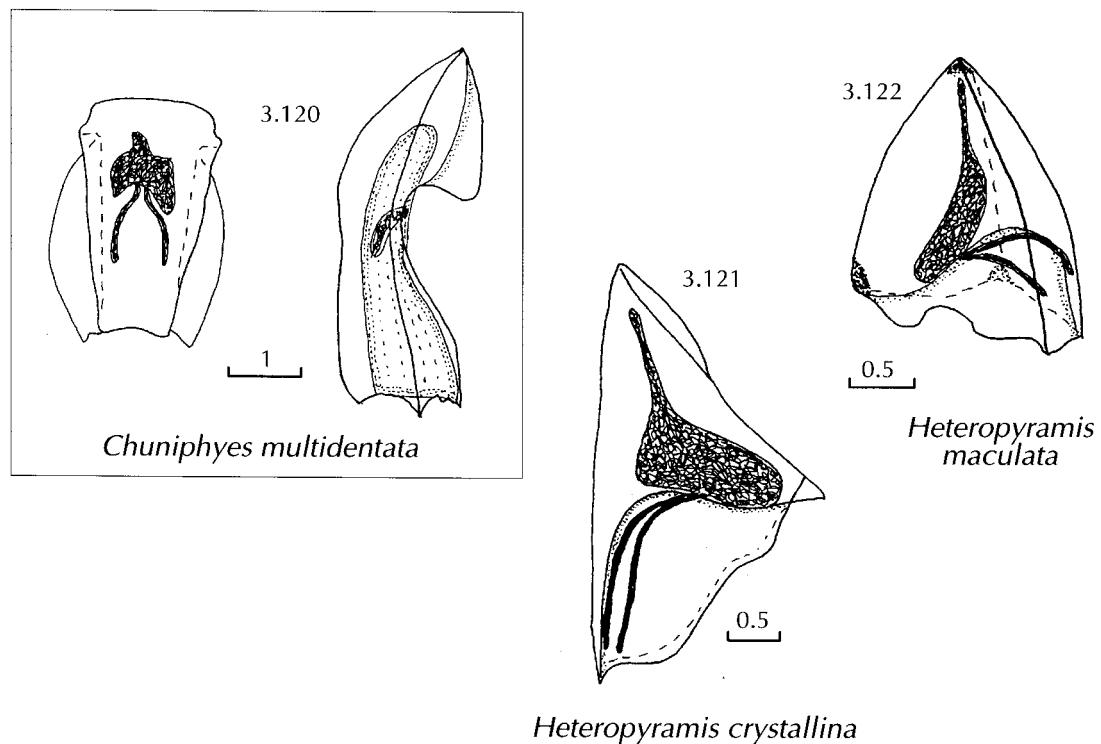
**Lateral views of anterior nectophores of Calycophorae of the family Clausophyidae**



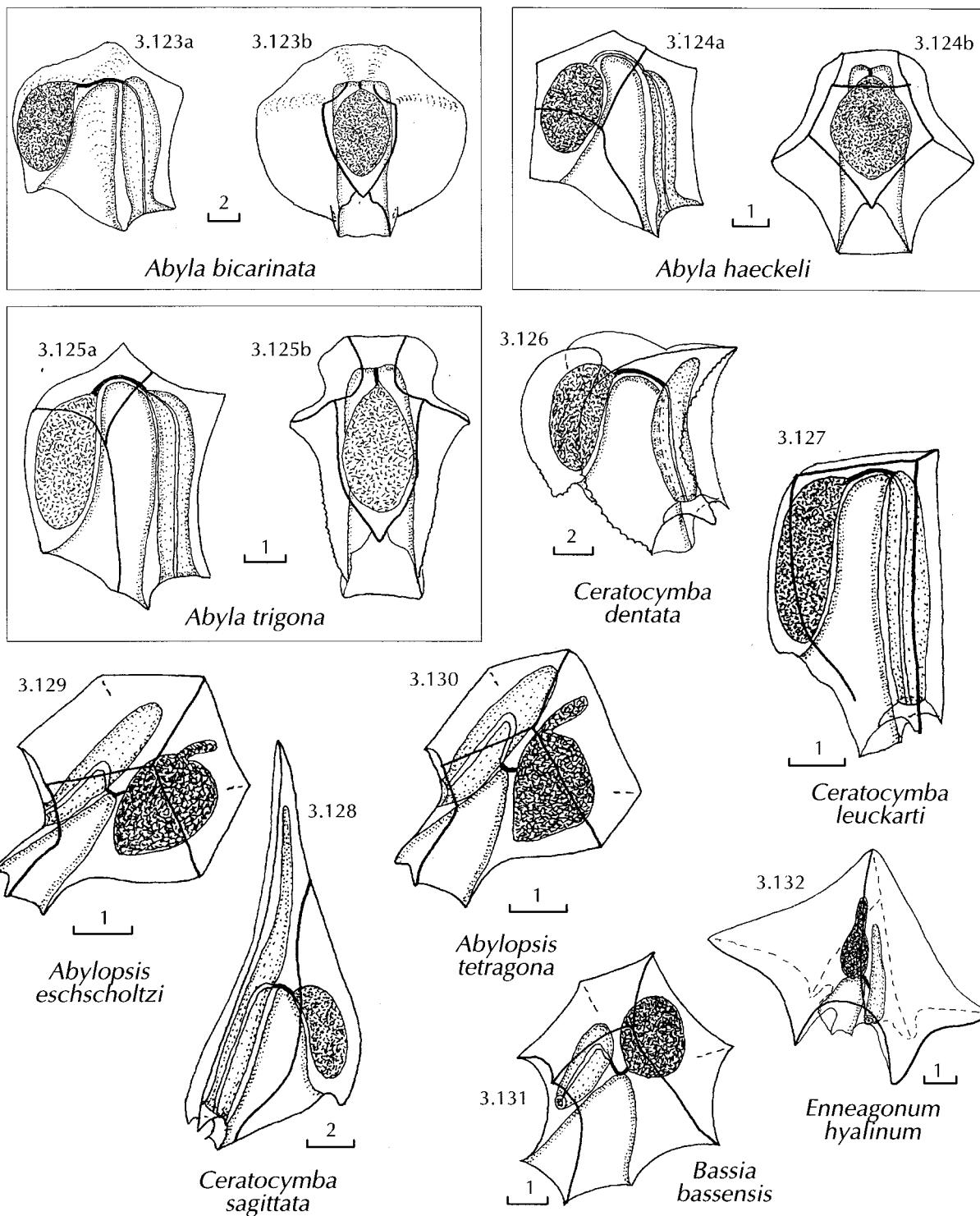
**Lateral views of anterior nectophores of Calycophorae of the family Clausophyidae**



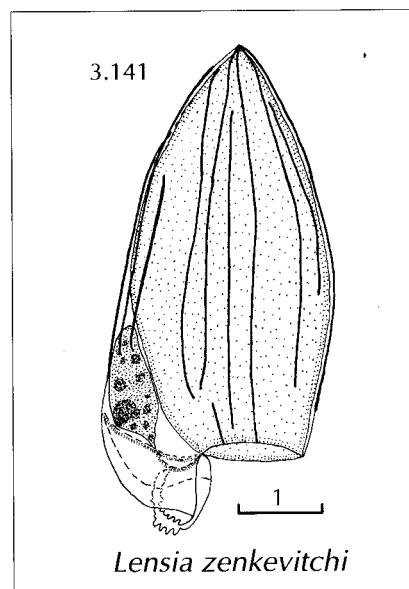
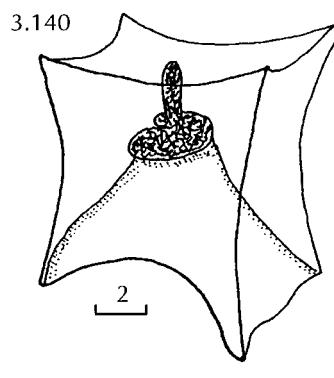
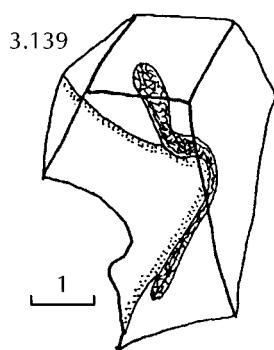
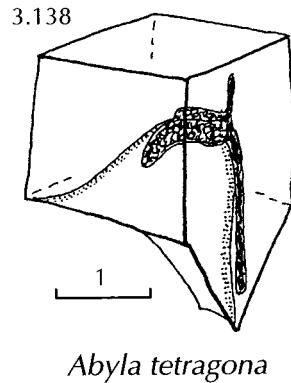
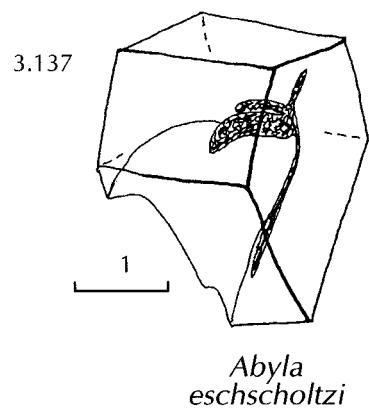
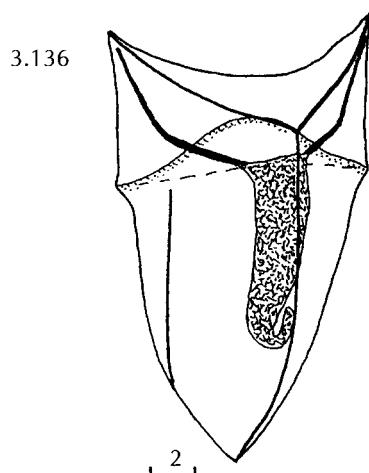
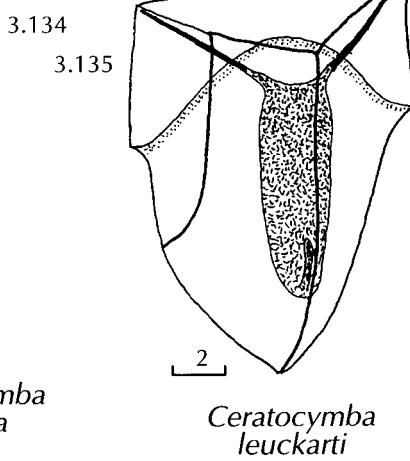
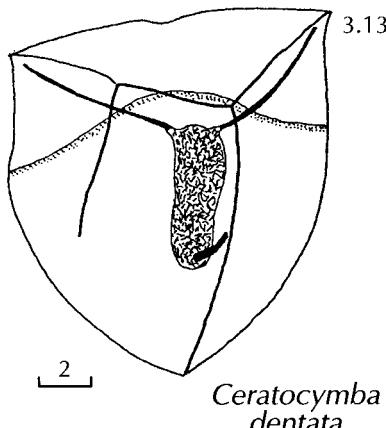
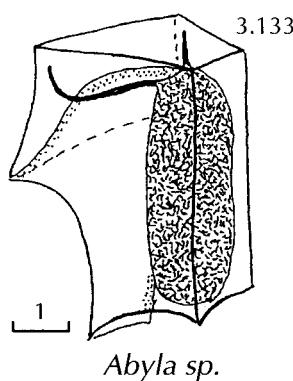
**Bracts of Calycophorae of the families  
Clausophyidae and Sphaeronectidae**



**Ventral (a) and lateral (b) views of anterior nectophores of Calycophorae  
of the family Abylidæ**



## Bracts of Calycophorae of the family Abylidæ



- *Abylopsis eschscholtzi* (Huxley, 1859) (Fig. 3.129, 3.137). Dorsal and ventral facets of anterior or nectophore relatively more regularly pentagonal and of nearly equal size. Strongly serrated ridges. Lateral radial canals on nectosac without ascending loop. Posterior nectophore less than twice as long as wide, with relatively large apical apophysis. Dorsal facet of cuboidal bract forms a regular pentagon; apico-lateral facets rectangular.
- *Abylopsis tetragona* (Otto, 1823) (Fig. 3.130, 3.138). Dorsal and ventral facets of anterior nectophore relatively less regularly pentagonal. Ridges less strongly serrated. Lateral radial canals on nectosac with ascending loop. Posterior nectophore 3 times as long as wide. Two conspicuous basal teeth. Dorsal facet of bract elongate and less regularly pentagonal; apico-lateral facets trapezoidal.

#### Genus *Bassia* L. Agassiz, 1862

Monotypic genus for *Bassia bassensis*.

- *Bassia bassensis* L. Agassiz, 1862 (Fig. 3.131, 3.139). Anterior nectophore without an apical diverticulum to the somatocyst, and with the hydroecium not extending below the basal facet. Posterior nectophore with 4 ridges ending in short basal teeth. Bract with median apical ridge. Phyllocyst is a long tube, swollen apically, without apico-lateral branches. This species somewhat resembles *Abylopsis eschscholtzi* but there are clear differences. There is usually a bluish tinge to the ridges of all parts.

#### Genus *Enneagonum* Quoy and Gaimard, 1827

Monotypic genus for *Enneagonum hyalinum*.

- *Enneagonum hyalinum* Quoy and Gaimard, 1827 (Fig. 3.132, 3.140) [=*Enneagonum searsae* Alvariño, 1968]. The large, pyramidal anterior nectophore is the only one developed. The conical somatocyst is situated above the hydroecium, and extends to a greater height than the nectosac. The bract is cuboidal, with slightly concave facets. Swollen somatocyst with 2 lateral and an apical processes.

#### Acknowledgements

Drs Hermes Mianzan and Claudia Girola (INIDEP, Mar del Plata, Argentina), and Dr. Mark Gibbons (Univ. of Cape Town, South Africa) kindly allowed me to use some of their unpublished data.

#### Suggested readings

- Bigelow H.B. 1911. The Siphonophorae. Mem. Mus. Compar. Zool., Harvard Coll., 38:173-402.  
 Kirkpatrick P.A., Pugh P.R. 1984. Siphonophores and Velellids. Synopses of the British Fauna, 29:1-154.  
 Mackie G.O., Pugh P.R., Purcell J.E. 1987. Siphonophore biology. Advances Mar. Biol., 24:97-262.  
 Pagès F., Gili J.-M. 1992. Siphonophores (Cnidaria, Hydrozoa) of the Benguela Current (southeastern Atlantic). Scientia Marina, 56 (Supl. 1):65-112.  
 Totton A.K. 1954. Siphonophora of the Indian Ocean together with systematic and biological notes on related specimens from other oceans. Discovery Rep., 27:1-162.  
 Totton A.K. 1965. A Synopsis of the Siphonophora. British Mus. Natur. Hist., London, pp. 1-230.

#### Note added in proof

*Lensia zenkevitchi* Margulis, 1970 (Fig. 3.141). Anterior nectophore with variable number of often incomplete longitudinal ridges. Hydroecium extends to or above ostial level and is open ventrally. Large ovate, often indistinct, somatocyst. Inner margins of mouth plate with distinct but variable coglike serrations; outer margins rounded. Posterior nectophore and eudoxid stage not known. Rare species only known from tropical waters.

Fig. 3. Illustrations of the species. All scales are in mm unless otherwise noted.

Figure sources: after Bédot (1895): 3.35. after Bigelow (1911): 3.7, 3.23, 3.31, 3.36, 3.37, 3.44, 3.62, 3.72; from Bigelow (1911): 3.17; from Bigelow (1931): 3.18; after Chun (1885): 3.46; after Leloup (1934): 3.120; after Moser (1925): 3.106, 3.107; after Russell (1938): 3.85; after Sears (1953), by courtesy of the Museum of Comparative Zoology, Harvard University: 3.123-3.140; after Totton (1965): 3.6, 3.13, 3.15, 3.21, 3.27, 3.30, 3.32, 3.33, 3.38, 3.39, 3.61, 3.64, 3.66, 3.70, 3.74, 3.75, 3.76, 3.78, 3.81, 3.82, 3.83, 3.84, 3.87, 3.88, 3.89, 3.90, 3.92, 3.93, 3.97, 3.102, 3.104, 3.105, 3.109, 3.110, 3.111, 3.112, 3.121.