

CNIDARIA: COLONIAL HYDROZOA (SIPHONOPHORAE)

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1 Introduction

The order Siphonophorae encompasses highly polymorphic, colonial, mainly marine Hydrozoa. With very few exceptions, siphonophores are pelagic organisms that can be found the whole year round, sometimes in a characteristic season, inshore and offshore at all latitudes and depths (Alvariño, 1971). As in all hydrozoans, they carry tentacles equipped with stinging cells (*nematocysts*), which are used by the colony to immobilize and kill their prey.

About two-thirds of the 160 currently known species belong to the suborder Calycophorae (Dunn et al., 2005a), which tend to dominate in samples collected by nets. More fragile Physonectae are often seriously damaged or destroyed by the nets, but the increased use of imaging systems or other *in situ* survey/sampling techniques has shown that the abundance and diversity of this group has been largely underestimated.

2 Life Cycle

According to Totton (1965), the fully grown colonial siphonophore is an enlarged larval nurse carrier, which buds off the sexually mature individuals, called *gonophores*. Most siphonophores are *monoecious*, i.e. they release gonophores of both sexes, even though not necessarily at the same time. Few exceptions include *Physalia physalis*, which being *dioecious* releases gonophores of only one sex.

In calycophoran siphonophores (e.g. *Muggiaea kochi*), the sexual stage (*eudoxid*) is released by the colony before the sexual maturation of the gonophore (Fig. 95A). Female/male eudoxids feed and develop independently. At full maturity they release the gametes for the external fertilization that produces a free-living planula larva, which matures into a *calyconula* larva and subsequently develops into a new colony (Fig. 95A). Physonect siphonophores have a similar development (Fig. 95B), even though their late larva, called a *siphonula*, is morphologically different from the calyconula, being equipped with an apical, gas-filled float (*pneumatophore*).



FIGURE 94: Siphonophorae: Calycophorae *Chelophyes appendiculata*.
Photo courtesy of C. Carré

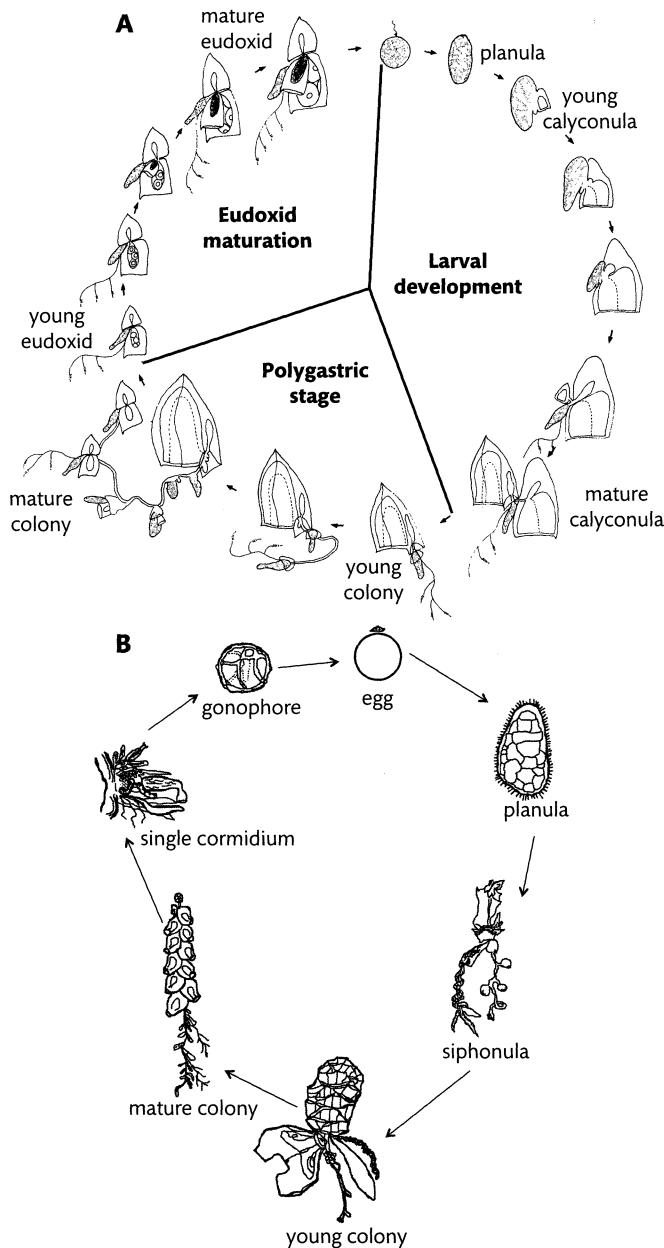


FIGURE 95: Life cycle of Siphonophorae. A, The calycophoran siphonophore *Muggiaea kochi*. B, The physonect *Agalma* sp. Modified from Carré and Carré (1991); B, Courtesy of A. Fischer.

3 Ecology

Siphonophores are amongst the most abundant carnivores in the marine system (Mackie et al., 1987 and references therein; Mapstone, 2009). They are generally passive, ambush predators that deploy a network of tentacles and then remain motionless, capturing prey that come into contact with their nematocyst batteries (Mackie et al. 1987). The polygastric stage of *M. atlantica* employs a specialized swimming behaviour that spreads the siphosome and tentacles into a three-dimensional helical

structure, which represents the 'fishing posture'. This behaviour has been named the 'veronica', after the classic toreador movement that it resembles. Calycophoran siphonophores eat primarily small copepods, but also other plankton including ostracods, molluscs, chaetognaths, and larvae of euphausiids and fish (Mapstone, 2009 and references therein). In turn, they are prey of bigger cnidarians, ctenophores, heteropods, and of several fish species (Mapstone, 2009). Assimilation efficiencies of oceanic Calycophorae are typically higher than other planktonic carnivores: 87–90% for carbon and 90–96% for nitrogen (Purcell, 1983).

Because of their colonial morphology, siphonophores may rapidly become dominant under favourable conditions, as they are able to release hundreds of eudoxids, each one producing a new colony. Swarms of siphonophores can have a significant predatory impact on the abundance of other planktonic organisms including small fish (Mackie et al., 1987; Purcell, 1997), causing massive mortalities of farmed fish (Greve, 1994; Båmstedt et al., 1998).

4 General Morphology

Each siphonophore colony, otherwise called the *polygastric stage*, is composed of a collection of zooids (Fig. 96A): (i) medusozoid zooids, i.e. asexual swimming bells (*nectophores*) and sexual *gonophores*, which alone or in clusters constitute the reproductive unit (*gonozooid*); (ii) polypoid zooids, which are used to regulate the buoyancy of the colony (*pneumatophore*), for feeding and digestion (*gastrozooids*) or for manipulation (*dactylozooids* and *palpons*). All zooids are arranged along a contractile *stem*, which is a tube surrounding the main gastrovascular canal. The apex of the stem, or *anterior/aboral* pole, carries the nectophores and is called the *nectosome*; the distal *posterior/oral* pole, which carries the remaining zooids and ends with the oldest larval zooids, is called the *siphosome* (Fig. 96A). The Siphonophora are divided into three suborders based on the presence/absence of the pneumatophore and of nectophores. Thus, Cystonectae siphonophores only have a pneumatophore, Calycophorae lack a pneumatophore but develop nectophores, whereas Physonectae have both (Fig. 96). The morphology of the nectosome and in particular of the nectophores is an important taxonomic character. Nectophores can be attached to either the dorsal/upper or ventral/lower side of the nectosome, depending on the family. Each nectophore, corresponding to a highly modified medusa, is composed predominantly of mesoglea, which is often characterized by ridges or folds useful for taxonomic identification. The internal cavity or *nectosac* corresponds to the sub-umbrella and bears the *radial canals* (two lateral, one upper, and one lower) that have different shapes and lengths depending on the species and can be connected through a pedicular canal to a *pallial or mantle canal* (MC) (Fig. 97). The mantle canal always has an ascending branch (AMC) and sometimes also has a descending branch (DMC), which is a feature of taxonomic importance to distinguish different groups of Physonectae. The nectosac is open externally

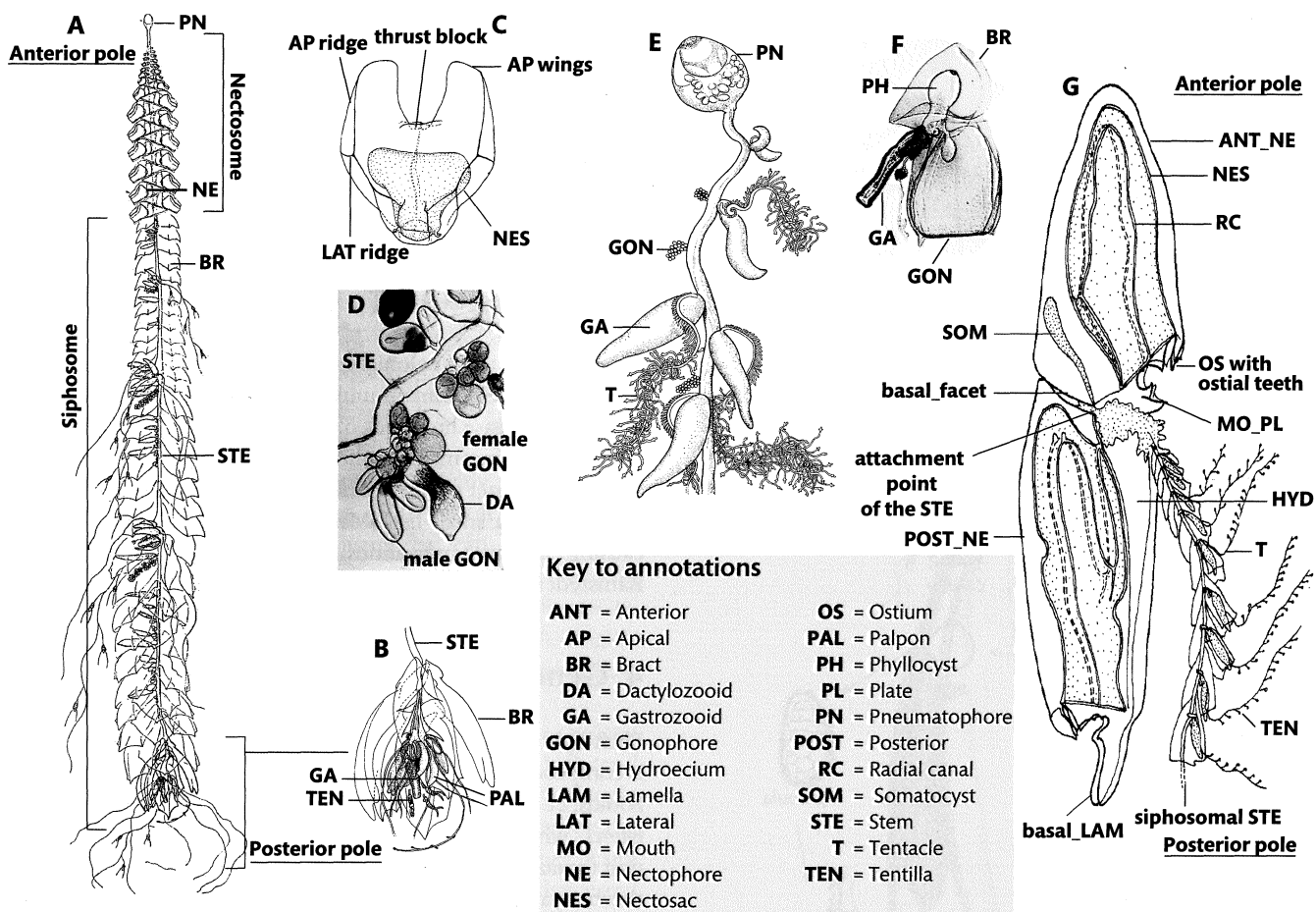


FIGURE 96: General structure of siphonophores. A–D, Physonectae. A, *Agalma elegans*, whole animal, lateral view. B, Distal/posterior part of the siphosome. C, Nectophore, upper view. D, *Nanomia bijuga*, detail of stem bearing gonophores and dactylozooids. E, Cystonectae, *Rhizophysa filiformis*, lateral view. F, G, Calycophorae. F, *Muggiaea kochi*, young eudoxid, lateral view. G, *Sulculeolaria quadrivalvis*, polygastric stage, lateral view. A–C, Totton (1965); D, photo C. Carré; E, Pagès and Gili (1992); F, Carré and Carré (1991); G, Carré (1979).

to the *ostium*, which is surrounded by a *circular* or *ring canal*. On the lower side of the nectophore lies a cavity called the *hydroecium* that, in the Calycophorae, serves to protect the siphosomal budding zone when the whole or a part of the stem is retracted into it, for defense or during locomotion. In calycophorans, from the hydroecium runs the *somatocyst*, sometimes containing oil droplets, that is an extension of the original larval gastrovascular system and is connected with the radial canals. The *mouth plate* or *basal lamella* is a lower/ventral process below the ostium.

Calycophorans usually have one or two nectophores only (i.e. the *anterior* and *posterior* nectophores, Fig. 96G), whereas physonects have variable numbers of nectophores, depending on the species (Fig. 96A).

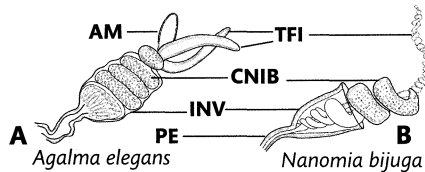
The siphosome is generally much longer than the nectosome, up to many metres in some physonect species. Several units called *cormidia* are arranged along the ventral/lower side of the siphosome, and can be retained or progressively released free from the distal part of the siphosome once they have reached sexual maturity. Each *cormidium* is composed, at a minimum, of: a single gastrozooid, carrying a tentacle; a male/female

gonophore; and a *bract* (absent in cystonects hippopodids, most Clausophyids and some other scattered species), characterized by a reduced gastrovascular canal (*phyllocyst*), that has floatation functionality and may contain metabolic reserves. Tentacles are long and typically bear a number of branches or *tentillae*, armoured with nematocysts. The structure of the tentillum is taxonomically important, as it differs in different physonect taxa (Fig. 97). A tentillum typically comprises a *pedicel*, often an *involucrum*, a *cnidosac* with a *cnidoband* and one or more *terminal filaments*. In physonects the tentillum might include swollen vesicle/s called *ampulla*/ae.

In physonects and in the calycophoran genus *Stephanophyes*, the cormidium also includes a few dactylozooids or palpons. Each palpon typically bears an unbranched tentacle called a *palpacle*, while dactylozooids have no palpacles. In the calycophorans the detached cormidium is called an *eudoxid* (or *monogastric stage*).

Cystonect and a minority of physonect colonies (e.g. Apolemiidae, Erennidae, *Marrus*, Pyrostephidae, Rhodaliidae, Stephanomiidae) bear gonophores of only one sex, whereas in

Families/genera

AGALMATIDAE
sensu strictu

TEN

MFZ

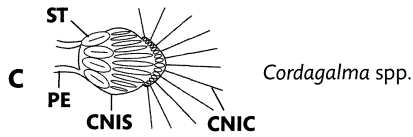
DMC

TEN with INV, tricornuate (i.e. with 2 TFI and AM) in *Agalma*. Unicornate (1 TFI) in the other genera. CNIB tightly coiled.

NO

YES

CORDAGALMATIDAE

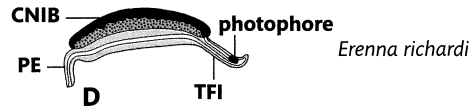
*Cordagalma* spp.

Larval type TEN, without INV, without TFI in *Cordagalma* (except *C. ordinatum*). TEN bilobate, with INV and spiralled CNIB in *Cardianecta*.

NO

YES

ERENNIDAE

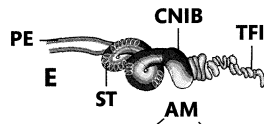
*Erenna richardi*

TEN without INV, with straight CNIB. TFI large and stiff with central axial canal, without N.

YES

NO

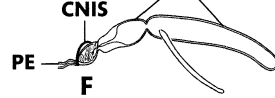
FORSKALIIDAE

*Forskalia edwardsi*

TEN with long pedicel, without INV, with coiled CNIB. TFI flexible.

NO

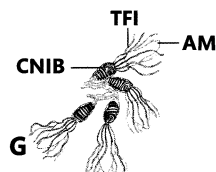
YES

Frillagalma spp.*Frillagalma vityazi*

TEN made by 2 consecutive AM after CNIS. No INV, CNIB, TFI.

NO

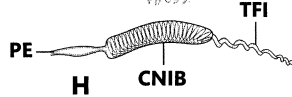
YES

Lychnagalma spp.*Lychnagalma utricularia*

TEN with complete INV, with complexly coiled red CNIB. 8 TFI around large AM.

NO

YES

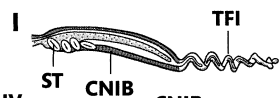
Marrus spp.*Marrus orthocanna*

TEN without INV, with straight/loosely coiled CNIB. TFI flexible.

YES

NO

PYROSTEPHIDAE

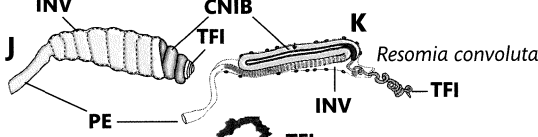
*Bargmannia elongata*

TEN without INV, with straight CNIB. TFI flexible.

YES

NO

RESOMIIDAE

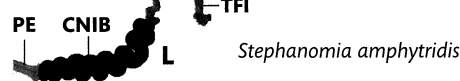
*Resomia convoluta*

2 types of TEN with complete INV: with coiled CNIB proximally and zigzagged CNI distally.

NO

YES

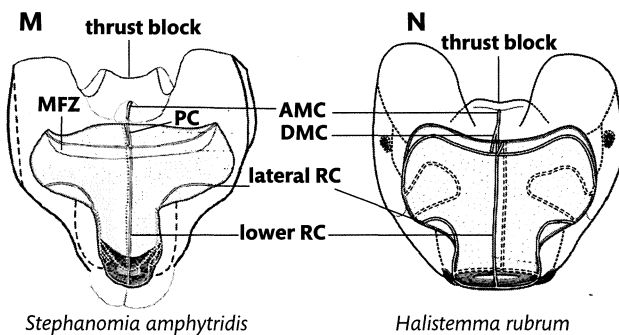
STEPHANOMIIDAE

*Stephanomia amphitridis*

TEN without INV, with loosely coiled CNIB. TFI long and flexible.

YES

NO

*Stephanomia amphitridis**Halitemma rubrum*

Key to annotations

AM = Ampulla

AMC = Ascending mantle canal

CNIB = Cnidoband

CNIC = Cnidocils

CNIS = Cnidosome

DMC = Descending mantle canal

INV = Involutum

MFZ = Muscle free zone

N = Nematocyst

PC = Pedicular canal

PE = Pedicel

RC = Radial canals

ST = Stenotele

TEN = Tentilla

TFI = Terminal filament

FIGURE 97: Characteristics of taxonomic importance to identify Physonectae families in Group III (see Fig. 100). A–L, schematic representation of tentilla, lateral views; M, N, nectophores, lower views. A–C, H, Mapstone (2009); D–F, I–K, Mapstone (2014); G, Pugh and Harbison (1986); L, modified from Pugh and Baxter (2014); M, N Pugh and Baxter (2014).

calycophorans and most physonects the colonies are hermaphrodite as they bear gonophores of both sexes.

5 Systematics

Here we generally adopt the classification from the World Register of Marine Species, which is the most up-to-date classification of the group. Over the years the systematics of this group has been repeatedly revised and some authors have raised the order Siphonophora to a subclass of the class Hydrozoa (e.g. Pugh, 1999; Bouillon et al., 2006). Molecular phylogenetic analyses show that Cystonectae are separated from all other siphonophores (Dunn et al., 2005a; Dunn and Wagner, 2006). The physonect family Agalmatidae is a polyphyletic group that is slowly undergoing taxonomic revision (e.g. Pugh, 2016). Taking into account recent updates, we consider Agalmatidae *sensu strictu* (Mapstone, 2009; Pugh, 2016) separately from *Marrus* spp., *Frillagalma* spp. and *Lychnagalma* spp.

The keys for identification are based on the main morphological features of nectophores and bracts, as those are the components of the colony that are usually caught using plankton nets.

Box 1 Classification of Siphonophorae

Phylum Cnidaria

Class Hydrozoa

Order Siphonophorae

Suborder Cystonectae

Family Physaliidae

Family Rhizophysidae

Family Bathypysidae

Suborder Physonectae

Family Agalmatidae

Family Apolemiidae

Family Cordagalmatidae

Family Erennidae

Family Forskaliidae

Family Physophoridae

Family Pyrostephidae

Family Resomiidae*

Family Rhodaliidae

Family Stephanomiidae

Suborder Calycophorae

Family Abylidae

Family Clausophyidae

Family Diphyidae

Family Hippopodiidae

Family Prayidae

Family Sphaeronectidae

* North Atlantic species not known in this family. Families in bold are covered in this chapter.

SIPHONOPHORA GROUP I - Suborder: CYSTONECTAE (*), PHYSONECTAE

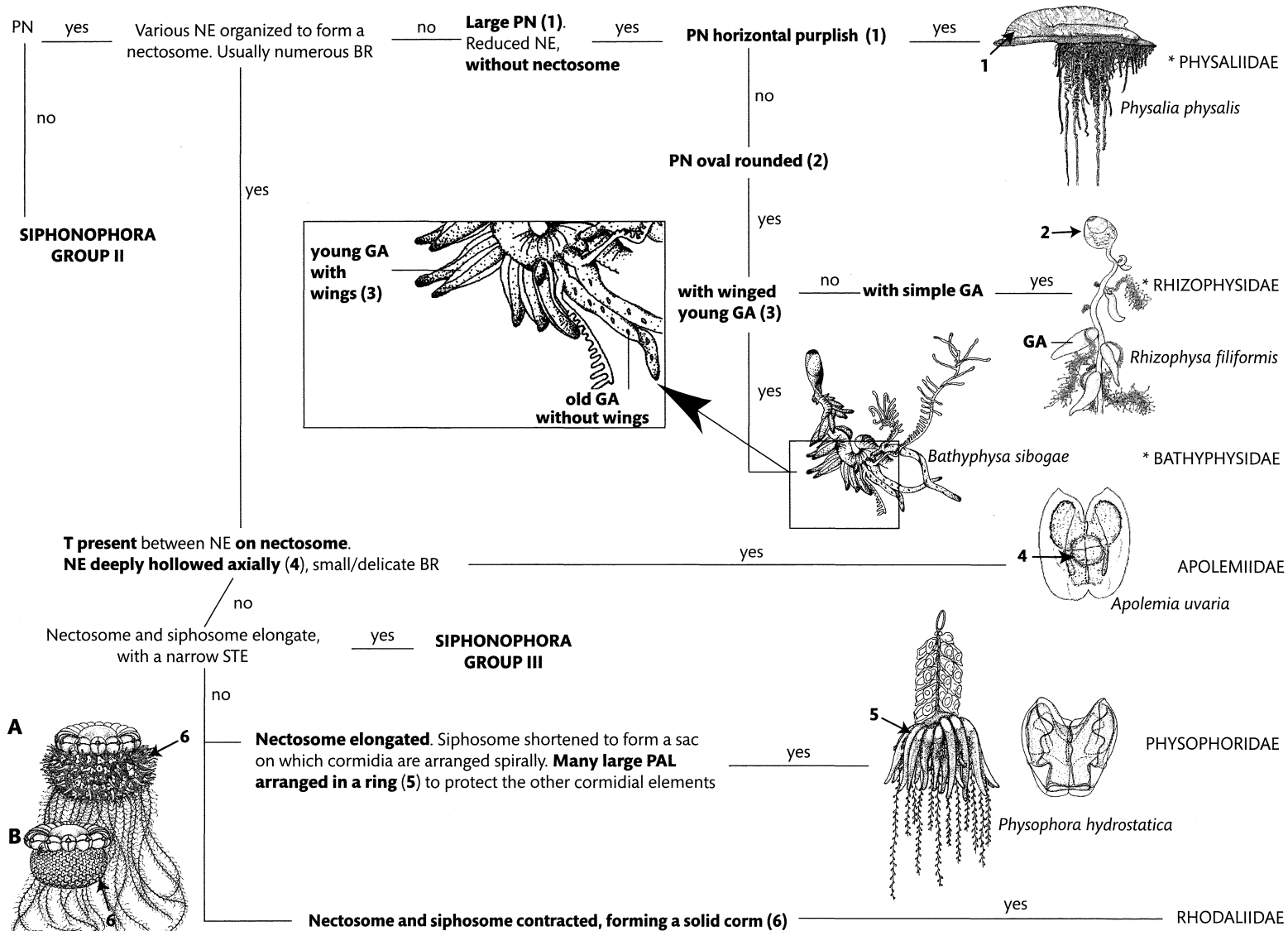


FIGURE 98: Siphonophora group I: suborder Cystonectae(*), Physonectae. *Physalia physalis*, *Stephalia corona* (a,b), after Totton (1965); *Rhizophysa filiformis*, after Pagès and Gili (1992); *Bathypysa sibogae*, after Biggs and Harbison (1976); *Apolemia uvaria*, *Physophora hydrostatica*, after Kirkpatrick and Pugh (1984).

SIPHONOPHORA GROUP II - Suborder: CALYCOPHORAE

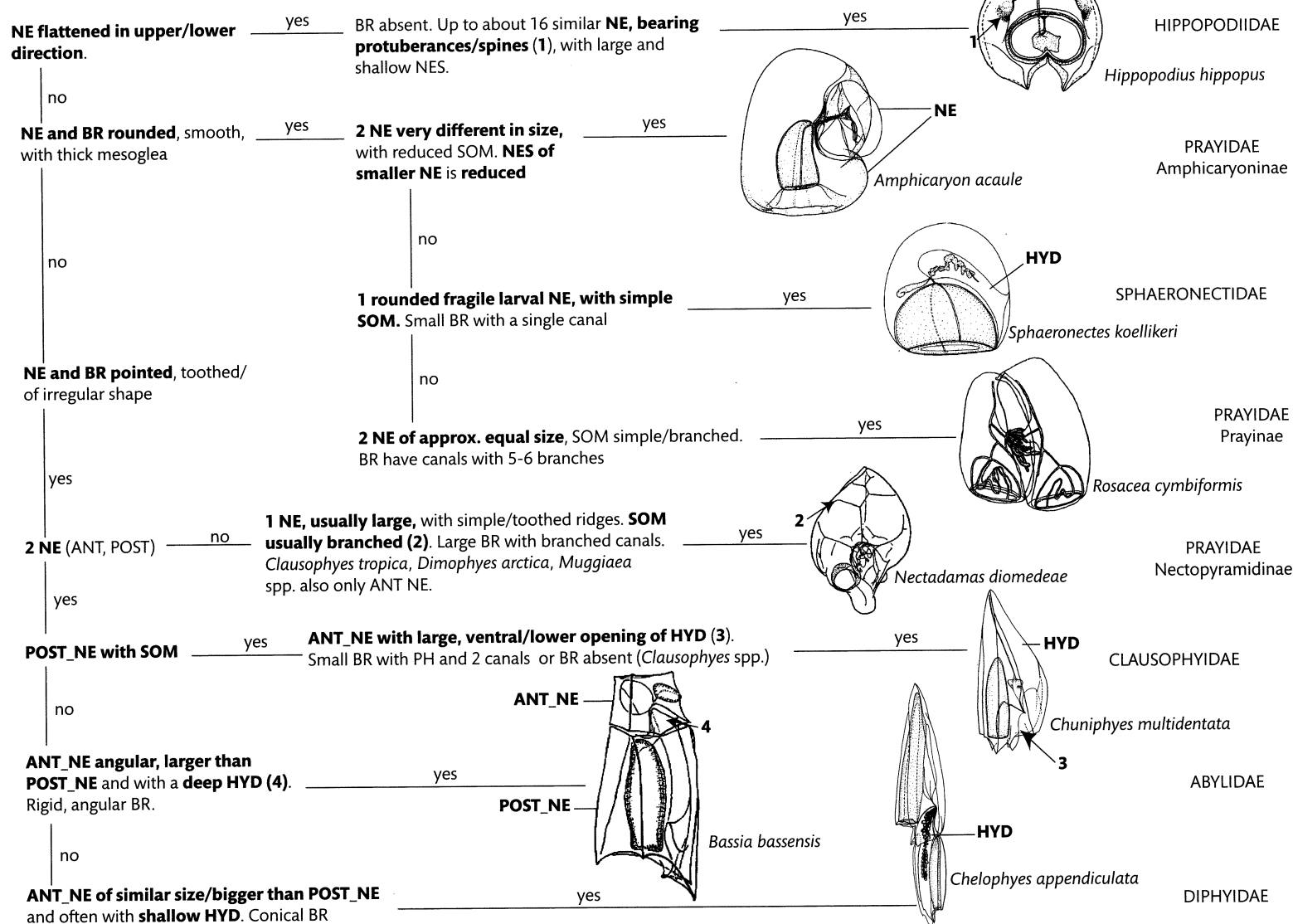


FIGURE 99: Siphonophora group II: suborder Calycophorae. *Hippopodius hippopus*, *Amphicaryon acaule*, *Sphaeronectes koellikeri*, *Chuniphyes multidentata*, *Chelophyes appendiculata*, after Kirkpatrick and Pugh (1984); *Rosacea cymbiformis*, after Tregouboff and Rose (1957); *Nectopyramis diomedae*, after Totton and Fraser (1955a); *Bassia bassensis*, after Totton and Fraser (1955b).

SIPHONOPHORA GROUP III - Suborder: PHYSONECTAE

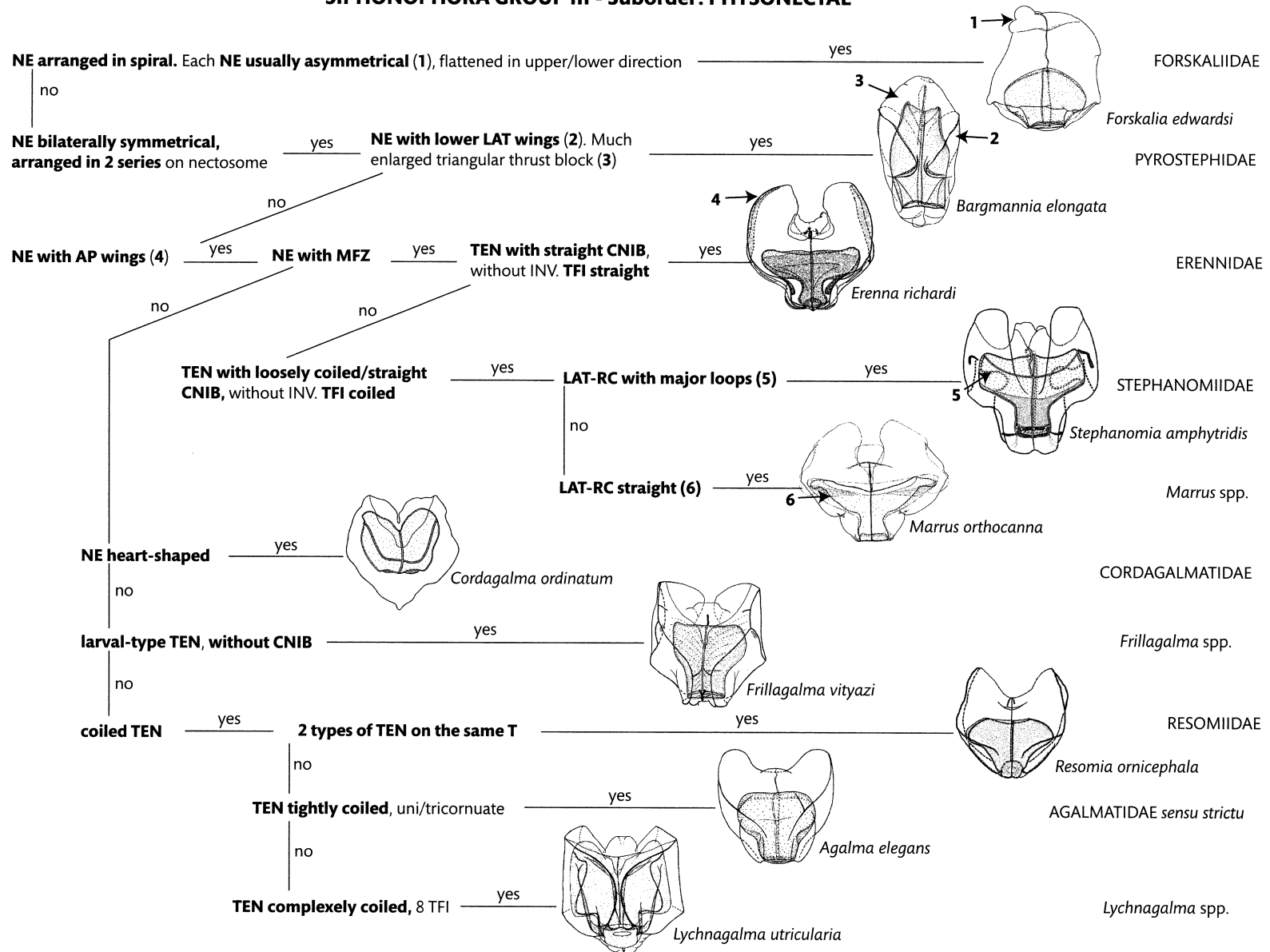


FIGURE 100: Siphonophora group III: suborder Physonectae. *Forskalia edwardsi*, *Bargmannia elongata*, *Agalma elegans* after Kirkpatrick and Pugh, (1984); *Erenna richardi*, after Pugh (2001); *Stephanomia amphytridis*, after Pugh and Baxter (2014); *Cordagalma ordinarum*, after Pugh (2016); *Frillagalma vityazi*, after Pugh (1998); *Resomia ornicephala*, after Pugh and Haddock, (2010); *Lychnagalma utricularia*, after Pugh and Harbison (1986); *Marrus orthocanna*, after Dunn et al. (2005b); *Agalma elegans*, after Kirkpatrick and Pugh (1984).

KEY TO MAIN CALYCOPHORAE SPECIES

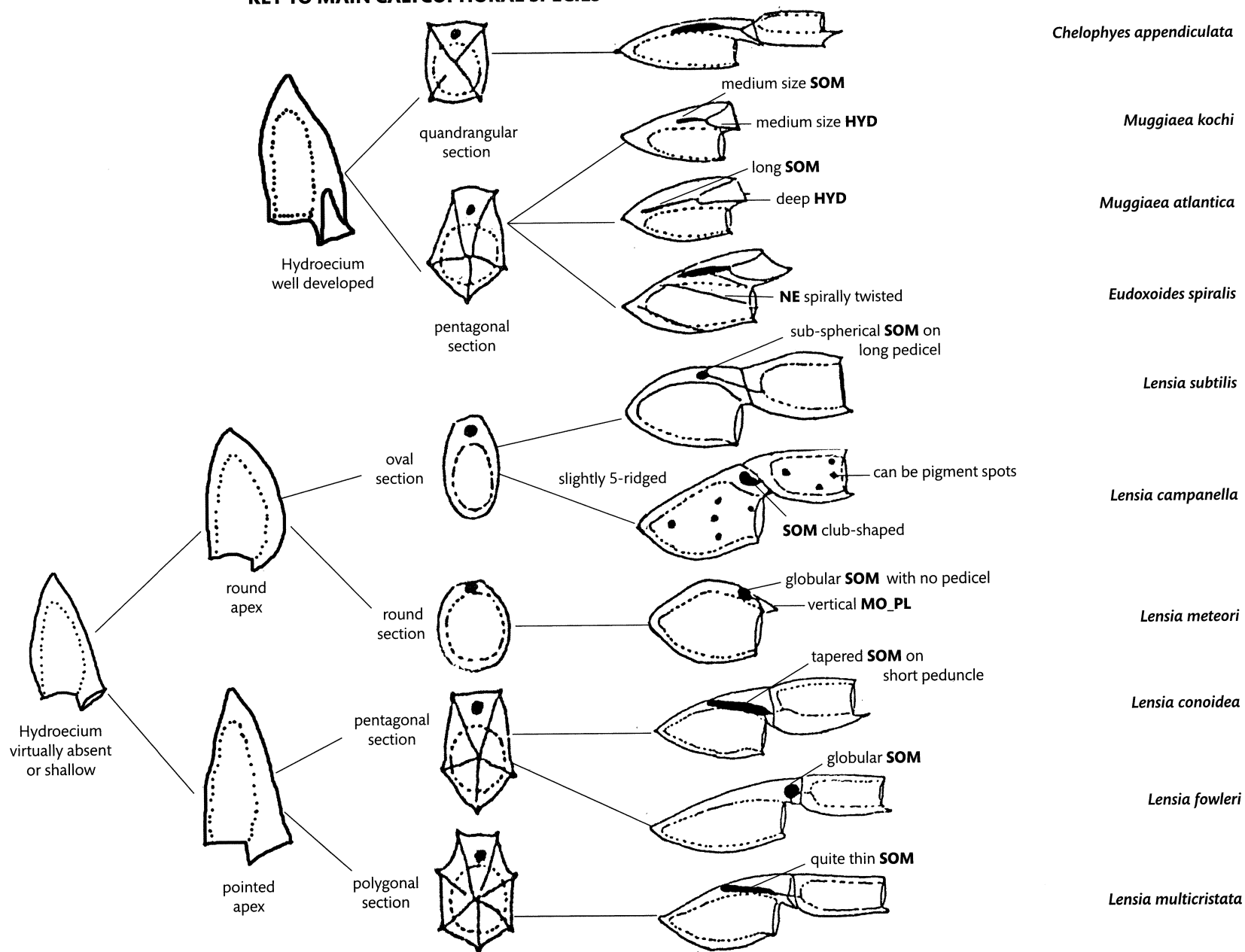
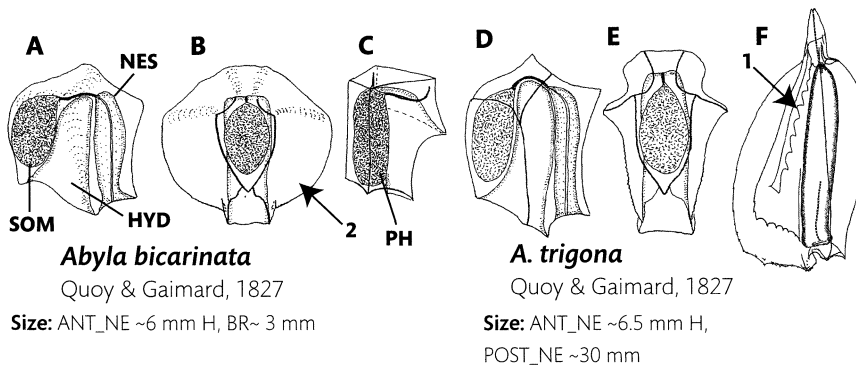


FIGURE 101: Key to main Calycophorae species.

Order Siphonophora Suborder Calycophorae Family Abylidae

Rigid, angular NE. POST_NE without SOM, usually much larger than the ANT_NE, with serrated ridges and teeth. SOM in ANT_NE usually curved ventrally.

Abyla spp.



ANT_NE: with 10/11 facets. AP facet divided by a transverse ridge, with ridges often serrated

NES: long, up to the apex of NE

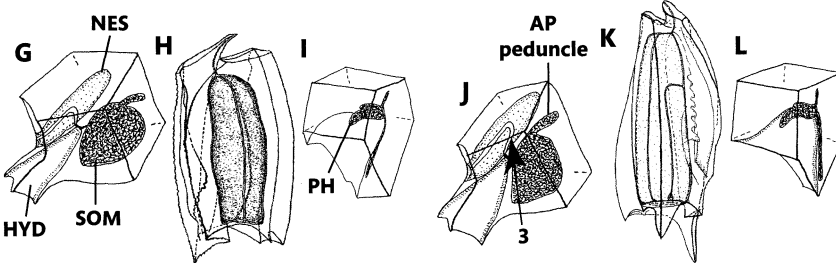
HYD: long, up to the apex of NE

SOM: large, oval, lies on lower side

POST_NE: with long AP apophysis. It has only 4 ridges, lower ones highly serrated basally. Toothed comb on left wing of HYD (1). 5 serrated OS teeth

BR: prismatic, with 6 facets, the upper one rectangular. PH very large

Note: ANT_NE of *A. bicarinata* has wing-like processes (2) and edges of facets rounded. In *A. trigona* most of the ridges are heavily serrated



Abylopsis spp.

ANT_NE: 7 facets, without AP facet. Pentagonal upper/lower facets

NES: cylindrical shape

HYD: partly between SOM and NES.

SOM: with AP peduncle

POST_NE: short, curved AP apophysis. 5 ridges. Toothed comb on both wings of HYD

BR: with 7 facets. PH with 2 swollen LAT branches, 1 narrow descending branch and 1 AP peduncle

Note: in the ANT_NE of *A. tetragona* LAT_RC form an ascending loop (3), absent in *A. eschscholtzii*

Abylopsis eschscholtzii

(Huxley, 1859)

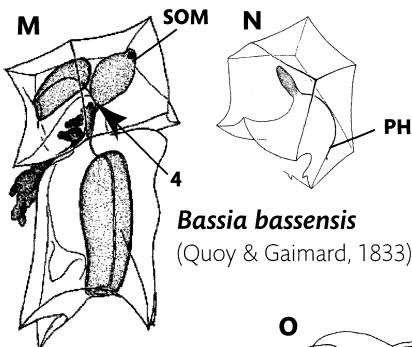
Size: ANT_NE ~5 mm H, POST_NE 6.5 mm H, BR 3 mm H

Distribution: Both species found in epipelagic waters in NATR and NWCS. *A. tetragona* also common in CNRY, NASE, NASW

A. tetragona

(Otto, 1823)

Size: ANT_NE up to 5 mm H, POST_NE 20 mm H, BR 4 mm H



Bassia bassensis

(Quoy & Gaimard, 1833)

Size: ANT_NE up to 4 mm H, POST_NE 15 mm H, BR 5 mm H

Distribution: Epipelagic in CNRY, NASE, NADR, NASW, NATR, NECS, NWCS

Bassia spp.

ANT_NE: polyhedric. **NES:** cylindrical shape

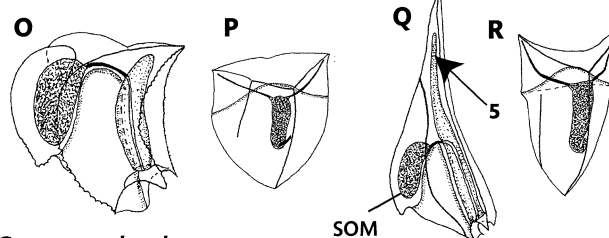
HYD: does not reach SOM and NES

SOM: without AP peduncle

POST_NE: 4 ridges, with basal teeth

BR: with 7 facets, rhomboidal on upper face and pentagonal on lower. PH is a long tube swollen at the apex

Note: in the ANT_NE of *B. bassensis* the HYD does not reach the zone between SOM and NES (4)



Ceratocymba dentata

(Bigelow, 1918)

C. sagittata

(Quoy & Gaimard, 1827)

Ceratocymba spp.

ANT_NE: 7 facets, AP facet undivided

POST_NE: long and narrow, without wing-like expansions. Short upper ridge ends on an upper tooth

BR: characteristic shape, roughly triangular with a concave AP facet, prominent LAT horns and a median dorsal ridge. PH with 2 thin ventro-LAT branches

Note: ANT_NE of *C. sagittata* has pointed apex and NES much longer than SOM (5). ANT_NE of *C. dentata* has LAT_margins deeply bowed and serrated

Size: *C. dentata* ANT_NE ~12.5 mm H, BR ~13 mm

Size: *C. sagittata* ANT_NE ~19 mm H, BR ~21 mm

Distribution: both species found in the epipelagic in CNRY, NASE, NASW, NATR. *C. sagittata* also in NADR

FIGURE 102: *Abyla bicarinata*: A, B, anterior nectophore, lower and lateral views; C, eudoxid, lateral view. *A. trigona*: D, E, anterior nectophore, lower and lateral views; F, posterior nectophore, lateral view. *Abylopsis eschscholtzii*: G, anterior nectophore, lower view; H, posterior nectophore, lateral view; I, bract, lateral view. *A. tetragona*: J, anterior nectophore, lower view; K, posterior nectophore, lateral view; L, bract, lateral view. *Bassia bassensis*: M, polygastric stage, lower view; N, bract, lateral view. *Ceratocymba dentata*: O, anterior nectophore, lower view; P, bract, lateral view. *C. sagittata*: Q, anterior nectophore, lower view; R, bract, lateral view. A-E, G, I-J, L, O-R, Pugh, (1999); F, Totton (1965); H, modified from Gili (1986); K, Kirkpatrick and Pugh (1984); M-N, Pagès and Gili (1992).

Order Siphonophora Suborder Calycophorae Family Clausophyidae

ANT_ and POST_NE have a SOM and are streamlined. HYD more prominent than in the diphyids. BR usually has PH with 2 fine basal branches extending down into the neck shield.

Distribution and ecology: Siphonophores from this family mainly live in deep waters.

Chuniphyes spp.

ANT_NE: with 4 ridges at the pointed apex and 8 ridges at the base, ending in prominent teeth. **POST_NE:** 3 ridges at the apex and 6 at base, ending in distinct teeth. HYD extends the whole length, with 2 large asymmetrical flaps in its upper half (1)

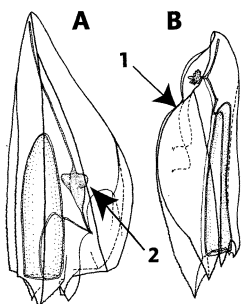
BR: flattened, not identifiable at species level. PH with 2 LAT branches

Note: *C. multidentata* is characterized by the shape of the SOM (2)

Kephyes spp.

Presently monotypic genus for *K. ovata*

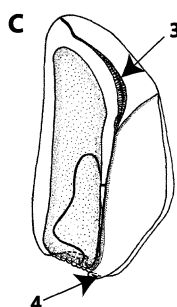
ANT/POST_NE: smooth, ridgeless, laterally compressed. NES >2/3 of NE length has slightly looped RC. SOM reaches ANT_NE apex (3). In ANT_NE the extensive HYD reaches the OS (4). **BR:** conical, with rounded apex and long neck-shield. PH reaches the apex



Chuniphyes multidentata
Lens & van Riemsdijk, 1908

Size: ANT_NE up to 35 mm H, POST_NE 40 mm H, BR 2 mm

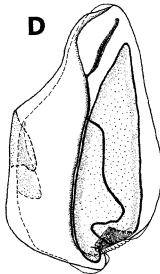
Distribution: epi-mesopelagic in ARCT, CNRY, NADR, NASE, NASW, NECS, NWCS, SARC



Kephyes ovata
(Keferstein & Ehlers, 1860)

Size: ANT/POST_NE up to 14 mm H, BR 8 mm

Distribution: meso-bathypelagic in CNRY, NASE, NECS, SARC



Order Siphonophora Suborder Calycophorae Family Diphyidae

ANT and POST_NE have similar size (or POST is smaller), both streamlined but dissimilar. ANT_NE has usually large NES and often

SOM with oil droplets. Diphyidae is a polyphyletic group assembling species with many different combinations of characters.

Chelophyes spp.

ANT_NE: rigid, with 5 ridges, the upper one only shortly above ostium. Only 3 ridges reach the apex. MO_PL divided

HYD: talon-shaped

SOM: ~ 1/2 of NE length, spindle-shaped, on a peduncle.

POST_NE: apically pointed, with 4 serrated ends. MO_PL divided in 2 strong, asymmetric teeth (5)

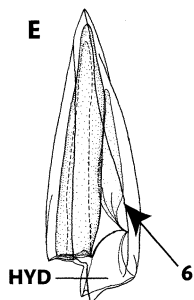
BR: conical with small/rounded neck shield

HYD: deep, ~ 1/2 of whole L. Cylindrical PH, reaching apex of BR

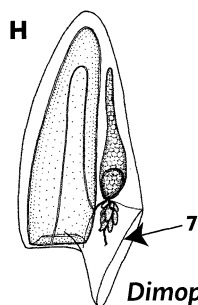
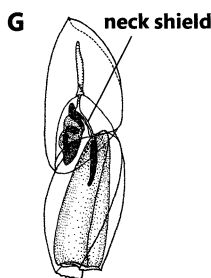
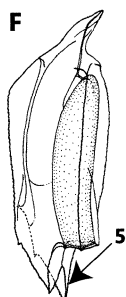
NOTE: *C. appendiculata* is characterized by ANT_NE with a straight SOM (6) and POST_NE with characteristic MO_PL

Size: ANT_NE up to 20 mm H, POST_NE 8 mm H, BR 4 mm H

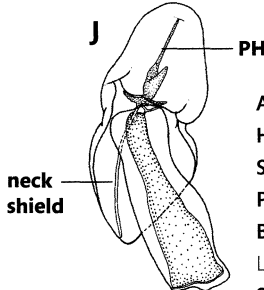
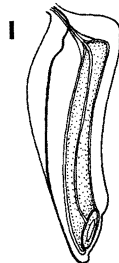
Distribution: Epi-mesopelagic in CNRY, NASE, NASW, NATR, NECS, NWCS



Chelophyes appendiculata
(Eschscholtz, 1829)



Dimophyes arctica
(Chun, 1897)



Dimophyes spp.

Presently monotypic genus for *D. arctica*

ANT_NE: smooth, without ridges. MO_PL undivided (7)

HYD: large, extending above OS

SOM: carrot-shaped, ~ 2/3 of NE length

POST_NE: reduced. NES opens upper-basally

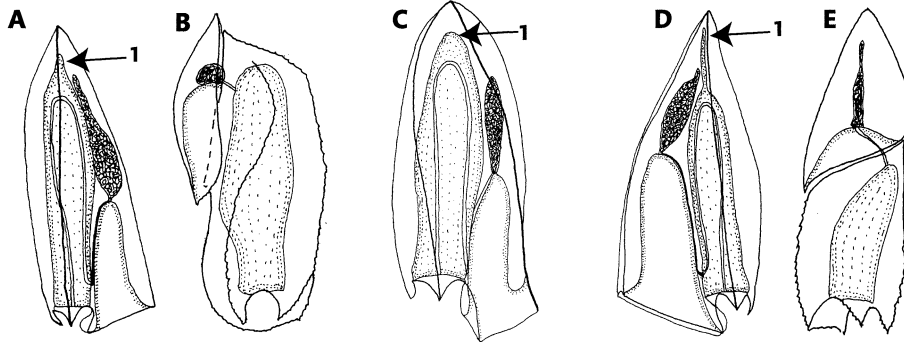
BR: conical, with extensive neck shield. PH with AP- and LAT horns

Size: ANT_NE up to 15 mm H, BR 10 mm H

Distribution: epi-mesopelagic in ARCT, CNRY, GFST, NADR, NASE, NASW, NECS, NWCS, SARCS

FIGURE 103: *Chuniphyes multidentata*: A, anterior and B, posterior nectophores, lateral views. *Kephyes ovata*: C, anterior and D, posterior nectophores, lateral views. *Chelophyes appendiculata*: E, anterior and F, posterior nectophores, lateral views; G, eudoxid, lateral view. *Dimophyes arctica*: H, anterior and I, posterior nectophores, lateral views; J, eudoxid, lateral view. A–B, E–J, Kirkpatrick and Pugh (1984); C–D, Pugh (2006).

Diphyes spp.



Diphyes bojani
(Eschscholtz, 1825)

Size: ANT_NE ~10 mm H,
POST_NE 7 mm H, BR 4 mm H

D. chamissonis
Huxley, 1859

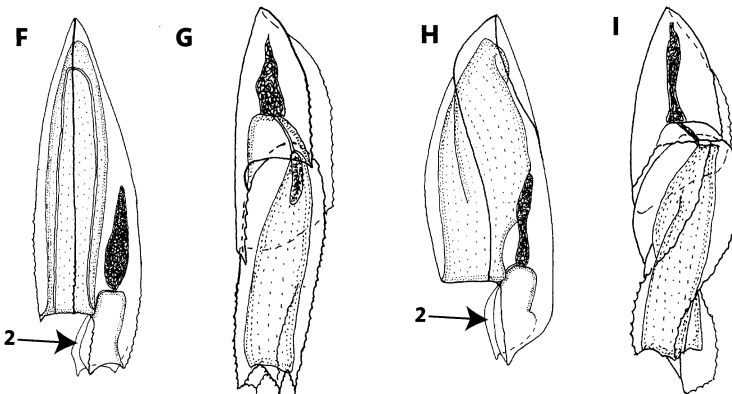
Size: ANT_NE ~12 mm
H, BR 5 mm H

D. dispar
Chamisso &
Eysenhardt, 1821

Size: ANT_NE ~36 mm H,
POST_NE 27 mm H,
BR 8 mm H

ANT_NE: with 5 ridges and 3 prominent ostial teeth. **HYD:** deep. **SOM:** spindle-shaped. **POST_NE:** with long AP apophysis and 3 ostial teeth (unknown for *D. chamissonis*). **BR:** helmet-shaped. Note: ANT_NE of different species characterized by depth of HYD (1/3 NE length in *D. bojani*, 1/2 NE length in the other species), SOM length and shape of NES apex (1) (rounded in *D. chamissonis*, with a diverticulum in *D. dispar*, pyramidal in *D. bojani*)

Eudoxoides spp.



Eudoxoides mitra
(Huxley, 1859)

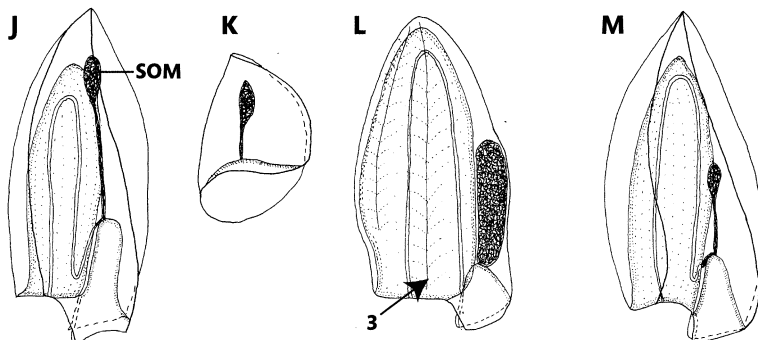
Size: ANT_NE ~8 mm H,
BR 4 mm H

E. spiralis
(Bigelow, 1911)

Size: ANT_NE up to 12 mm
H, BR 4 mm H

ANT_NE: rigid, with 5 ridges, usually serrated, not always reaching the apex (4 AP-ridges in *E. spiralis*). Might be spirally twisted. MO_PL divided (2). No ostial teeth. **HYD:** 1/2 NES length, less deep than in *Chelophyes*. **POST_NE:** with curved furrow between apex and apical apophysis. Absent in *E. spiralis*. **BR:** hood-shaped, with PH long reaching the apex. Long neck-shield. GON twisted with serrated edges. **Note:** ANT_NE and GO of *E. spiralis* typically spirally twisted. SOM carrot-shaped in *E. spiralis*, pear-shaped in *E. mitra*. **Distribution:** both species are epipelagic in CNRY, NASE, NASW, NATR, NWCS. *E. spiralis* also found in NADR and NECS

Muggiaea spp.



Muggiaea atlantica
Cunningham, 1892

Size: ANT_NE ~5 mm H,
BR 2 mm H

M. bargmannae
Totton, 1954

Size: ANT_NE ~9 mm H

M. kochi
(Will, 1844)

Size: ANT_NE ~4 mm
H, BR 2 mm H

ANT_NE: pyramidal, with 5 ridges. Oblique, divided MO_PL. **HYD:** deep, not open ventrally. **SOM:** very close to NES wall. **POST_NE:** not developed. **BR:** small/conical, with asymmetrical base. Shallow HYD, PH club-shaped. **Note:** species identified by different shape and length of SOM. ANT_NE of *M. bargmannae* with LAT folds in place of ridges (3). **Distribution:** epipelagic. *M. atlantica* found in CNRY, NASE, NECS, NWCS, SARC; *M. bargmannae* in ARCT, NARC, SARC; *M. kochi* in NASE, NASW, NECS

FIGURE 104: *Diphyes bojani*: A, anterior nectophore, lateral view; B, eudoxid, lateral view. *D. chamissonis*: C, anterior nectophore, lateral view; D, anterior nectophore, lateral view; E, eudoxid, lateral view. *D. dispar*: D, anterior nectophore, lateral view; E, eudoxid, lateral view. *Eudoxoides mitra*: F, anterior nectophore, lateral view; G, eudoxid, lateral view. *E. spiralis*: H, anterior nectophore, lateral view; I, eudoxid, lateral view. *Muggiaea atlantica*: J, anterior nectophore, lateral view; K, bract. *M. bargmannae*: L, anterior nectophore, lateral view. *M. kochi*: M, anterior nectophore, lateral view. A–M, Pugh (1999).

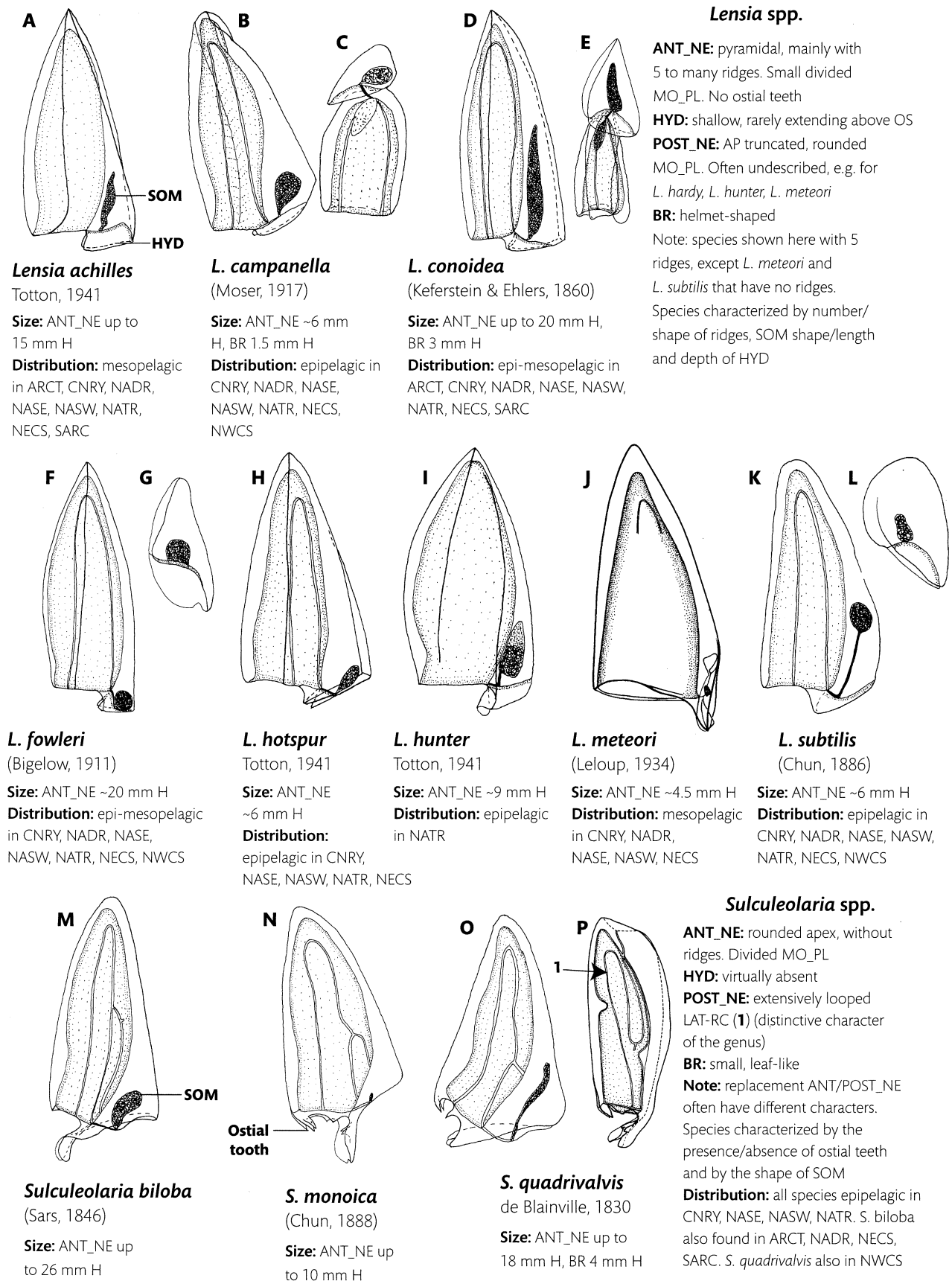


FIGURE 105: *Lensia achilles*: A, anterior nectophore, lateral view. *L. campanella*: B, anterior nectophore, lateral view; C, eudoxid, lateral view. *L. conoidea*: D, anterior nectophore, lateral view; E, eudoxid, lateral view. *L. fowleri*: F, anterior nectophore, lateral view; G, eudoxid, lateral view. *L. hotspur*: H, anterior nectophore, lateral view. *L. hunter*: I, anterior nectophore, lateral view. *L. meteori*: J, anterior nectophore, lateral view. *L. subtilis*: K, anterior nectophore, lateral view; L, bract, lateral view. *Sulculeolaria biloba*: M, anterior nectophore, lateral view. *S. monoica*: N, anterior nectophore, lateral view; O, anterior and P, posterior nectophore, lateral views. A–P, Pugh (1999).

Order Siphonophora Suborder Calycophorae Family Hippopodiidae

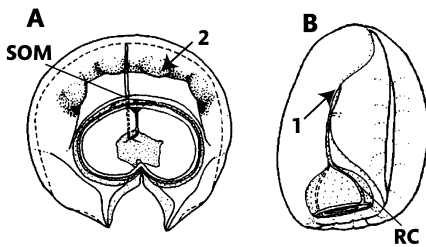
Up to 16 NE flattened in upper-lower axis, arranged in series of two. NE bear protuberances or spines. BR absent, GO directly arise from the siphosome. Larval NE similar to that of Prayidae-Prayinae,

can be distinguished by the shape of SOM, curving smoothly over mid-dorsal surface of HYD (1).

Hippopodius spp.

NE: horseshoe-shaped, with 4 rounded protuberances (2) forming an arc above ostium; Larval NES with only 2 RC

Distribution: epi-mesopelagic in CNRY, NADR, NASE, NASW, NATR, NECS, NWCS



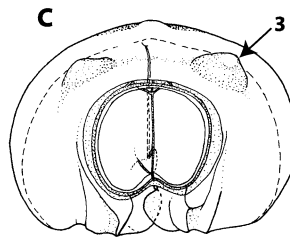
Hippopodius hippopus
(Forsskål, 1776)

Size: NE diam. up to 20 mm. larval NE ~5 mm H

Vogtia spp.

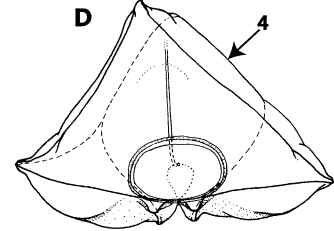
NE: with protuberances (3), spines or ridges (4). Larval NES with 4 RC

Distribution: both mesopelagic in ARCT, CNRY, NADR, NASE, NASW, NATR, NECS. *V. glabra* also in NWCS



Vogtia glabra
Bigelow, 1918

Size: NE diam. up to 30 mm



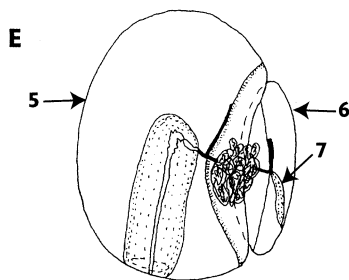
V. serrata
(Moser, 1925)

Size: NE diam. up to 40 mm

Order Siphonophora Suborder Calycophorae Family Prayidae

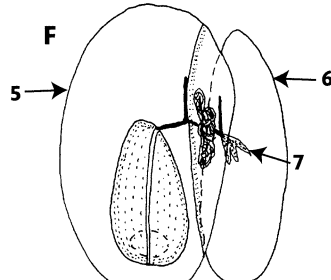
NE quite large and usually rounded. Larval NE sometimes retained in the polygastric stage (e.g. in the subfamily Amphicaryoninae) or replaced by 1–4 definitive NE that have a SOM often complexly

branched. In subfamily Prayinae specimens have usually 2 (up to 4) smooth NE, while only 1 large NE characterizes the subfamily Nectopyramidinae. BR rounded and unridged.



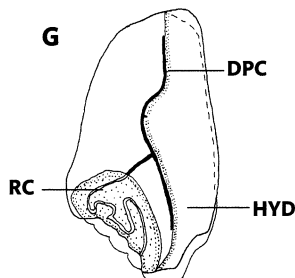
Amphicaryon acaule
Chun, 1888

Size: larger NE diam. ~10 mm



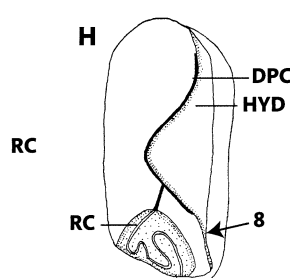
A. peltifera
(Haeckel, 1888)

Size: larger NE diam. ~4 mm



Rosacea cymbiformis
(Delle Chiaje, 1830)

Size: NE ~ 11 mm H



R. plicata
Bigelow, 1911

Size: NE up to 30 mm H

Amphicaryon spp.

NE: 2 different. Larger NE, possibly the retained larval NE (5), in *A. acaule* partly encloses the reduced vestigial definitive NE (6), which has a NES without an ostium
BR: with 2 LAT HYD-canals

Note: species can be identified by the size of the NE and shape of the vestigial RC (7)

Distribution: both epipelagic in NADR, NASE, NASW, NATR. *A. acaule* also NECS, NWCS

Rosacea spp.

NE: 2 medium, rounded NE with simple SOM without side branches. Sinuous LAT RC on NES

BR: kidney-shaped, with characteristic arrangement of canals

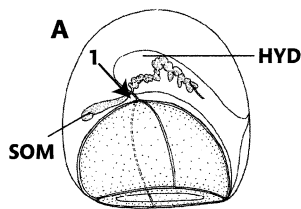
Note: species can be identified by the extension of the HYD, that in *R. plicata* does not reach the base of NE (8)

Distribution: *R. cymbiformis* epipelagic, *R. plicata* meso-pelagic. Both in NADR, NASE, NECS. *R. cymbiformis* also in CNRY, *C. plicata* also in NATR

FIGURE 106: *Hippopodius hippopus*: A, definitive nectophore, lower view; B, larval nectophore, lateral view. *Vogtia glabra*: C, definitive nectophore, upper view. *V. serrata*: D, definitive nectophore, upper view. *Amphicaryon acaule*: E, polygastric stage, lateral view. *A. peltifera*: F, polygastric stage, lateral view. *Rosacea cymbiformis*: G, definitive nectophore, lateral view. *R. plicata*: H, definitive nectophore, lateral view. A–D, Kirkpatrick and Pugh (1984); E–H Pugh (1999).

Order Siphonophora Suborder Calyphorae Family Sphaeronectidae

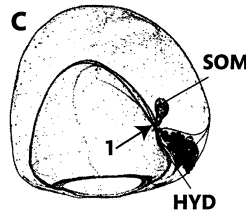
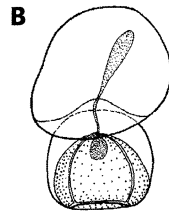
Small, fragile rounded/conical larval NE, the only one in the polygastric stage. BR small, rounded. See recent revision of the genus in Pugh (2009) and Grossmann et al. (2012).



Sphaeronectes koellikeri

Huxley, 1859

Size: ~6 mm (NE diameter), ~2 mm (BR)



S. irregularis

(Claus, 1873)

Size: ~3 mm W

***Sphaeronectes* spp.**

See family characteristics.

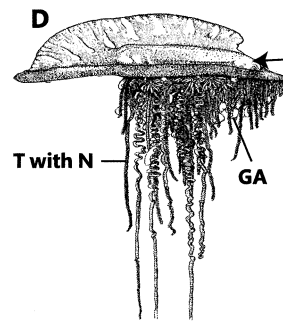
Note: species can be identified by the shape of SOM, position of the intersection and form of RC (1), NES height and HYD extension

Distribution: *S. koellikeri* epipelagic in GFST, NASE, NECS, NWCS; *S. irregularis* epi-pelagic in SARC

Order Siphonophora Suborder Cystonectae Family Physaliidae

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

Distribution and ecology: *Physalia* floats on the surface of the sea. Its float responds actively to wind, adopting a characteristic 'sailing posture' together with erection of the crest.



Physalia physalis

(Linnaeus, 1758)

Huge, asymmetric, horizontal purplish-blue PN (2), with an erectile diagonal 'sail' at the top. Cormidia attached to one side of the float. T can be more than 10 m long

Size: float up to 30 cm in length

Distribution: epipelagic in CNRY, NADR, NATR, NECS, NWCS

FIGURE 107: *Sphaeronectes koellikeri*: A, definitive nectophore, lateral view; B, bract, lateral view. *S. irregularis*: C, definitive nectophore, lateral view. *Physalia physalis*: D, whole animal. A, B, Kirkpatrick and Pugh (1984); C, Carré (1968), D, Totton (1965).

Order Siphonophora Suborder Physonectae Family Agalmatidae sensu strictu

It includes the genera *Agalma*, *Halistemma*, *Nanomia*, *Athorybia* and *Melophysa*, the last two being short-stemmed forms with, in the genus *Athorybia*, the total suppression of the nectosome.

Dorsal nectosome (i.e. NE budded off on dorsal side of the stem). NE have DMC and no MFZ. Adult TEN are involucrate tricornuate in *Agalma*, or unicornuate in the other genera.

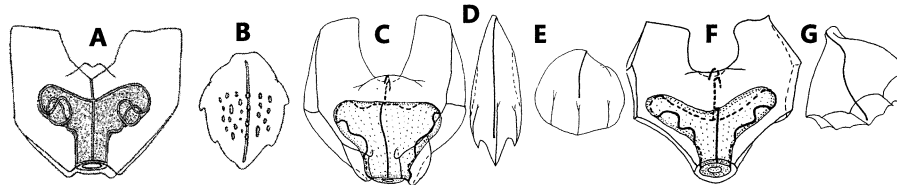
***Agalma* spp.**

NE: V-shaped. Triangular NES, T-shaped (*A. elegans*) or Y-shaped (*A. clausi* and *A. okenii*). LAT-RC distinctly looped. **TEN:** tricornuate.

BR: foliaceous

Note: *A. clausi* and *A. okenii* without LAT_ridges

Distribution: epi-mesopelagic. *A. elegans* and *A. okenii* in CNRY, NATR, NWCS. *A. elegans* also in GFST, NADR, NASE, NASW, NECS. *A. clausi* in NWCS


Agalma clausi

Bedot, 1888

Size: NE ~16 mm H

A. elegans

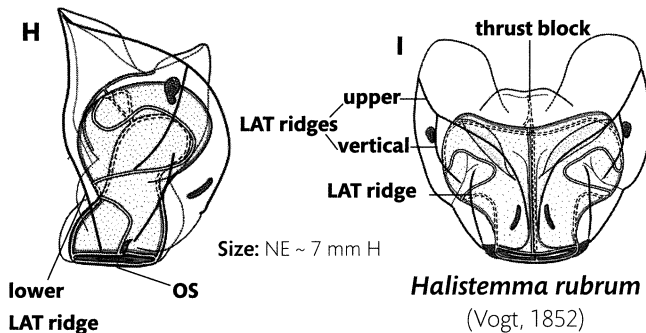
(Sars, 1846)

Size: NE ~5-7 mm H.
Colony up to 1 m L

A. okenii

Eschscholtz, 1825

Size: NE ~4.5 mm H



Size: NE ~7 mm H

Halistemma rubrum

(Vogt, 1852)

***Halistemma* spp.**

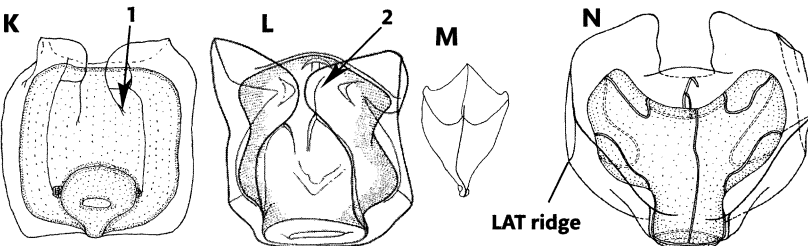
NE: large thrust block. Characteristic arrangement of ridges, i.e. ≥1 pair of vertical LAT ridges, 1 pair of upper and lower LAT and 2 pairs of LAT ridges. Typical sinuous arrangement of RC

TEN: unicornuate, with very reduced INV

BR: foliaceous, of 2 different types

Note: *H. rubrum* characterized by 1 pair of incomplete vertical LAT_ridges, not joining upper and lower LAT_ridges. MO_PL absent. **Size:** Colony up to a few meters length

Distribution: epi-mesopelagic in ARCT, CNRY, NADR, NASE, NASW, NATR, NECS, NWCS


Nanomia bijuga

(Delle Chiaje, 1844)

Size: NE ~3 mm H. Colony up to 10-30 cm L

N. cara

Agassiz, 1865

Size: NE up to 10 mm H

***Nanomia* spp.**

NE: Upper LAT_ridges incomplete (1). LAT_ridges complete. LAT_RC form loops.

TEN: unicornuate, with incomplete INV.

BR: thin and leaf-like.

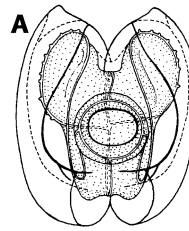
Note: *N. bijuga* has squared NES hollow in the middle, NE with AP wings folded (2). *N. cara* has Y-shaped NES and NE with only 1 LAT_ridge on each side.

Distribution: epi-mesopelagic. Both species found in NECS, NWCS; *N. bijuga* also in NASE and NASW, while *N. cara* in ARCT, NADR, NECS, SARC

FIGURE 108: *Agalma clausi*: A, definitive nectosophore, upper view; B, bract, upper view. *A. elegans*: C, definitive nectosophore, upper view; D and E, two bracts of different shape, upper views. *A. okenii*: F, definitive nectosophore, upper view; G, bract, upper view. *Halistemma rubrum*: H, definitive nectosophore, lateral view; I, definitive nectosophore, upper view; J, bract, upper view. *Nanomia bijuga*: K, definitive nectosophore, upper view; L, young nectosophore, lower view; M, bract, upper view. *N. cara*: N, definitive nectosophore, upper view. A, B, Bedot (1888); C, L, N, Totton (1965); D, E, J, K, M, Pugh (1999); F, G, Bigelow (1911); H, I, Pugh and Baxter (2014).

Order Siphonophora Suborder Physonectae Family Apolemiidae

One T or groups of T present between NE on nectosome. NE deeply hollowed axially, forming a pair of large AP wings. NES large with S-shaped LAT_RC.

***Apolemia uvaria***
(Lesueur, 1815)

Groups of 5–6 T on nectosome, between each pair of NE. LAT_RC with short branches on the upper loop. BR covered by opaque spots.

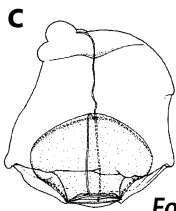
Size: NE 15–20 mm H. BR ~6 mm. Colony up to 20–30 m L

Distribution: epipelagic in NATR, NECS, SARC

Order Siphonophora Suborder Physonectae Family Forskaliidae

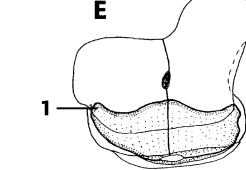
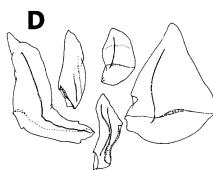
Cylindrical/cone-shape nectosome, with NE arranged spirally. NE flattened in upper-lower axis, often asymmetrical. NES restricted to

basal half, with straight RC. BR of variable shapes of four types: stem, bolster and two kinds of knee shaped.

***Forskalia edwardsii***

Kölliker, 1853

Size: NE up to 7 mm H

***F. contorta***

(Milne Edwards, 1841)

Size: NE up to 10 mm H

***Forskalia* spp.**

See family characters

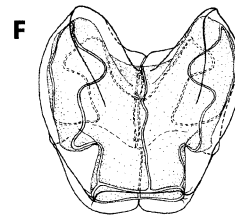
Note: left AP wing is large in *F. contorta* and small in *F. edwardsii*, without apical incision in both species. In *F. contorta* NES has marked LAT wings (1), while *F. edwardsii* has small yellow spots on OS where RC meet ring canal.

Size: colony up to 5–10 m long

Distribution: *F. edwardsii* epipelagic in NASE, NATR, NECS. *F. contorta* epi-mesopelagic in CNRY, NASE, NASW, NATR

Order Siphonophora Suborder Physonectae Family Physophoridae

NE apparently ridgeless, with an extensive NES, which has characteristic looped LAT_RC. Upper and lower canals are sinuous. Siphosome shortened to form a sac on which cormidia are arranged spirally. Each cormidium has one large PAL. Two species have been described: *Physophora hydrostatica* (without BR) and *P. gilmeri* (with BR)

***Physophora* spp.**

See family characters

Size: NE up to 20 mm H.

Colony up to 10 cm long

Distribution: mesopelagic in ARCT, CNRY, NADR, NASE, NASW, NECS, NWCS, SARC

Physophora hydrostatica

Forsskål, 1775

FIGURE 108 (CONTINUED): *Apolemia uvaria*: A, definitive nectophore, upper view; B, bract, lateral view. *Forskalia edwardsii*: C, definitive nectophore, upper view; D, bracts, upper views. *F. contorta*: E, definitive nectophore, upper view. *Physophora hydrostatica*: F, definitive nectophore, upper view. A, E, Pugh (1999); B, Totton (1965); C, D, F, Kirkpatrick and Pugh (1984).

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