

# Systematics of Siphonophores

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## Abstract

Siphonophores are the most complex of all pelagic medusozoan hydrozoan cnidarians, bearing various types of zooids on a long stem and often termed “string jellyfish.” They are extremely fragile and live almost exclusively in the open ocean. They vary in length from 50 m down to 10–20 mm. Most species bear swimming bells (nectophores) for locomotion, some have a float (pneumatophore), and all have a long stem of iterative units termed cormidia for feeding, reproduction, and also protection and buoyancy. Tentacles from the cormidia bear stinging cells (nematocysts) for prey capture, either in simple groups or lines or in more complex nematocyst batteries on side branches known as tentilla. In life, tentacles and their side branches extend into a three-dimensional net for fishing, into which prey either blunders by accident or, in a few species, is attracted by lures. Such great diversity has led to a complex systematics based on a range of morphological characters, recently enhanced by the first molecular study of the group. From this a new phylogeny has been proposed, for 17 valid families (one semi-benthic) and 177 valid species (some unassigned). Characters of these families are reviewed in two tables and 17 summaries, including diagnostic characters, number and variety of species, and, where appropriate, habitat preferences and relative success in today’s seas. Figures and images showing different types of siphonophores, their morphology, stinging organs, and appearance in life accompany the main text.

## Keywords

Siphonophores; Cystonects; Physonects; Calyphorans; Hydrozoa; Nematocysts; Nectophores; Cormidia, pneumatophore; Tentacles; Eudoxid

## Introduction

Siphonophores are complex pelagic cnidarians in the medusozoan group Hydrozoa. They are carnivorous “sit and wait” predators, some of which can lure prey into their tentacles by mimicking shoals of small copepods, medusae, or fish. They rapidly stun their prey with toxins delivered from batteries of nematocysts on the tentacles or tentacle side branches. This is essential because, otherwise, the siphonophore itself would be damaged by struggling prey attempting to escape.

Individuals possess enormous powers of extension, contracting their stem and tentacles completely for swimming and then relaxing them to the maximum for feeding. This relaxation allows formation of an enormous three-dimensional fishing net, or web, often with the aid of swirling swimming movements to “set the trap.” Once set, many siphonophores simply remain stationary in the water until prey blunders into their net. Others may lure them in either by drawing copepod-like stinging batteries through the water or by flicking red lures resembling shoaling fish to attract prey.

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Cnidaria are an ancient lineage, characterized by the presence of cnidae, or stinging cells, most of which are nematocysts. In siphonophores, nematocysts are grouped into either pads on the tentacles (e.g., *Physalia*, the Portuguese man-of-war) or, in most other species, complex nematocyst batteries on side branches from the tentacles termed tentilla.

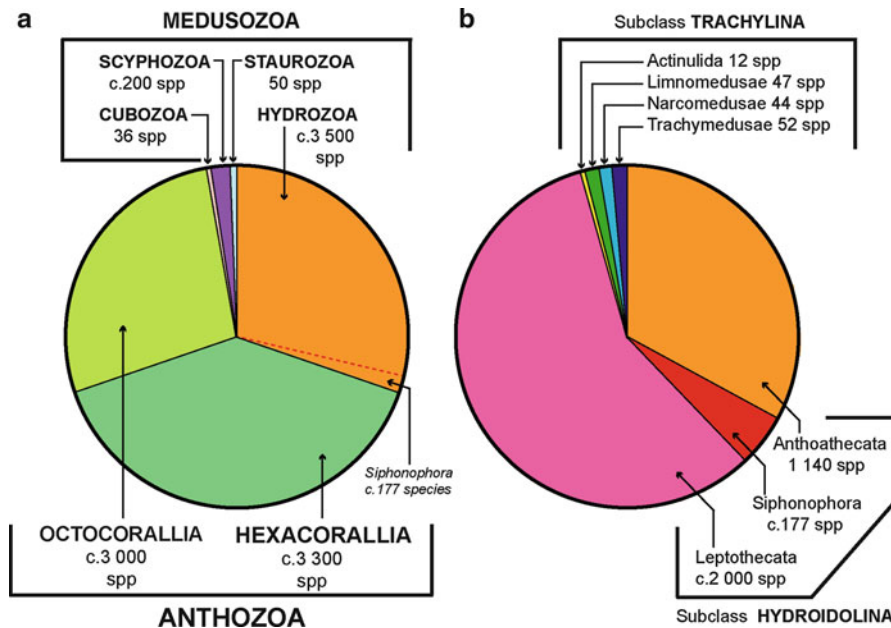
Siphonophores are often called string jellyfish, or chain jellyfish, to distinguish them from true jellyfish and hydromedusae, which are mostly disk shaped. All belong to one of two major clades which comprise the Cnidaria, namely, the Medusozoa. This clade includes Hydrozoa, Scyphozoa, Cubozoa, and Staurozoa. Most jellyfish in these groups have a bottom-living stage in their life cycle that restricts them to the shelves around most continents. Siphonophora, however, are holopelagic (except one family), meaning that they pass through their entire life cycle in the water column, without having a benthic stage. This has enabled them to penetrate all oceans, and most exhibit a worldwide, or cosmopolitan, distribution. Some species are restricted to tropical latitudes, others to temperate latitudes, and a few are truly cosmopolitan, with records from all around the globe from Arctic to Antarctic waters (Mapstone 2014, Tables 2 and 3).

Siphonophore specimens are difficult to obtain, because they inhabit the deep sea, and are therefore absent from net catches used to monitor coastal waters. Today most are collected by either blue-water SCUBA (self-contained underwater breathing apparatus) or remotely operated vehicles (ROVs), but in the past when nets were used, specimens were often fragmented and damaged and the importance of siphonophores in pelagic assemblages not fully appreciated. Gelatinous animals have traditionally been preserved in buffered formaldehyde to preserve their shape, and vast collections are present at a few locations around the world, including the Natural History Museum, London, but these are of little use for molecular work, which requires alcohol-preserved material.

Siphonophores are colonial polymorphic hydrozoans with physiological integration of zooids and a complex morphology. They also exhibit a diversity of body form. An understanding of their morphology is therefore needed to investigate their systematics, and morphology was very well explained in a seminal monograph of 1965 by A.K. Totton. Little then changed until the first molecular analyses of the group by Dunn et al. (2005b), which revealed some new relationships and diagnostic characters within the group. Characters not previously thought to be important were found to be diagnostic, including the presence or absence of swimming bells, the sexual state of the family or species, the presence or absence of a muscular free zone in the wall of the nectosac of the nectophores, and the type of cormidia present on the stem. These, and other more traditional characters, are reviewed below.

## Taxonomic Status

Siphonophora are a small monophyletic group in the phylum Cnidaria and members of the diverse clade Hydrozoa, comprising c. 3,500 species (Fig. 1a). The Hydrozoa includes the large subclass Hydroidolina (3,317 species) and the much smaller subclass Trachylina (155 species) (Fig. 1b). The Siphonophora are a small group of c. 177 species within the Hydroidolina, while the remainder of this subclass comprises the much larger groups Anthoathecata and Leptothecata (c. 3,140 species). These latter two clades are mostly meroplanktonic, with a bottom-living polypoid “hydroid” stage in the life cycle. As noted above, this restricts their geographical distribution and makes them species-rich. Siphonophores, in contrast, are depauperate species-poor clade and in this respect resemble the other two holopelagic hydrozoan groups Trachymedusae and Narcomedusae, which together comprise c. 96 species (Fig. 1b) (World Hydrozoa Database).



**Fig. 1** Position of Siphonophora within the phylum Cnidaria. (a) the c. 10,000 Cnidaria species (excluding Myxozoa) subdivided into clades; (b) the c. 3,500 Hydrozoan species, subdivided by ranks (Modified from © Gillian Mapstone (2014), Fig. 2A, B; see legend for this figure and Mapstone (2015) for origins of other numbers used in a and b)

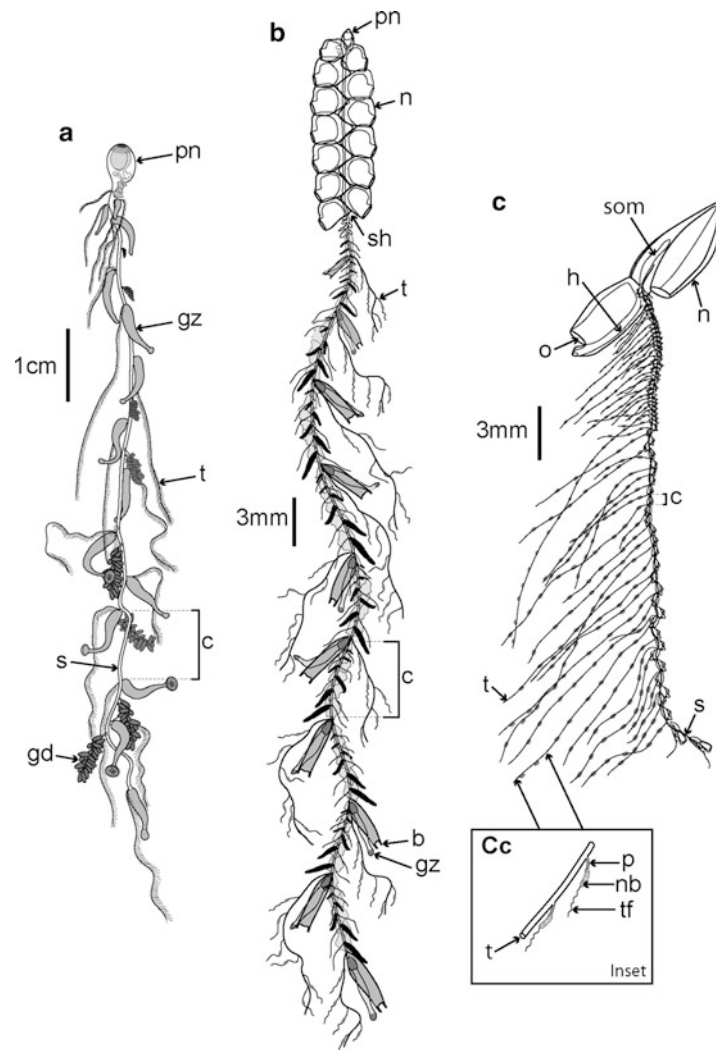
## Typical Body Plans and Cormidia

The basic morphology of siphonophores is best explained with reference to the body plans of three typical species from the groups Cystonecta, Physonectae, and Calyphorae (Fig. 2). An anterior-posterior axis related to the direction of swimming is recognized in all siphonophores (reviewed by Mapstone 2009), which in Fig. 2 is oriented vertically, with the anterior end uppermost.

All three types have a long stem, the siphosome, which bears repeating, or iterative, groups of zooids known as cormidia. One cormidium always includes a gastrozooid with tentacle for feeding and one or more sexual zooids for reproduction, often on a tree-like stalk known as a gonodendron. In addition, the cormidia of physonects and calyphorans also include one or more bracts (Fig. 2b, c). A float, the pneumatophore, is present in cystonects and physonects (Fig. 2a, b), and swimming bells, the nectophores, are present in physonects and calyphorans (Fig. 2b, c). An additional length of stem, the nectosome, carries the nectophores in Fig. 2b (see definition in Mapstone 2009, p. 72).

The pneumatophore is filled with carbon monoxide secreted by a gas gland, and this provides buoyancy for cystonects and physonects. Additional buoyancy is gained from gelatinous tissues in physonects and calyphorans, particularly from bracts in the cormidia; these tissues have a lowered specific gravity from the partial replacement of sulfate ions by chloride ions in the mesoglea (Mackie et al. 1987).

Propulsive zooids, the nectophores, are characteristic of physonects and calyphorans, and each contains a muscular nectosac which undergoes repeated contractions during swimming to facilitate active locomotion through the water (water exits via the ostium). Nectophores are absent in cystonects, which can only drift passively, and, by repeated contraction and expansion of the stem and tentacles, extend their tentacles to form a very basic fishing net for feeding.

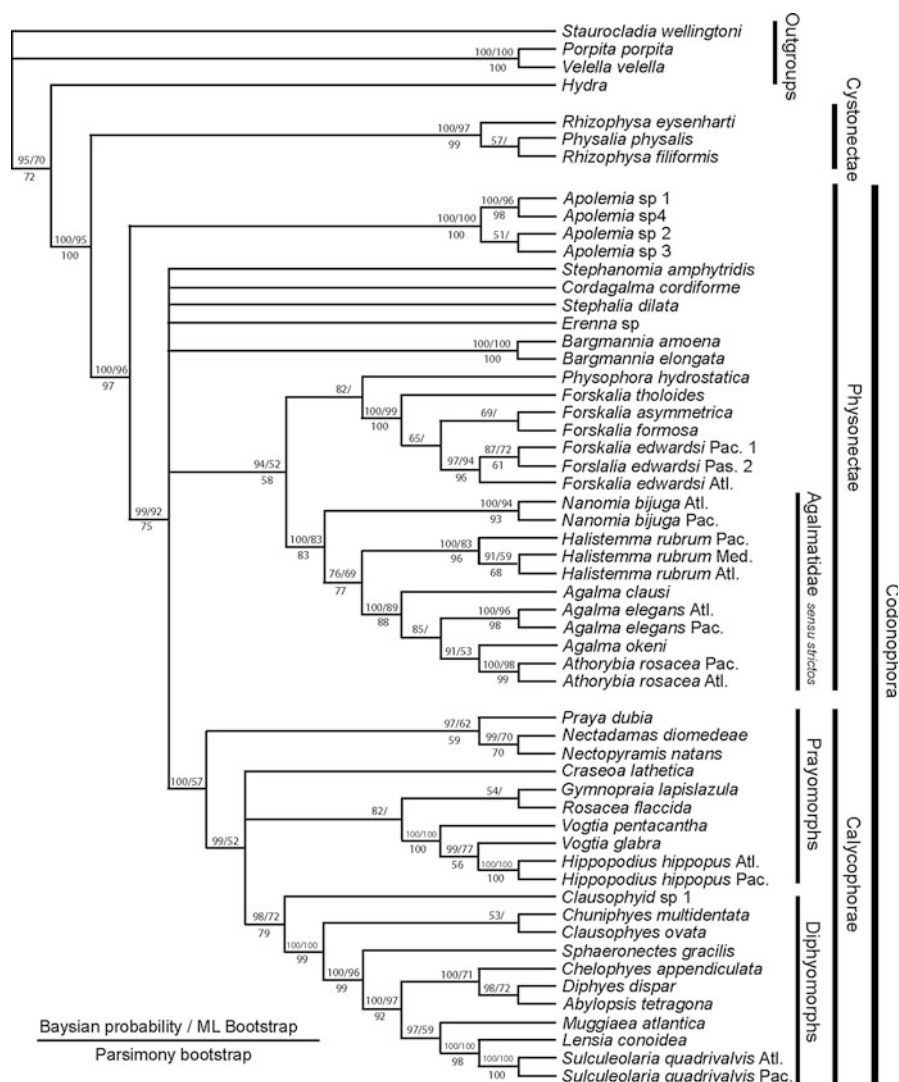


**Fig. 2 Siphonophore morphology. Three typical body plans:** (a) long-stemmed cystonect *Rhizophysa eysenhardti*, (b) long-stemmed physonect *Nanomia bijuga*, and (c) typical calycophoran *Lensia conoidea*; *inset Cc* shows two tentilla attached to one tentacle. Labels: *b* bract, *c* cormidium, *gz* gastrozooid, *gd* gonodendron, *h* hydroecium, *n* nectophore (swimming bell), *nb* nematocyst battery (a cnidoband), *o* ostium, *p* pedicel, *pn* pneumatophore (float), *s* stem, *sh* siphosomal horn (growth or budding zone), *som* somatocyst, *t* tentacle, *tf* terminal filament (Derived from © Gillian Mapstone (2014), Fig. 3; refer to this figure legend for details of published figures and references from which drawings derived)

All zooids are formed by budding in budding (or growth) zones present in various parts of the siphonophore individual or “colony.” Buds mature into particular zooids, for example, those in a cormidium, as they move down the stem toward the posterior end and the stem simultaneously lengthens. The budding zone is often contracted and difficult to identify in preserved material, but in Fig. 2b of a typical physonect, the siphosomal budding zone is clearly visible.

## Molecular Phylogeny and Valid Taxa

The new molecular phylogeny of Siphonophora by Dunn et al. (2005b) is based on the nuclear small subunit ribosomal RNA gene 18S and the mitochondrial large subunit ribosomal RNA gene 16S. It shows that Cystonecta (as Cystonectae), without nectophores, is sister to all other siphonophores, termed the



**Fig. 3 Molecular phylogeny of Siphonophora from Dunn et al. (2005b, Fig. 6).** Consensus tree of all trees for the Bayesian analysis of the combined data set (from an initial 20 million trees). The *left score* above the branch is the Bayesian posterior probability (%), the *right score* above the branch is the ML bootstrap support value (%), and the score below the branch is the MP bootstrap support value (%). The bars to the *right* of the species names indicate clades and grade taxa. Abbreviations: *Atl* Atlantic, *Med* Mediterranean, *Pac* Pacific. For full details of analyses and consensus tree computations, refer to Dunn et al. (2005b) (© Mapstone 2014, Fig. 9)

Codonophora, or bell-bearers, with nectophores (Fig. 3). The phylogeny also shows the Physonectae to be paraphyletic, whereas the Calycophorae are a monophyletic clade within the Codonophora.

Sexual state has been found to be an important character in determining relationships within the Codonophora. Cystonects are all dioecious (separate sexes), and five discrete physonect families and one unascribed genus within the Codonophora also display dioecy (Table 1). The remaining four discrete physonect families, three further unascribed physonect genera, and all calycophoran families are monoecious, with both sexes developing on the same individual, albeit at different times, to prevent self-fertilization. Monoecy enables cross fertilization between individuals in the deep sea where populations can be very small and mating opportunities limited.

In codonophorans, cormidia first arise as “pro-buds” on a swelling at the anterior end of the siphosome known as the “horn” or siphosomal growth zone (Fig. 2b). In cystonects there is no horn, and zooids arise

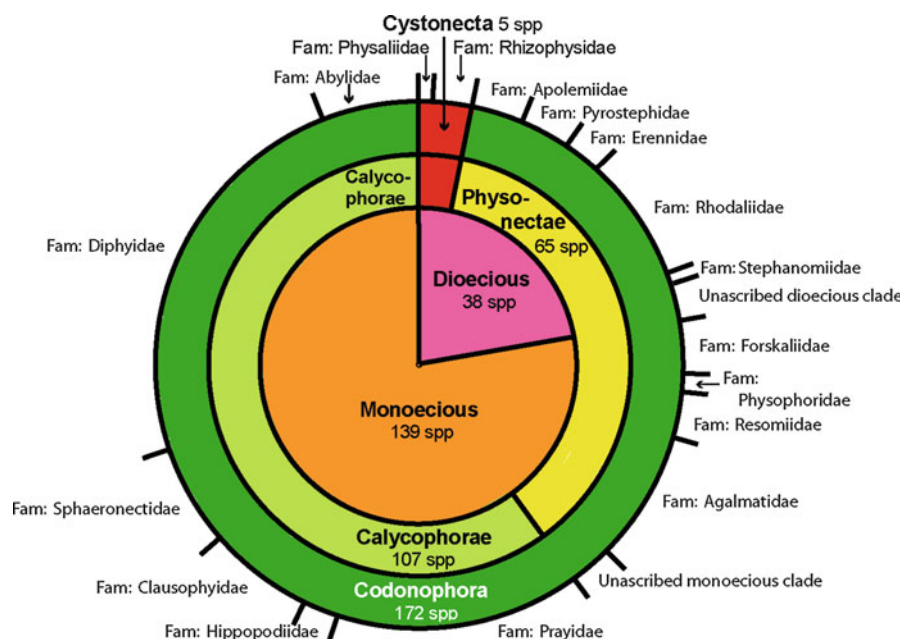
**Table 1** Siphonophora systematics: higher ranks, valid families, and genera (Extracted from © Mapstone 2014, Table 3, with Stephanomiidae added and a question mark added to *Rudjakovia*; see Table 2)

High rank	Family and subfamily	Genera
<b>I – Cystonecta</b>	01. Physaliidae	<i>Physalia</i>
	02. Rhizophysidae	<i>Bathypphysa</i> , <i>Rhizophysa</i>
<b>II – Codonophora</b>		
<b>Physonectae</b>		
Dioecious families	03. Apolemiidae	<i>Apolemia</i>
	04. Erennidae	<i>Erenna</i> , <i>Parerenna</i>
	05. Pyrostephidae	<i>Bargmannia</i> , <i>Pyrostephos</i>
	06. Rhodaliidae	<i>Angelopsis</i> , <i>Aranciala</i> , <i>Dromalia</i> , <i>Archangelopsis</i> , <i>Steleophysema</i> , <i>Stephalia</i> , <i>Thermopalina</i> , <i>Tridensa</i>
	07. Stephanomiidae	<i>Stephanomia</i>
	08. Unascribed dioecious genus	<i>Marrus</i>
Monoecious families	09. Forskaliidae	<i>Forskalia</i>
	10. Physophoridae	<i>Physophora</i>
	11. Resomiidae	<i>Resomia</i>
	12. Agalmatidae <i>sensu stricto</i>	<i>Agalma</i> , <i>Athorybia</i> , <i>Melophysa</i>
	13. Unascribed monoecious genera	<i>Cordagalma</i> , <i>Frillagalma</i> , <i>Lychnagalma</i> , and maybe <i>Rudjakovia</i>
<b>Calycophorae</b>		
Prayomorphs	14. Prayidae	
	S-f Amphycaryoninae	<i>Amphycaryon</i> , <i>Maresearsia</i>
	S-f Prayinae	<i>Craseoa</i> , <i>Desmophyes</i> , <i>Rosacea</i> , <i>Gymnopraia</i> , <i>Lilyopsis</i> , <i>Mistoprayina</i> , <i>Praya</i> , <i>Prayola</i> , <i>Stephanophyes</i>
	S-f Nectopyramidinae	<i>Nectadamas</i> , <i>Nectopyramis</i>
Diphyomorphs	15. Hippopodiidae	<i>Hippopodius</i> , <i>Vogtia</i>
	16. Clausophyidae	<i>Chuniphyes</i> , <i>Clausophyes</i> , <i>Crystallophyes</i> , <i>Kephyes</i> , <i>Heteropyramis</i>
	17. Sphaeronectidae	<i>Sphaeronectes</i>
	18. Diphyidae	
	S-f Sulculeolariinae	<i>Sulculeolaria</i>
	S-f Diphyinae	<i>Chelophyes</i> , <i>Dimophyes</i> , <i>Diphyes</i> , <i>Eudoxoides</i> , <i>Lensia</i> , <i>Muggiaea</i>
	S-f Giliinae	<i>Gilia</i>
	19. Abylidae	
	S-f Abylinae	<i>Abyla</i> , <i>Ceratocymba</i>
	S-f Abylopsinae	<i>Abylopsis</i> , <i>Bassia</i> , <i>Enneagonum</i>

as independent buds directly on the stem (Dunn and Wagner 2006). This synapomorphy makes the cormidia into integrated units in Codonophora and may explain the huge radiation and diversity within this group, in contrast to the Cystonecta.

One hundred seventy-seven species of siphonophore are considered valid at the time of writing (WoRMS Siphonophora List), and these are shown in relation to families, higher ranks, and sexual state in Fig. 4.





**Fig. 4 Siphonophora species.** The 177 valid Siphonophora species subdivided into ranks based on Table 1 (Derived from © Gillian Mapstone 2014, Fig. 2C)

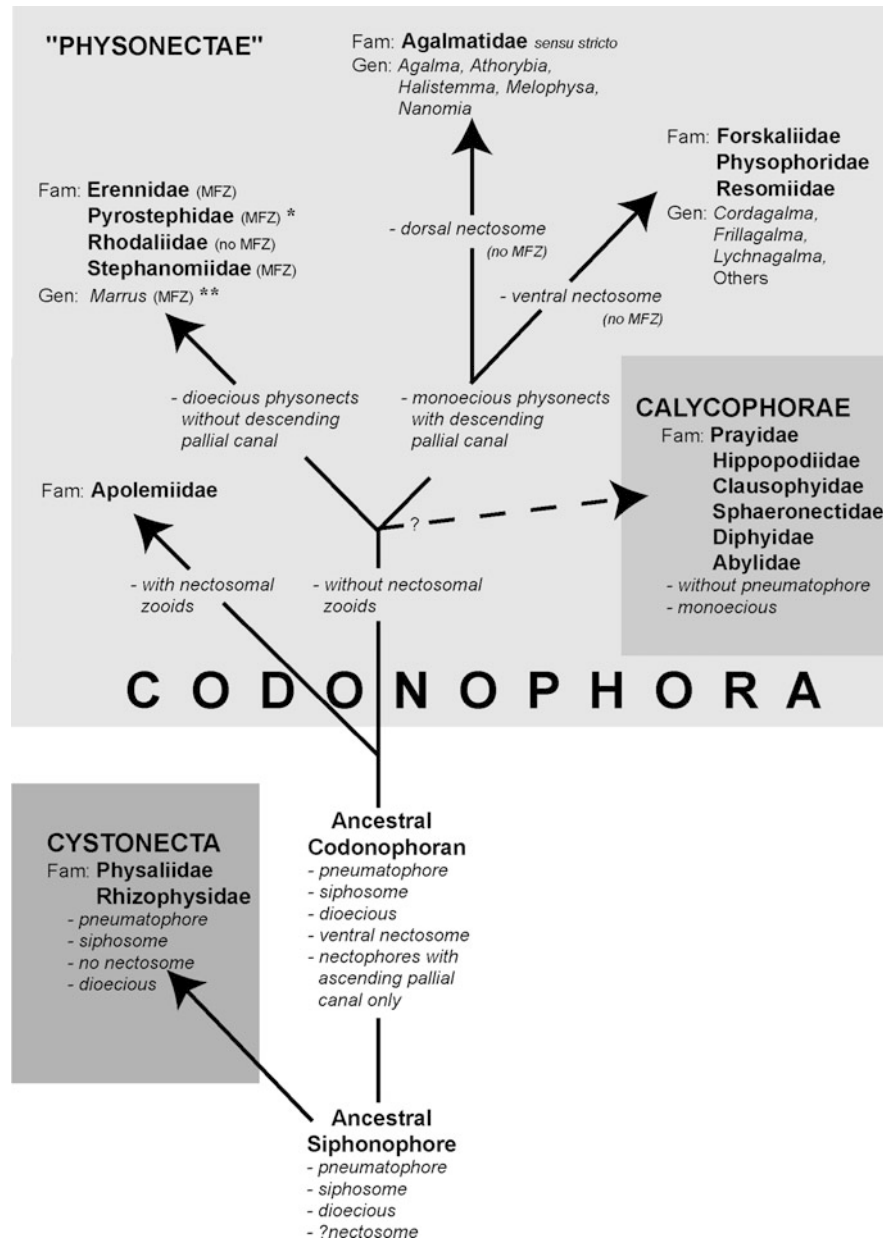
## Proposed Morphological Phylogeny of the Siphonophora

A tentative phylogeny of the Siphonophora derived from the molecular phylogeny in Fig. 3 is given in Fig. 5. It was proposed by Pugh (2006a) and is based on sexual state and several other morphological characters not previously considered important.

This phylogeny shows that particular diagnostic characters, including those discussed above, might have been important during siphonophore evolution. Other significant characters could have been the position of origin of the zooids on the siphonophore stem, the type of canals on the proximal surface of the nectophore, and the amount of musculature in the nectophore nectosac. Studies on budding (growth) zones and cormidial development in seven siphonophore taxa, together with earlier studies on three other taxa, led Dunn and Wagner (2006) to suggest several key transitions that could have occurred during siphonophore evolution. These include the appearance of a siphosome and pneumatophore in the ancestral siphonophore, the origin of the nectosome in the ancestral codonophoran, and a change from dioecy to monoecy during the evolution of the four monoecious physonect families (and three unassigned genera) and all calycophoran families (Fig. 5, and see Dunn and Wagner 2006, Fig. 7).

Dunn and Wagner (2006) also suggest that the nectosome of the ancestral codonophoran might first have appeared as a tandem duplication of the siphosome. Siphosomal zooids are taken, by convention, to arise from the ventral side of the stem (Haddock et al. 2005a), and nectosomal nectophores are also thought to have arisen from this same meridian in the first codonophorans (Fig. 5). Later during evolution, the nectosome appears to have twisted relative to the siphosome with the result that, in the family Agalmatidae *sensu stricto*, nectophores arise from the dorsal side of the stem (Fig. 5; Dunn and Wagner 2006).

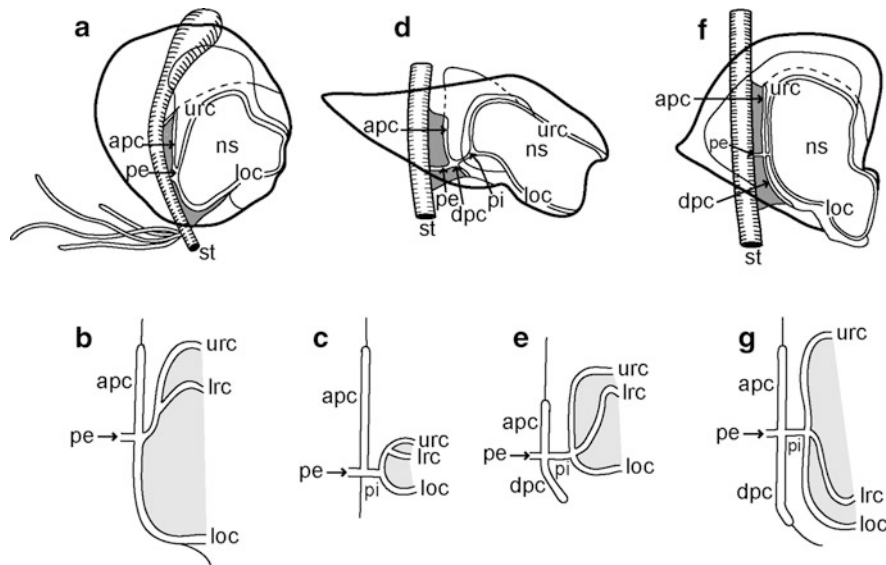
Another character of importance, which appears to have been modified during codonophoran evolution, is the type of canals present on the proximal surface of the nectophore. These canals, known either as the pallial canals (Mapstone 2014), the mantle canals (Pugh and Baxter 2014), or the ascending and descending diverticula (Mapstone 2009), are important for shedding, or self-amputation, of nectophores



**Fig. 5 Possible phylogeny of the Siphonophora** (Derived from Pugh 2006a, Fig. 21; Siebert et al. 2013; Pugh and Baxter 2014; © Mapstone 2014, Fig. 10); MFZ – muscle-free zone on nectophore; \* – dorsal nectosome and some undescribed species monoecious; \*\* – one species monoecious

and other zooids during autotomy (Mapstone 2009). Thus, they form what is sometimes termed an “autotomy joint.” Nectophores senesce (age) as they pass down the nectosome to the posterior end where they split off from the muscular lamella along the line of this canal (Fig. 6) one by one, as more nectophores are added in the nectophoral budding zone at the anterior end of the nectosome (Mapstone 2009). Nectophores may also be shed for defense, if startled by a predator, leaving loose zooids in the water to create confusion and enabling the siphonophore to retreat (Mackie et al. 1987). Only an ascending pallial canal is present in the dioecious Apolemiidae, Erennidae, Pyrostephidae, Rhodaliidae, and Stephanomiidae, whereas in monoecious physonects a second descending pallial canal is also developed (Figs. 5 and 6).





**Fig. 6 Pedicular and radial canal arrangements in nectophores of four physonect species.** All diagrams through nectophore midline. (a, b) Dioecious *Apolemia uvaria*; (c) dioecious *Bargmannia* sp.; (d, e) monoecious *Agalma elegans*; (f, g) monoecious *Nanomia bijuga*; *apc* ascending pallial canal (surface diverticulum), *dpc* descending pallial canal (surface diverticulum), *loc* lower radial canal, *lrc* lateral radial canal, *ns* nectosac, *pe* external pedicular canal, *pi* internal pedicular canal, *st* stem, *urc* upper radial canal; nectophoral muscular lamella shown in dark gray in (a, d, f); nectosac shown in pale gray in (b, c, e, g) (Derived from © Gillian Mapstone 2009, Figs. 5 and 6)

Other morphological characters of importance during siphonophore evolution are summarized in tabular form and discussed under family headings below (see Table 2).

## Cystonecta

A monophyletic clade that is sister to all other siphonophores, as noted above. Cystonects are dioecious, without a nectosome or any bracts in the siphosomal cormidia. The two families referable to this clade are Physaliidae and Rhizophysidae, and typical cystonect morphology is shown in Fig. 2a (long-stemmed cystonect) and Fig. 7 (Cystonect morphology).

The well-known and enigmatic Portuguese man-of-war cystonect, *Physalia*, is large, is pleustonic (lives at the surface) when mature, and has a much enlarged crested float (pneumatophore) propelled by the wind, but no stem (Fig. 7a). It is the only siphonophore with toxins sufficiently powerful to harm humans, although the envenomations reported worldwide in warmer waters rarely lead to death (Fenner 2000). Cormidia arise directly on the underside of the float and the long tentacles stream out to windward (Fig. 7b). Cormidia bud one from another in a series, each termed a “cormidial complex” (Fig. 7c). Indeed, *Physalia* displays the most prolific budding of any siphonophore. A mature specimen has 12 cormidial complexes arising in two groups (Fig. 7b), with, for example, one simpler complex in the oral region, giving a total of c. 13 cormidia. Most cormidia are tripartite, with a gastrozooid and gonodendron and a basigaster separated from the column of the gastrozooid to form a separate ampulla with tentacle (Fig. 7d); in the gastrozooids of all other siphonophores, the basigaster forms a thickened ring around the proximal end of this zooid itself (where nematocyst formation occurs). Most tentacles are convoluted (Fig. 7e) and supported by an extensible membrane, which allows them to contract up near to the float when not feeding. Nematocysts cover the tentacles and are particularly concentrated in the convoluted tentacles (Fig. 7f); however, these concentrations do not constitute true nematocyst batteries, which, in siphonophores, occur on the tentilla (side branches) of the tentacles of all codonophorans except the Apolemiidae (Mapstone 2009, p. 74). In *Rhizophysa*, nematocysts are variably distributed, forming a simple line along

**Table 2** Characters for cystonect and “physonect” families (Derived from © Mapstone 2014, Table 4, with Stephanomiidae added; see this paper also for additional references omitted below; see Fig. 5 for details of fundamental siphonophore characters mentioned below)

	Family	Comments
01.	Physaliidae	Monotypic for <i>Physalia physalis</i> ( <i>P. utriculus</i> considered a junior synonym, Bardi and Marques 2007)
02.	Rhizophysidae	Long-stemmed family of four valid species; <i>Bathypphysa japonica</i> a junior synonym of <i>B. conifera</i> ; SEM (scanning electron microscope) studies of budding sequences described for <i>B. sibogae</i> , <i>Rhizophysa filiformis</i> , and <i>R. eysenhardtii</i> (Dunn and Wagner 2006)
03.	Apolemiidae	Long-stemmed family; monophyletic and sister to all other Codonophora, with unique nectophoral palpons on the nectosome. Nectophores distinctive and ridgeless, cormidia dispersed or discrete (pedunculate); gastrozooids with simple tentacles (no tentilla) resembling palpacles of palpons. Monogeneric for <i>Apolemia</i> . Two new species include <i>A. lanosa</i> and <i>A. rubriversa</i> (Siebert et al. 2013) and three older species <i>A. contorta</i> , <i>A. uvaria</i> , and <i>A. vitiazi</i> ( <i>Tottonia contorta</i> sensu Mapstone 2003 now referable to <i>A. lanosa</i> ). A number of other species are known to exist (Dunn et al. 2005b; Mapstone 2003, 2009; Siebert et al. 2013) and await full description
04.	Erennidae	Long-stemmed family erected for four species with large prominent straight tentilla, no involucre, and a rigid terminal process lacking nematocysts. Two genera: <i>Erenna</i> (three species) and <i>Parerenna</i> (one species). <i>E. richardi</i> Bedot, 1904, and a new species <i>E. laciniata</i> have large flattened nectophores and large tentilla held close to the body and vibrated to attract prey; two further new species <i>E. cornuta</i> and <i>Parerenna emilyae</i> have different and also unique tentilla and gastrozooids (Pugh 2001)
05.	Pyrostephidae	Long-stemmed family of five species in two genera: <i>Bargmannia</i> (four species), <i>Pyrostephos</i> (one species). Pugh (1999a) reviewed the family, introducing two new species ( <i>B. amoena</i> , <i>B. gigas</i> ) and revising two others ( <i>B. elongata</i> , <i>B. lata</i> ); <i>Mica micula</i> shown to be putative post-larva of a pyrostephid (Grossmann et al. 2013). Nectophores with unique lower-lateral wings and much enlarged triangular thrust block; in <i>B. elongata</i> two growth zones on stem and composition of the cormidia studied using SEM (Dunn 2005); pyrostephid cormidia either have oleocysts (modified tentacle-less palpons) (in <i>Pyrostephos</i> ) or none (in <i>Bargmannia</i> ) (Pugh 1999a)
06.	Rhodaliidae	Short-stemmed family of eight genera, with four new species including <i>Archangelopsis jagoa</i> , <i>Aranciaia captonia</i> , and two in the genus <i>Tridensa</i> , including <i>T. sulawensis</i> and <i>T. rotunda</i> . Genus <i>Sagamalia</i> reduced to junior synonym of <i>Steleophysema</i> (WoRMS Siphonophora List). First in situ feeding observations on four species (Hissmann 2005). <i>Dromalia alexandri</i> redescribed (Mapstone and Ljubenkov 2013)
07.	Stephanomiidae	Disbanded family reintroduced for single large long-stemmed dioecious species <i>Stephanomia amphitridis</i> (Pugh and Baxter 2014); nectosome ventral, nectosac of mature nectophores with muscle-free zone, and other characters (Fig. 5)
08.	Unascribed dioecious genus	Long-stemmed genus <i>Marrus</i> Totton, 1954, with muscle-free zone on nectosac and other characters (Fig. 5); new species <i>M. claudanielis</i> introduced (Dunn et al. 2005a)
09.	Forskaliidae	Long-stemmed and delicate monotypic family, probably sister to the Physophoridae (Dunn et al. 2005b). Recently revised (Pugh 2003) with two new species added ( <i>Forskalia asymmetrica</i> , <i>F. saccula</i> ) and one reduced to a <i>species inquirenda</i> (WoRMS Siphonophora List)
10.	Physophoridae	Family with long nectosome but short corm-like siphosome; previously monotypic for <i>Physophora hydrostatica</i> with bract present only in larva; second species <i>P. gilmeri</i> added by Pugh (2005). Smaller, less colorful, and with bracts retained on adult colony. Tentilla of this family unique
11.	Resomiidae	Long-stemmed family newly introduced for two species previously referred to the Agalmatidae ( <i>Moseria convoluta</i> , <i>M. similis</i> ) and now transferred to a new monotypic genus <i>Resomia</i> (Pugh 2006a); two tentilla types uniquely present on each tentacle. Three new species <i>R. dunni</i> , <i>R. ornicephala</i> , and <i>R. persica</i> added by Pugh and Haddock (2010)

(continued)

**Table 2** (continued)

	Family	Comments
12.	Agalmatidae <i>sensu stricto</i>	Mostly long-stemmed and recently restricted to genera with dorsal nectosome (Fig. 5) and involucrate tricornuate or unicornuate tentilla with typically tightly coiled cnidoband which now includes two short-stemmed genera ( <i>Athorybia</i> , <i>Melophysa</i> ) (Dunn et al. 2005b), with two new species of <i>Halistemma</i> , <i>H. transliratum</i> , and <i>H. maculatum</i> introduced and four other <i>Halistemma</i> species redescribed (see Pugh and Baxter 2014 for details)
13.	Unascribed monoecious genera	Long-stemmed monotypic genera <i>Cordagalma</i> , <i>Frillagalma</i> , and <i>Lychnagalma</i> now removed from the Agalmatidae for their ventral nectosomes (Fig. 5); new species <i>C. tottoni</i> described; <i>Rudjakovia plicata</i> considered a valid species, with a dorsal nectosome but sex unknown; it may be transferred to Agalmatidae when more characters are elucidated (Pugh 2006a; Mapstone 2015)

each tentacle side branch in *R. eysenhardti* (Fig. 2a), and concentrated into small button-like clusters on the trifid tips of each tentacle side branch in *R. filiformis* (Fig. 7h, i) (Totton 1965).

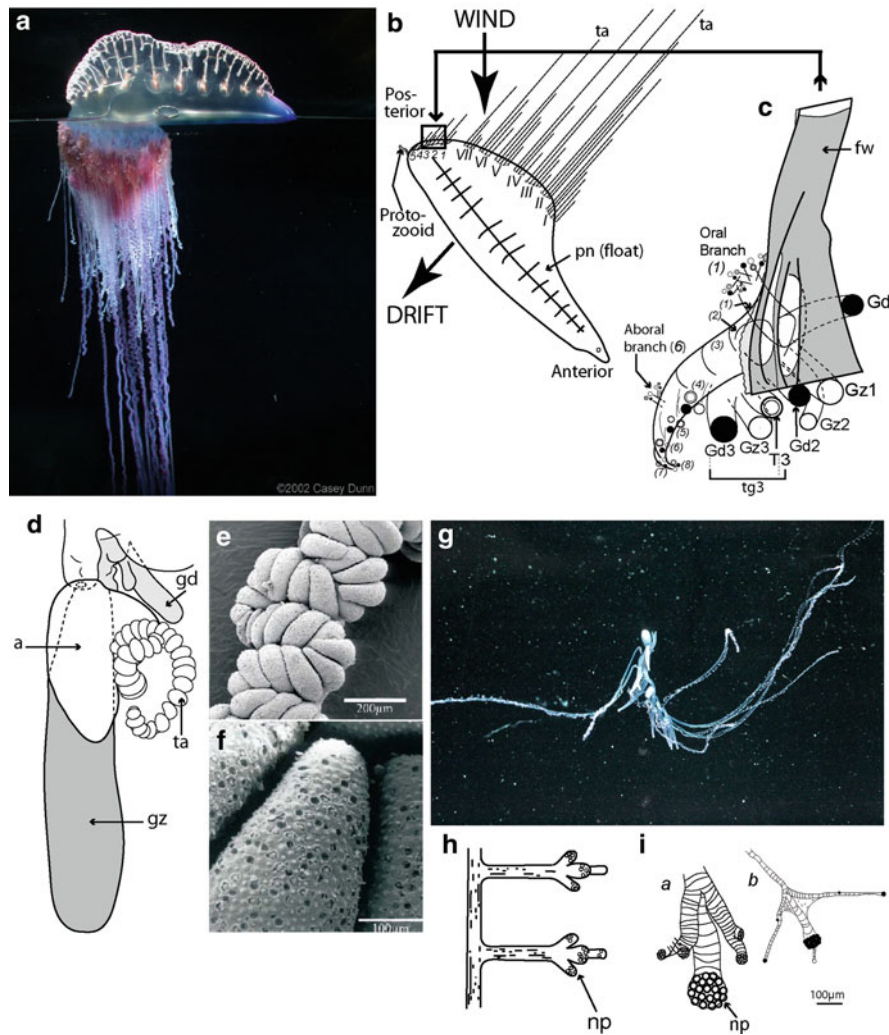
## Apolemiidae

The main characters of this family are summarized in Table 2, and the nectosomal palpons are shown in Fig. 8f. Apolemiids are unusual in growing to lengths of 30 m or more (Siebert et al. 2013), longer than any other known siphonophore (Fig. 8a, b). All zooids arise from the ventral meridian of the stem (Fig. 8c), giving apolemiids a ventral nectosome (Figs. 5 and 8c). The nectosome and cormidia are more complex than in other codonophoran families, with at least two different patterns of cormidial organization apparent in the three different *Apolemia* taxa so far investigated (Siebert et al. 2013). Dispersed cormidia occur in *A. lanosa* (Fig. 8a, b) where zooids spread out along the stem (Fig. 8d, g) as soon as the pro-bud leaves the siphosomal horn. In *A. rubriversa* (Fig. 8f) and *A. uvaria* (Fig. 8e), cormidia are pedunculate, with all zooids of one cormidium arising from the peduncle (or pedicel) of the first gastrozooid to be formed, on the siphosomal horn (Siebert et al. 2013). These fundamental features of zooid budding are concluded by Siebert et al. (2013) to be homoplastic in codonophorans.

In young specimens of *Apolemia uvaria*, pedunculate cormidia are clearly separated from others by bare lengths of stem (Fig. 8e). As growth proceeds, the naked stem portions become partially or completely obscured by prodigious budding of the pedunculate cormidia, as well shown by Siebert et al. (2013, Fig. 18c). In *A. lanosa* the siphosome becomes very long and extends a prominent curtain of “tentacles” for feeding (Fig. 8g). This curtain comprises mainly palpacles from the numerous palpon clusters on the stem, and also many fewer thin tentacles from the gastrozooids (Siebert et al. 2013). Each simple palpacle or tentacle bears a narrow band of nematocysts down one side for catching prey (Mapstone 2003, Fig. 12e, f) but no true tentilla. Stem length is further increased in *A. lanosa* during growth by interpolation of secondary gastrozooids and more palpon clusters, as shown in Fig. 8d.

## Erennidae

In this, and all remaining codonophorans, taxa are characterized by the presence of tentilla, or complex stinging batteries, on the side branches of their tentacles. For physonects, these tentilla are diagnostic, but calycophoran tentilla are rather uniform and of little or no diagnostic value. Each tentillum includes a pedicel, thickened cnidoband, and (usually) a thin extensible terminal filament. Each cnidoband is packed with rows of nematocysts, with more on the terminal filament(s) of almost all species. It is the nematocysts, or cnidae, which deliver toxins to the prey, either by penetration or entanglement, and more nematocyst types are found in siphonophores than in any other hydrozoans. Different types of

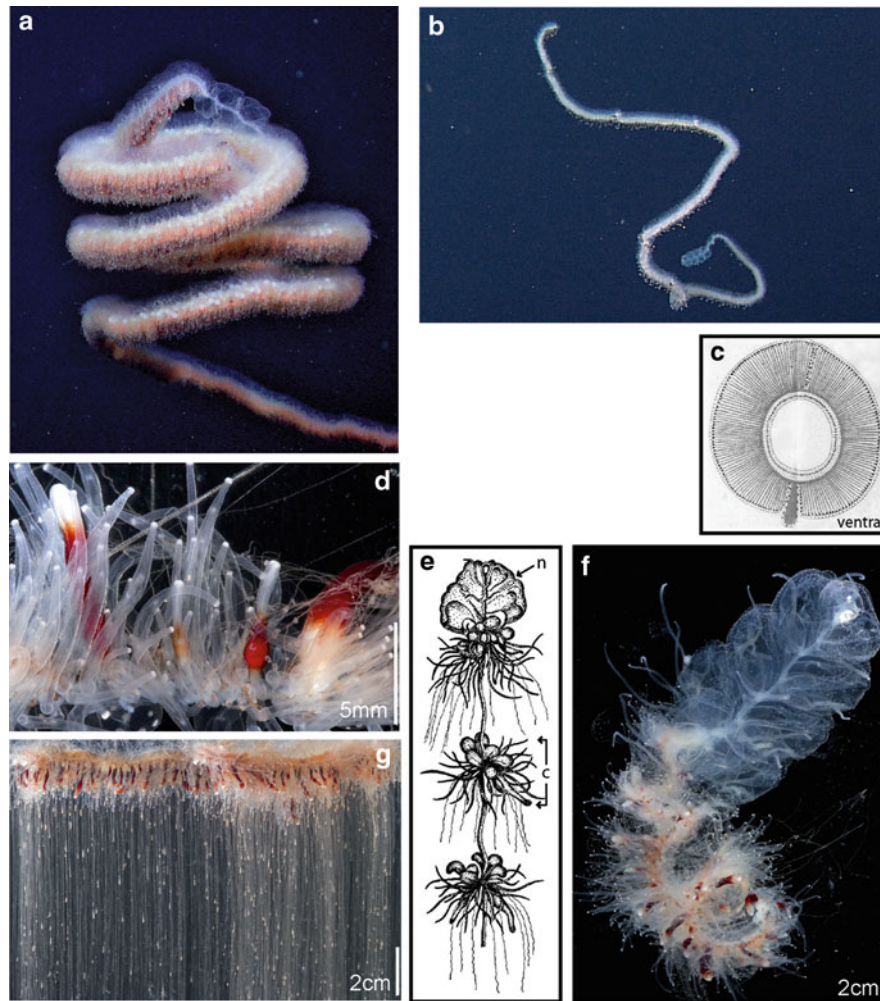


**Fig. 7 Cystonect morphology.** (a) Atypical *Physalia physalis*, pleustonic (lives at surface), with much enlarged pneumatophore, no stem, cormidia arising directly from underside of pneumatophore; (b) left-handed drifting specimen viewed from above – added numbers 1–5 identify oral cormidial groups, while numbers I–VII identify main cormidial groups – note how *Physalia*’s surface float drifts to starboard with the wind on a broad reach; (c) oral cormidial complex number 2 viewed from inside the float – note groups 3–8 are tripartite, with more tripartite groups on oral and aboral side branches – with numbers in brackets added to identify tripartite groups; (d) a developing tripartite group from main cormidial complex number VI; (e) SEM of part of contracted *Physalia* tentacle; (f) detail from (e), with darker holes marking discharged nematocysts; (g) *Rhizophysa filiformis* (see Fig. 2 legend for long-stemmed cystonect features); (h, i) *R. filiformis* trifold nematocyst pads; Labels: *a* ampulla (basigaster), *fw* float wall, *gd* gonodendron, *gz* gastrozoid, *np* nematocyst pad, *pn* pneumatophore (float), *t* tentacle, *ta* tentacle with ampulla (basigaster), *tg* tripartite group (a © Casey Dunn Brown; b–d, i © Gillian Mapstone 2014, Fig. 2 insets Aa, Ab, Fig. 7; for details of published figures and references from which drawings were derived, see relevant figure legends; e, f from Bardi and Marques 2007, with permission from Iheringia Série Zoologia; g © Larry Madin WHOI; h: Kawamura 1910, Fig. 5d)

nematocysts, their distribution across siphonophore families, and suitability for different types of prey are summarized by Mapstone (2014, Table 6).

Erennids have unique and exceptionally large tentilla, with a straight cnidoband of small haploneme nematocysts, but no larger heteroneme nematocysts (typical of other codonophorans). Also, uniquely, the thick terminal filament completely lacks nematocysts and instead, in one species at least, bears a pair of distal red lures to attract prey (Table 2, Fig. 9b). Species are dioecious, with nectophores having only an

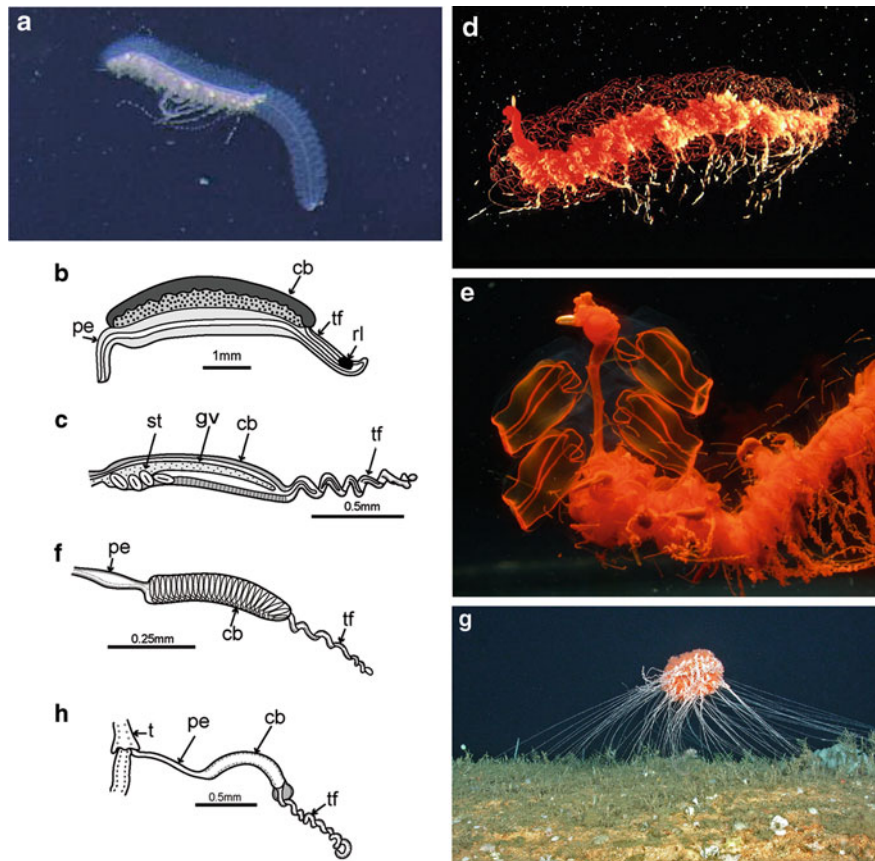




**Fig. 8 Apolemiid morphology.** (a, b, d, g) *Apolemia lanosa* from Monterey Bay, (a) whole colony, from 1,150 m (© 2005 MBARI); (b) whole colony, from 670 m (© 2011 MBARI); (c) *A. uvaria* TS through stem showing ventral zooid meridian (Korotneff 1883, pl. 14 Fig. 9); (d) *A. lanosa* detail of cormidium with two large gastrozooids (large red zooids), many longer palpons, and a secondary gastrozooid (small red zooid) (© Stefan Siebert); (e) *A. uvaria* young colony, showing pedunculate cormidia (Gegenbaur 1853, pl. 18 Fig. 1); (f) *A. lanosa* nectosome with siphosome fragment; note nectophoral palpons emerging from between the nectophores (© Stefan Siebert); (g) *A. lanosa* part of siphosome with extended “tentacle” curtain (no tentilla); note many red gastrozooids (© Stefan Siebert)

ascending pallial canal on the proximal surface (see Fig. 6c) and a muscle-free zone (MFZ) at the proximal end of the nectosac (Fig. 5). The nectosome is typically long (Fig. 9a) to very long, without any nectosomal polyps, and the nectophores typically large and flattened, often with black pigment on the radial canals and other zooids (Pugh 2001). Erennids live at great depths, in the twilight zone where prey is scarce. In the species with red lures, and probably also the other *Erenna* species (Pugh 2001), the siphosome is permanently contracted, and the tentilla always held close to the body. The lures emit red light (from bioluminescence) and together resemble a shoal of small deep-sea fish in the water. These attract deep-sea bristlemouth fish, which are of similar size and color. These fish are thought to swim into the lures, to be immediately stunned by nematocysts on the long straight cnidobands and then ingested by the gastrozooids, together with some lures (Haddock et al. 2005b).





**Fig. 9 Morphology of other dioecious physonects.** (a) *Erenna laciniata* (© JAMSTEC, <https://fbox.jamstec.go.jp/public/XMH0AAAdKtcvAt7cBnXVJOhXGd3gQe6hkGsJUttHV-1> Si; the organism in this image was identified by Dr. Dhugal Lindsay based on examination of the collected specimen); (b) *Erenna richardi* tentillum; (c) *Bargmannia elongata* tentillum; (d) *Marrus claudanielis* colony, nectophores autotomized (© Marsh Youngbluth); (e) *Marrus orthocanna*, nectosome, and first part of siphosome (© Casey Dunn); (f) *Marrus orthocanna* tentillum; (g) *Dromalia alexandri* (permissions@wiley); (h) *Tridensa sulawensis* tentillum (b, c, f, and h © Gillian Mapstone 2014, from Fig. 12). Labels: cb cnidoband, gv gastrovascular canal, pe pedicel, rl red lure, st stenotele nematocysts, t tentacle, tf terminal filament

## Pyrostephidae

Most family characters are summarized in Fig. 5 and Table 2. Additionally, pyrostephids lack palpacles (palpon tentacles), and each cormidium contains only either a single unique siphosomal tentacle (or tentaculozoid) (*Bargmannia*) or a modified palpacle-less palpon termed an oleocyst (*Pyrostephos*) (Dunn 2005; Pugh 1999a). This latter zooid contains an oil-filled vesicle which gives extra support to the heavy, vermilion red stem (Totton 1965). Tentilla are also unique in pyrostephids, with a cnidoband of mostly very small nematocysts (desmonemes and acrophores) and only a few larger stenoteles at the proximal end (Fig. 9c). An axial gastrovascular canal penetrates the length of the terminal filament and is probably used to extend the cnidoband during prey capture, since pyrostephid tentilla lack the paired elastic strands found in the tentilla of most other siphonophores (Totton 1965). Pyrostephid terminal filaments bear many small nematocysts similar to those present in the cnidoband (Mapstone 2014, Table 7).

The cormidial composition of *Bargmannia elongata* was revealed during an elegant SEM study by Dunn, who also identified two growth zones: a siphosomal horn on which pro-buds develop, with subdivision of each pro-bud into one cormidium, and a nectophoral growth zone where individual nectophores develop (Dunn 2005, Table 2). Each cormidium was found to be completely regular and also directionally asymmetric.

The distribution of *Bargmannia* species is variable and for some species difficult to assess due to problems of past misidentification (Pugh 1999a). Both *B. elongata* and *B. amoena* occur in the Atlantic, as does *B. lata* (Pugh 1999a), while in the Pacific only *B. elongata* and *B. lata* have so far been positively identified (Mapstone 2009). *Pyrostephos vanhoeffeni*, in contrast, is restricted to the southern hemisphere (Mapstone 2014, Table 1) with an extensive distribution map published recently by Lindsay et al. (2014). These authors found young specimens of *P. vanhoeffeni* concentrated close to the Antarctic coast (nectophores previously misidentified as *B. elongata*), while larger and more mature nectophores were found further north, in the open ocean. Indeed, there are records from as far north as 35°S in the Atlantic and Pacific (Lindsay et al. 2014, map 3). Despite this, the name *P. vanhoeffeni*, meaning “spiral of fire,” was originally applied to some big specimens collected not too far from the coast, near to the ice edge at 90°E. These were brightly colored, up to several meters long, and first described by Moser (1925), with more color notes being given by Totton (1965, p. 78), who pointed out that the stem, gastrozooids, and tentilla are all bright red, while the nectophores are pale pink with bright red ostia.

## Rhodaliidae

This is one of the most species-rich “physonect” families, comprising 14 species in eight genera (Fig. 4; Table 2; WoRMS Siphonophora List). Rhodaliids have undergone more speciation than long-stemmed and pelagic physonects due to their semi-benthic habit, which has led to greater geographical isolation and more restricted ranges for all species (see Mapstone 2014, Table 1, for summaries of two rhodaliid distributions and abundances: *Dromalia alexandri* and *Rhodalia miranda*). The larvae and life cycles of rhodaliids are unknown, and main diagnostic characters differ from those of pelagic physonects in that nectophores are simple and lack any surface ridges and have a nectosac that is muscular throughout and a siphosome which is coiled up into a near-spherical corm with cormidia crowded around it in whorls and growing outward rather than being spread along a long linear stem.

Important diagnostic characters for rhodaliids include shape and surface texture of the enlarged pneumatophore and its associated gas gland or aurophore, type of corm developed (thin walled, thick walled, or solid throughout), type of siphosomal cormidia present (on separate stems or several on a common stem), and type of bracts developed. In *Dromalia alexandri*, from off Southern California (Fig. 9g), the pneumatophore is turreted, the aurophore is papillate, and several siphosomal cormidia develop on common stems called cormidial units, with up to three cormidia per stem. Furthermore, growth of cormidia continues throughout life, with units circling around the corm up to eight times in total. *D. alexandri* has a unique body form, has been recently redescribed by Mapstone and Ljubenkov (2013), and its characters compared to those of six other similar genera (Mapstone and Ljubenkov 2013, Table 3).

Siphosomal cormidia of rhodaliids are either monogastric (each arising separately on an individual stem), or polygastric, with several cormidia arising from a common stem and somewhat resembling a tree. These structures are termed “cormidial units,” and mature units from the first and second whorls of *Dromalia alexandri* are illustrated by Mapstone and Ljubenkov (2013, Figs. 7 and 8). In other rhodaliids, cormidia production ceases once two whorls are formed. An important character of rhodaliids is the presence of two types of gastrozooids instead of one: type II gastrozooids each have a long tentacle bearing many tentilla for prey capture, while type I gastrozooids have either only a small tentacle or none, and lack any tentilla. When a rhodaliid attaches to the substrate, it deploys many type II tentacles in a three-dimensional array (Fig. 9g), and prey blunders into this net to be stunned and held by the tentilla. Type I gastrozooids then extend out to these tentilla, “hoover up” the prey, and digest it. Feeding has been described in three rhodaliid species by Hissmann (2005), who identified prey items from small copepods and amphipods to larger amphipods and fish larvae, which are captured by the type II gastrozooids and digested by the type I gastrozooids.

Tentilla of rhodaliids are of typical physonect structure, with a pedicel, elongate cnidoband (sometimes with a bilobed distal end; see Fig. 9h) of mostly larger and sometimes also smaller nematocysts, and an elongate terminal filament of many small nematocysts, of one or two types (where known) (Mapstone 2014, Table 7). Bracts occur in the cormidia, typically arise from elongate bracteal lamellae, and are species-specific for those species in which cormidia have been collected and studied (Mapstone and Ljubenkov 2013).

### Stephanomiidae

This family has only recently been reinstated by Pugh and Baxter (2014) for a single large species *Stephanomia amphytridis* (Table 2) first figured from the siphosome only in 1807 by Lesueur and Petit, and subsequently found with nectosomal zooids at a number of temperate and tropical locations worldwide (except the South Pacific). The name Stephanomiidae was introduced by Huxley for a second siphosome he found off the east coast of Australia in 1859, which was found again by Bigelow in the tropical east Pacific in 1911, and again by Mapstone from the Flores Sea in Indonesia in 2004, this time with the nectosome as well. All these latter specimens have since been referred to the agalmatid species *Halistemma foliacea* (see below).

*Stephanomia amphytridis* is a large and prominent species reaching up to 5 m in length, with 25 or more very large nectophores and a distinctive semirigid orange siphosome which is enclosed by many robust bracts (Pugh and Baxter 2014). The orange color in the siphosome is due to pigmented gastrovascular fluid (Dunn et al. 2005b) and not to orange pigment in the stem and zooids, as in the two *Marrus* species discussed below. *S. amphytridis* is dioecious (with separate sexes), with a ventral nectosome, a muscle-free zone on the nectosacs of mature nectophores, sinuous lateral radial canals, and only an ascending pallial canal on the proximal nectophore surface (see Fig. 5). The pattern of nectophore ridges is similar to that of *Halistemma* species, but the vertical-lateral ridges form a complex that is unique to *S. amphytridis*. The tentilla of the long tentacles also somewhat resemble those of *Halistemma* species, since the cnidoband is loosely coiled and there is only a single terminal filament; but an involucre is absent and the nematocysts also seem to be different. In the cnidoband nematocysts are all large, with thin ones filling most of the cnidoband, but unidentifiable and fatter ones, which could be stenoteles, flanking it on both sides. Similarly, two types of smaller nematocysts occur on the terminal filament, but these could not be positively identified, although it is certain that they were not the usual acrophores and desmonemes (Pugh and Baxter 2014, and see Mapstone 2014, Table 6, for summary of typical physonect nematocysts).

Amongst the material of *Stephanomia amphytridis* studied by Pugh and Baxter (2014), seven small *Nectalia* postlarvae were identified and described, each about 7–8 cm in length. Their nectophores resembled those of the mature individuals, but the siphosome was very short and had only just started to grow. It comprised a single gastrozoid (the protozoid) with its tentacle, surrounded by some distinct elongate larval bracts. The tentacle bore a number of unique larval tentilla unlike those found in any other physonect, and these contained three types of nematocysts. Species of *Halistemma* also pass through a *Nectalia* stage in their life cycle, but have quite different larval tentilla.

### Unascribed Dioecious Genus

The genus *Marrus* was assigned to this group by Pugh (2006a, Fig. 21) for the muscle-free zone on the nectosac (Fig. 5). *Marrus* is an enigmatic genus, with two well-recognized species (*M. claudanielis* and *M. orthocanna*; see Dunn et al. 2005a), one doubtful species (*M. antarcticus*; see Mapstone 2009), and a fourth which requires transfer to a different genus (*M. orthocannoides*; see discussion in Dunn et al. 2005a; Mapstone 2009). Two recently studied species are striking *in vivo*. *M. claudanielis* (Fig. 9d) was introduced and described by Dunn et al. (2005a); it has a stiff stem which never relaxes (similar to *Agalma okeni*, see below) and a thick red zooid-covered siphosome that spirals around to the

posterior end and is surrounded by a characteristic “halo” of transparent bracts (Fig. 9d). The appearance of *M. orthocanna* is similar (Fig. 9e). *Marrus* species are very fragile and often autotomize their zooids when illuminated or otherwise disturbed. The colony in Fig. 9d has already lost its nectophores, but in the small *M. orthocanna* colony shown in Fig. 9e, the nectophores are still intact. Other images of *M. orthocanna* taken under the Arctic ice (see Mapstone 2009, frontispiece A-B) show a larger individual with at least 12 nectophores, and up to 37 nectophores or more have been recorded in other specimens (Andersen 1981).

Nectophores of *Marrus* species are ridged, with straight red pigmented radial canals and a pair of red-yellow chromatophores on each side of the ostium (possibly for disruptive coloration). The nectosac has a large muscular-free zone, and there is only an ascending pallial canal (surface diverticulum) on the proximal nectophore surface. Nectophore ridges are of diagnostic importance in many physonect species, and in *Marrus* upper-lateral ridges divide distally in *M. orthocanna*, but not in *M. claudanielis* (Dunn et al. 2005a). Circa 30 mature gastrozooids have been found in the largest *Marrus* colonies studied, and the tentilla on their tentacles are either straight (Fig. 9f) or only loosely coiled. Gonodendra are also numerous on the siphosome and include equal numbers of male and female gonophores in *M. orthocanna* (Andersen 1981), which is monoecious, but gonophores of only one sex in *M. claudanielis*, which is dioecious (Dunn et al. 2005a). Bracts are large and kite-shaped in both species, with a prominent orange band of nematocysts and associated ectodermal cells on the upper surface. In *M. orthocanna*, this band is relatively short and straight (Fig. 9e), while in *M. claudanielis* it is longer and arc-shaped (Fig. 9d); this character is particularly useful for separating the two species *in vivo*.

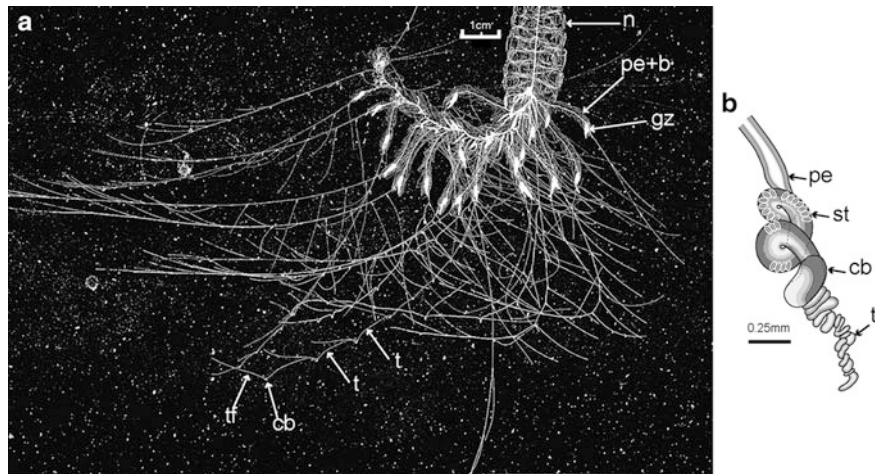
## Forskaliidae

This is the first monoecious physonect family listed in Tables 1 and 2 and has a ventral nectosome and a descending pallial canal (descending surface diverticulum) on the proximal nectophore surface (Fig. 5). It is monotypic for *Forskalia* and includes six valid species (WoRMS Siphonophora List). The “pallial canals” are shorter than those shown in Fig. 6d (see Totton 1965, Figs. 57 and 58b) and the internal pedicular canal (pi) much longer (see Pugh 2003, Figs. 2, 9, 17, 25, 34, and 40), because nectophores are particularly flattened along the upper-lower axis and extended along the proximal-distal axis (see Mapstone 2009, Fig. 1b for axes).

Forskaliids are fragile animals and distributed around the globe chiefly in the warmer waters of tropical and warm-temperate latitudes. SCUBA divers have frequently observed them in the Mediterranean and western Atlantic, although forskaliids have also been collected by manned submersibles in the Alboran Sea (western Mediterranean) and the Bahamas (Pugh 2003). Observations on colonies show them to be mostly snake-like and elongate, with the siphosome longer and broader than the nectosome (see WoRMS Siphonophora List image of *Forskalia edwardsi*), although in some *Forskalia* species (Fig. 10a), the siphosome appears to be short (*F. tholoides*, *F. asymmetrica*; Pugh 2003). One species, *F. formosa* has been observed in the Mediterranean swimming powerfully and simultaneously rotating anticlockwise (Pugh 2003). However, in general, *Forskalia* species swim more slowly than most other physonects, because of their long and broad siphosome, and have a small pneumatophore for greater maneuverability (Biggs 1977). The specimen in Fig. 10a is relaxed for feeding, with the nectosome uppermost, although other forskaliids have been observed hanging vertically in the water with the siphosome uppermost (Biggs 1977).

The family review of Pugh (2003) noted that *Forskalia edwardsi* could easily be distinguished from *F. contorta* in the field by the presence of a small distinctive sulfur-yellow spot at the junction of the upper radial canal and the ostial ring canal. Both species have been collected in the Mediterranean and western North Atlantic, and also from the Indian Ocean and Far Eastern seas (Pugh 2003). Another less common species from off India, which is also present in the Gulf of California and the North Atlantic (although not the Mediterranean), is *F. tholoides*, with a distinctive bell-shaped (or fir cone-like) nectosome of





**Fig. 10 Morphology of monoecious physonecetes 1. Forskaliidae.** (a) *Forskalia* sp. (© Inter-Research, revised from Luo et al. 2014); (b) *Forskalia edwardsi* tentillum (© Gillian Mapstone 2014, Fig. 12H). Labels: *cb* cnidoband, *gz* gastrozoid, *n* nectophores, *pe* pedicel of gastrozoid, *pe + b* gastrozoid pedicel with bracts, *st* stenotele nematocysts in the cnidoband, *t* tentacle, *tf* terminal filament

nectophores that lack axial wings; this species was introduced in 1888 by Haeckel ([WoRMS Siphonophora List](#)). A fourth species is *F. formosa* of which 20 specimens have been collected in the western Mediterranean and two in the Bahamas (Pugh 2003). *F. asymmetrica*, a fifth species, is of similar abundance with 15 specimens known so far from the western Mediterranean, Bahamas, and canyons off Woods Hole in the NW Atlantic (see [WoRMS Siphonophora List](#)); the mean depth for this species is 598 m. The final forskaliid species, *F. saccula*, is known only from one young specimen collected close to the surface in the Sargasso Sea and introduced by Pugh (2003).

In forskaliids, gastrozooids are held away from the siphosomal stem on long pedicels, and the tentacles dangle down outside this cylinder as shown by Pugh (2003, Fig. 16). Bracts occur on both the gastrozoid pedicels and the stem (Fig. 10a, Biggs 1977), and those on the pedicels provide buoyancy for the heavy gastrozooids. Four types of bracts have been found in most species: three types on the gastrozoid pedicels and a fourth on the stem; these are illustrated and described by Pugh (2003) for all six forskaliid species. Also on the stem are gonodendra, comprising gonophores of both sexes (monoecious – sexes maturing at different times), and gonopalpons, which can be species-specific (Pugh 2003).

The tentacles of forskaliids have regularly spaced tentilla, typically 15 per tentacle spaced 5 mm apart (Fig. 10a, Biggs 1977). Each tentillum (Fig. 10b) has a short pedicel, as seen in Fig. 10a, no involucre, and a loosely coiled orange-red cnidoband composed mainly of homotrichous anisorhizas with some larger lateral stenoteles (Mapstone 2014, Table 7). Beyond the cnidoband, a very long terminal filament extends for feeding (Fig. 10a), and each such filament bears a repeating pattern of small nematocysts including a pair of desmonemes, two pairs of acrophores, a pair of desmonemes, and so on (Mapstone 2014, Table 6). Forskaliids are known to sting fishermen and SCUBA divers badly when contact is made with the tentacles. Copepods are the main prey, together with various other small planktonic organisms (Purcell 1983).

## Physophoridae

This family is monoecious, with a ventral nectosome, a siphosome reduced to a corm, and unique encapsulated tentilla which may be jiggled like small copepods to act as lures. It is monogeneric for the genus *Physophora* and includes two species, *P. hydrostatica* and *P. gilmeri*. *P. hydrostatica* is ubiquitous with a truly cosmopolitan distribution (Mapstone 2014, Table 1), while *P. gilmeri* is rare (Table 2) and



known so far only from nine specimens around the Bahamas (Pugh 2005) and one off Japan (Lindsay and Miyake 2009).

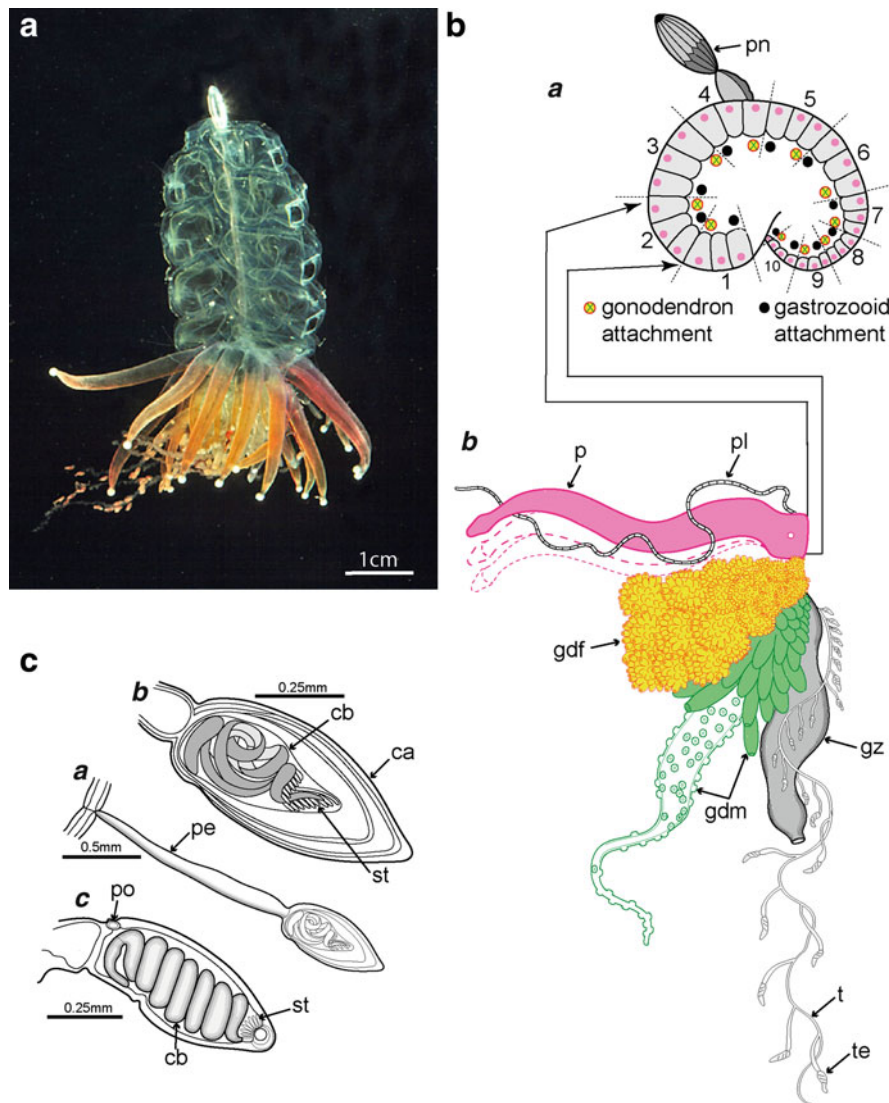
The nectosome is typical of long-stemmed physonects and bears up to 12 nectophores arranged in two rows (although all originate from a single ventral meridian). A ring of up to 36 prominent palpons fringes the outer edge of the spherical corm below, each terminating in an ampulla of large microbasic mastigophore nematocysts, which can inflict a painful sting. The ampulla of each palpon is white in *P. hydrostatica* (Fig. 11a) and orange in *P. gilmeri*. Each mature cormidium comprises three palpons, one smaller gastrozoid with tentacle, and a reproductive body on a single stalk which subdivides immediately into a male gonodendron branch and a female gonodendron branch (Fig. 11bb). In addition, the cormidia of *P. gilmeri* each contain one or more bracts of two types (Pugh 2005). In *P. hydrostatica*, a single bract develops only in the larva, for buoyancy until some large palpons develop, when the bract is lost (Totton 1965). In *P. gilmeri* buoyancy provided by the palpons is apparently supplemented in mature colonies by the large bracts; whether a single larval bract is produced in the larva of this species is unknown.

The tentilla of physophorids differ from those of all other codonophorans in being enclosed within a capsule on a long pedicel, and lacking any terminal filament. The cnidoband is up to 5 mm long, of many small anisorhizas flanked by a few larger microbasic mastigophores (Mapstone 2014, Table 7); it inverts during growth and then unwinds into a chaotic spiral and discharges through a pore near the proximal end of the capsule (Fig. 11c).

## Resomiidae

This small family, introduced in 2006 and summarized in Table 2, includes five long-stemmed species which are very fragile, have a rigid stem, and are transparent except for buttons or arcs of nematocysts at the tips of the bracts, faintly tinted gastrozooids, and palpons (Pugh and Haddock 2010). They also have remarkable tentilla which transform during growth from a spirally coiled form into a (typically) zigzag form. This has been studied in detail in all species, and the process somewhat resembles cnidoband rearrangement in the capsulate tentilla of species in the physonect genus *Physophora*, although the latter differs in having a shortened swollen siphosome and no terminal filament on the tentilla, as described above. In *Resomia*, after coiling, a transparent involucre typically grows over the entire cnidoband and extends on to form a distal tube into which the terminal filament is withdrawn when not feeding. Once covered, the cnidoband uncoils and rearranges itself into three zags, with the double elastic band (employed during tentillum activation) connecting only the proximal and distal ends of the cnidoband (see Pugh 2006a, Figs. 11 and 18). One exception to this growth pattern is *R. ornicephala* in which the involucre grows out to float above the cnidoband instead of enclose it, and is pigmented. The pigment fluoresces under violet and blue excitation making the involucre resemble a bird's beak, with a central green strip flanked by two pairs of yellow spots (Pugh and Haddock 2010). In the field the long tentacles are repeatedly relaxed and tugged up through the water in a jiggling movement. *R. ornicephala* inhabits a restricted depth range 164–298 m in Monterey Bay and must compete with the more abundant small physonect *Nanomia bijuga* for food. In the dim downwelling light at this depth, the lure of *R. ornicephala* may either fluoresce to attract krill prey or resemble a shoal of krill in outline when all the tentacles are extended (Pugh and Haddock 2010).

Few resomiids have been collected worldwide, with two species found only in the Southern Ocean and the remainder in warmer oceanic waters, mainly the NE Pacific, either off or within Monterey Bay, in the Gulf of California, or in the Tongue of the Ocean region of the Bahamas in the Atlantic. Although a lure has been postulated for attracting prey in *Resomia ornicephala*, the type of prey captured by other resomiids is unknown. Prey must be immediately stunned by the formidable battery of nematocysts on the long and folded cnidoband (Mapstone 2014, Tables 6 and 7), using the method described for other



**Fig. 11 Morphology of monoecious physonecids 2. Physophoridae.** (a) *Physophora hydrostatica* (© Larry Madin WHOI); (ba) diagram of posterior surface of corm bearing ten cormidia; (bb), one cormidium exploded; (c) tentilla, a whole tentillum, with long pedicel; b mature tentillum capsule with cnidoband reversed, uncoiled chaotically and ready for discharge; c less mature capsule with cnidoband already reversed but still spirally coiled (© Gillian Mapstone 2014, Fig. 6Ba, b; Fig. 12Fa–c; see these figure legends for references from which drawings were derived). Labels: ca capsule, cb cnidoband, gz gastrozoid, gdf female gonodendron, gdm male gonodendron, p palpon, pe pedicel, pl palpacle, po pore, pn pneumatophore, st stenotele nematocysts, t tentacle, te tentillum

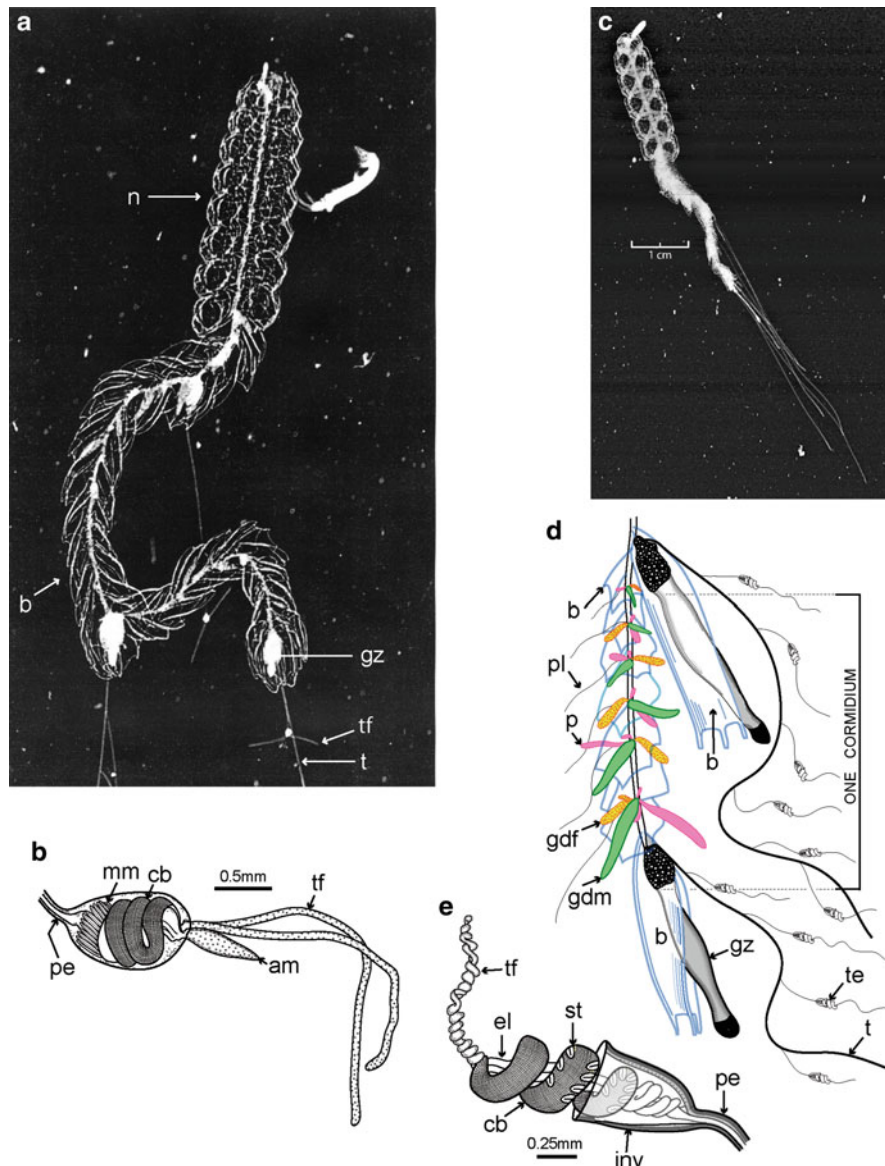
physonecids by Mapstone (2014). So far, feeding in situ has not been observed in any resomiid, and, indeed, in one species, *R. dunni*, only a single well-developed gastrozoid is present on the siphosome.

### Agalmatidae Sensu Stricto

This most species-rich pelagic family of all physonecids (Fig. 4) was shown to be a distinct monophyletic clade by Dunn et al. (2005b, Fig. 3) and was delimited by Pugh (2006a) to five genera only. Diagnostic features of the family are listed in Table 2, with the most distinctive being the twisting of the nectosome relative to the siphosome resulting in nectophores arising from the dorsal side of the stem and siphosomal cormidia from the ventral side. This is well illustrated in *Halistemma foliacea* by Pugh and Baxter (2014, Fig. 60). The small species *Nanomia bijuga* is the most common physonect worldwide (Fig. 12c) between

55°N and 59°S, with numerous records from all oceans except the North Atlantic (Mapstone 2014, Table 1). The arrangement of zooids in one cormidium is shown in Fig. 12d, and detailed zooid composition of the cormidia is given by Dunn and Wagner (2006). The tentillum comprises a red cnidoband of circa three coils, with an involucre covering the first coil, and a single distal terminal filament (Fig. 12e).

*Nanomia bijuga* feeds on a range of small prey, including copepods, decapod larvae, and, in Monterey Bay in particular, various young stages of krill (Pugh and Haddock 2010). As the physonect remains motionless in the water with its tentacles extended for feeding, prey becomes entangled in the long dangling terminal filament; its movements cause discharge of the cnidoband, which unwinds and slaps



**Fig. 12 Morphology of monoecious physonects 3. Two common species of the family Agalmatidae *sensu stricto*.** (a) *Agalma elegans* (© Jessica Luo/Cowen Lab); (b) *A. elegans* tentillum (© Mapstone 2014, Fig. 13Aa); (c) *Nanomia bijuga* (© Inter-Research, revised from Luo et al. 2014); (d) *N. bijuga* cormidium; (e) *N. bijuga* tentillum (© Gillian Mapstone 2014, Figs. 6A, 13C). Labels: *am* ampulla, *b* bract, *cb* cnidoband, *el* elastic band, *gdf* female gonodendron, *gdm* male gonodendron, *gz* gastrozooid, *inv* involucre, *mm* microbasic mastigophore, *n* nectophore, *pe* pedicel, *p* palpon, *pl* palpacle, *st* stenotele, *t* tentacle, *te* tentillum, *tf* terminal filament



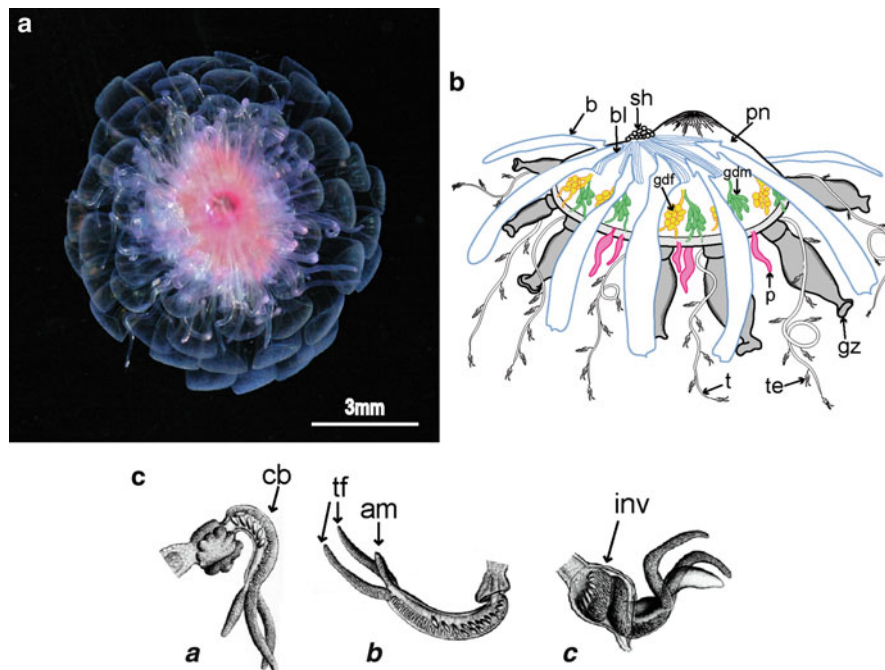
onto the prey, stunning it instantly, as described in Mapstone (2014, Fig. 15a–c). Recently, the juvenile squid *Chiroteuthis calyx* has been found to mimic *Nanomia bijuga* in Monterey Bay, where it avoids predators by hanging vertically among *N. bijuga*, a species shunned by predators because of its stinging batteries (the tentilla) and low food value (Burford et al. 2014).

Other well-known but less abundant species in the family Agalmatidae *sensu stricto* include *Agalma elegans*, *A. okeni*, and *Halistemma rubrum*. In the past, loose nectophores of *A. elegans* have sometimes been difficult to distinguish from those of *H. rubrum*, but a recent and comprehensive review of the genus *Halistemma* by Pugh and Baxter (2014) has resolved this problem. *Halistemma* nectophores are more truncate than those of *Agalma* species when mature, with much shorter more truncate axial wings separated by a prominent thrust block (see Pugh and Baxter 2014, Fig. 115). *H. rubrum* nectophores display a distinctive pattern of incomplete ridges on the upper surface, whereas all those of *A. elegans* are complete (see Mapstone 2009, Fig. 19a). Pugh and Baxter (2014) also introduce a new species *H. maculatum* and redescribe *H. rubrum*, *H. cupulifera*, *H. striata*, *H. foliacea*, and *H. transliratum* from complete specimens, most collected in exceptionally good condition by submersible vehicles. Ridge patterns are clarified in both young and mature nectophores, bract types described (from two to five in this genus), and tentilla compared and contrasted. The cnidoband of *Halistemma* species is long (sometimes up to nine coils), with a very small cup or disk-shaped involucre proximally and a single terminal filament distally; the latter often, but not always, terminates in a swollen acorn-shaped sinker. *Halistemma* tentilla are figured for all species by Pugh and Baxter (2014) and that of *H. transliratum* also shown by Mapstone (2014, Fig. 13b).

Species in the long-stemmed genera *Agalma* and *Nanomia* have yet to be described from submersible material, if indeed it exists, although both are well-known genera. They have differently shaped nectophores, one or two transparent bract types on the siphosome, and distinctively different tentilla (Fig. 12b, e). Their cnidobands tend to be shorter than those of *Halistemma* species and are red and in *Agalma* species completely covered in a transparent sac known as the involucre (Fig. 12b), although in one rarer species (*Agalma clausi*) the involucre is open distally and the bracts apparently bear distinctive red spots. *Agalma elegans* (Fig. 12a) is a soft and flexible species, uncommon but cosmopolitan in temperate and tropical latitudes (Mapstone 2014, Table 1). *A. okeni*, in contrast, is rigid, with a short stem bearing prismatic nectophores and bracts, and is quite often collected in warmer waters worldwide (Pugh 1999b).

Two short-stemmed genera *Athorybia* and *Melophysa* are in the Agalmatidae *sensu stricto* family (see Fig. 5 and Table 2) because *Athorybia rosacea* is sister to the three species in the genus *Agalma* (Fig. 3). *Athorybia rosacea* is a small species without any nectophores, which resembles a floating flower (Fig. 13a) and comprises a large pink pneumatophore surrounded by several whorls of large bracts arising from a much reduced corm-like siphosome (Fig. 13b). Gastrozooids each bear a tentacle with tentilla, which hangs down from the lower side of the corm for feeding, and in *A. rosacea* the tentilla are of two types: dendritic, without an involucre and with dendritic growths (Fig. 13ca), and involucre, with a complete involucre when mature (Fig. 13cc) and a barely developed one when young (Fig. 13cb). Some dendritic tentilla also have a large protruding spur, which may act as a lure (Mapstone 2014, Fig. 16b). *Melophysa melo* (WoRMS Siphonophora List) differs from *A. rosacea* in having a short nectosoma bearing up to four functional nectophores, but has similar tricornuate tentilla (with a terminal ampulla and two lateral terminal filaments) and a coiled cnidoband partly covered by an involucre (Daniel 1985).

Totton (1965) concluded that *Athorybia rosacea* represents a young *Nanomia* or *Agalma* individual lying on its side, and this is because species of these two genera go through an *Athorybia* post-larval stage during their early development. Totton (1965) shows this stage in his Fig. 19 for *A. elegans*. The larva has a ring of larval bracts around the pneumatophore (but no nectophores) and a larval tentacle with a number of simple and different larval tentilla (shown for *Agalma elegans* in Mapstone 2014, Fig. 13Ab). In



**Fig. 13 Morphology of monoecious physonec 4: *Athorybia rosacea*.** (a) Live individual floating in the sea, from above (© Larry Madin WHOI); (b) lateral view of float with siphosomal horn (where the cormidia are formed) and attached cormidia (© Gillian Mapstone 2014, Fig. 6D; see figure legend for reference from which the drawing derived); (c) a, b dendritic tentilla and c involucrate tentillum (Bigelow 1911, pl. 20, Figs. 8, 9, and 10). Labels: am ampulla, b bract, bl bracteal lamella, cb cnidoband, gdf female gonodendron, gdm male gonodendron, gz gastrozoid, inv involucrum, p palpon, pn pneumatophore, sh siphosomal horn, t tentacle, te tentillum, tf terminal filament

*Halistemma* species, Pugh and Baxter (2014) have found a different developmental stage known as a *Nectalia* post-larva. This comprises a few nectophores and a ring of long larval bracts, with a larval tentacle bearing another type of larval tentillum, and has been shown so far for *H. rubrum* and *H. maculatum* (see Pugh and Baxter 2014, Figs. 23–25, 89, and 92), although is probably also found in the other *Halistemma* species. In addition, another *Nectalia* post-larva occurs in the dioecious physonec *Stephanomia amphitridis*, but in this species the larval tentilla are very different (see Pugh and Baxter 2014, Figs. 108, 111, and 112–113).

### Unassigned Monoecious Genera

Three genera with ventral nectosomes are now excluded from the Agalmatidae *sensu stricto* and are listed in Fig. 5 and Table 3. Each is summarized briefly below from information given by Mapstone (2009, 2014) and references quoted therein. *Cordagalma ordinata* is a flexible species up to 30 cm long with a maximum of 40 diminutive heart-shaped nectophores, distinctive kite-shaped bracts, palpons without palpules, and unique larval-type tentilla on the gastrozoid tentacles which are very small and lack a cnidoband (Mapstone 2014, Fig. 13d). *C. ordinata* feeds only on small copepods (Purcell 1980), which are trapped in an array of long cnidocils that project from the distal surface of the tentillum. The species inhabits all oceans and can sometimes be abundant in deep coastal fjords. It has been collected by submersible in the Alboran Sea in the western Mediterranean and studied in detail at Villefranche Marine Station. These and other worldwide records are summarized in Mapstone (2009).

*Frillagalma vityazi* is a small physonec with larger nectophores than those of *Cordagalma ordinata*, but a shorter and rigid siphosome. Nectophores bear pairs of ridges similar to those found in other physonecs (including a single pair of vertical-lateral ridges), a nectosac with simple looped lateral radial



**Table 3** Characters for calycophoran families (Derived from © Mapstone 2014, Table 5; see this paper also for additional references omitted below; see Fig. 5 for details of fundamental siphonophore characters mentioned below)

	Family	Comments
14.	Prayidae	Probably paraphyletic and includes nested family Hippopodiidae (Dunn et al. 2005b) (see below); <i>Praya dubia</i> (subfamily Prayinae) and subfamily Nectopyramidinae may be one lineage, with prayines <i>Craseoa</i> , <i>Gymnopraia</i> , and <i>Rosacea</i> another (Dunn et al. 2005b), but broader taxa sampling is needed (Mapstone 2009). Prayine name <i>Lilyopsis medusa</i> has precedence over <i>Lilyopsis rosea</i> (WoRMS Siphonophora List); new prayine species <i>Desmophyes haematogaster</i> , <i>Gymnopraia lapislazula</i> , <i>Lilyopsis fluoracantha</i> , <i>Rosacea repanda</i> , <i>R. limbata</i> , and <i>R. arabiana</i> introduced (see WoRMS Siphonophora List); subfamily Nectopyramidinae revised with <i>Nectopyramis thetis</i> and <i>N. natans</i> redescribed and new genus <i>Nectadamas</i> introduced (for <i>N. diomedae</i> and a new species <i>N. richardi</i> ). Prayine species <i>R. cymbiformis</i> also redescribed and nomenclature problems concerning <i>R. plicata</i> sensu Bigelow and <i>Desmophyes annectens</i> resolved. Eudoxids released in amphicaryonines and nectopyramidines, but not in prayines (Mapstone 2009). <i>Rosacea villafrancae</i> transferred to genus <i>Desmophyes</i> and <i>Prayoides intermedia</i> found to be a junior synonym of <i>Praya</i> species (Pugh 1992, WoRMS Siphonophora List). Unique bio-optical properties identified in <i>G. lapislazula</i> and <i>L. fluoracantha</i> , though their function is still unknown (Haddock et al. 2005a)
15.	Hippopodiidae	Found nested within prayines in first siphonophore phylogeny and <i>Hippopodius</i> nested within <i>Vogtia</i> (Dunn et al. 2005b); hippopodiid distribution correlated with feeding on various species of ostracods, unlike other calycophorans. Family characters recently summarized and the new axes applied, together with redescrptions given and synonymies listed for <i>V. serrata</i> , <i>V. spinosa</i> , and <i>V. pentacantha</i> (Mapstone 2009); <i>V. microsticella</i> considered a junior synonym of <i>V. glabra</i> and <i>V. kuruae</i> a junior synonym of <i>V. serrata</i> (WoRMS Siphonophora List; Mapstone 2009)
16.	Clausophyidae	The three diphyomorph families below may have arisen from this one (Dunn et al. 2005b). New species include <i>Clausophyes laetmata</i> and <i>Cl. tropica</i> , and two others redescribed include <i>Cl. galeata</i> and <i>Cl. moserae</i> ; a unique fuseudoxid life stage found in <i>Crystallophyes amygdalina</i> and a new genus <i>Kephyes</i> introduced for Moser's <i>Cl. ovata</i> , which, unlike <i>Clausophyes</i> species, has bracts with a pair of hydroecial canals (Pugh 2006b). Four clausophyids redescribed from NE Pacific and new axes applied (Mapstone 2009)
17.	Sphaeronectidae	Ten species now considered valid in this family with single retained larval nectophore. Family reviewed and history summarized (Pugh 2009); five new species introduced: <i>Sphaeronectes christiansonae</i> , <i>S. haddocki</i> , <i>S. tiburonae</i> (Pugh 2009), <i>S. pagesi</i> , and <i>S. pughi</i> . An old species <i>S. brevithecata</i> reinstated (Pugh 2009) and <i>S. bougisi</i> concluded to be a likely calyconula of <i>Lilyopsis medusa</i> (WoRMS Siphonophora List). <i>S. gracilis</i> relegated to a junior synonym of <i>S. koellikeri</i> and probably restricted to the tropics (Pugh 2009; WoRMS Siphonophora List); specimens reported from Jervis Inlet, British Columbia (Mapstone 2009), could be <i>S. haddocki</i>
18.	Diphyidae	Probably paraphyletic (Dunn et al. 2005b), vindicating earlier conclusions (Totton 1965), but based on only 5 of 45 likely valid species (WoRMS Siphonophora List). Two main clades identified in the molecular study, within one of which is nested the family Abylidae (Dunn et al. 2005b). New axes applied to all life stages of diphyids; muscular lamellae, median gastrovascular canals, and pedicular canal arrangements also schematically shown for two basic types of diphyids (Mapstone 2009). A new small species added to the genus <i>Lensia</i> ( <i>L. quadriculata</i> ), another redescribed in detail ( <i>L. asymmetrica</i> ), and a third ( <i>L. reticulata</i> ) transferred to a new genus <i>Gilia</i> within a new subfamily Giliinae, for the two clausophyid-like canals in the bract. An enigmatic species <i>Eudoxia macra</i> shown, using the mitochondrial 16S gene, to be sexual stage of a larger species <i>L. cossack</i> . A number of previously described <i>Lensia</i> species, several <i>Sulculeolaria</i> species, and one <i>Muggiaea</i> species all reduced to junior synonyms of various better known species (WoRMS Siphonophora List)
19.	Abylidae	Family nested with <i>Diphyes dispar</i> in one of two Diphyidae clades, based on 16S and 18S (Dunn et al. 2005b), but only <i>Abylopsis tetragona</i> tested and more taxa sampling needed. Ten valid species (WoRMS Siphonophora List), all present in the South Atlantic and summarized by Pugh (1999b); several species also redescribed from around South Africa. Junior synonyms (including those in a confusing abyloid review by Sears) given in the WoRMS Siphonophora List

canals and bioluminescent patches on the nectophore surface. Bracts are faceted and of three types, with three pairs per cormidium and, as in *C. ordinata*, the palpons lack palpacles and the tentilla are distinctive and diagnostic. Each tentillum comprises a very small proximal cnidosac with c. 33 nematocysts of two types, from which project two elongate and sausage-shaped sequential ampullae (Mapstone 2014, Fig. 13e). *F. vityazi* is a rare species worldwide (distribution summarized in Mapstone 2009) and has been collected with submersibles in the Bahamas, but prey consumed is so far unknown.

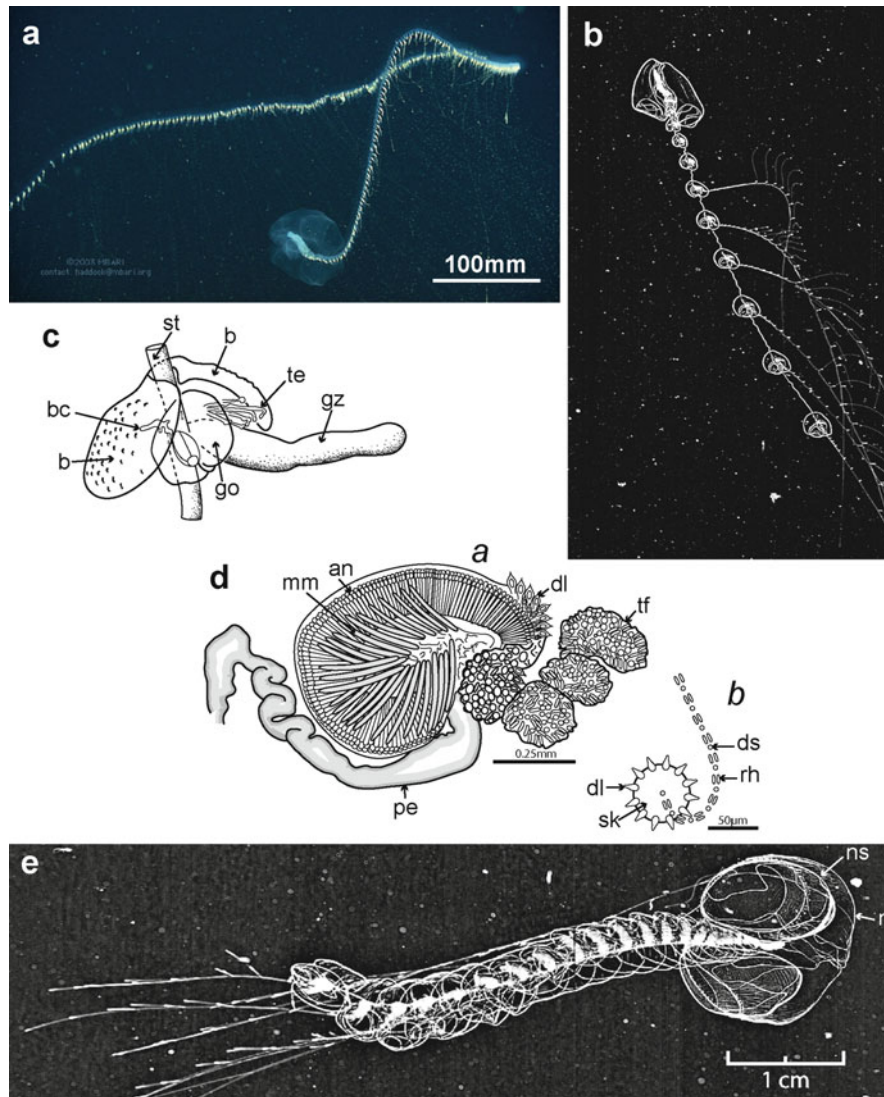
The third monotypic species in this group is *Lychnagalma utricularia*. It is very fragile and transparent and has only rarely been collected worldwide (WoRMS Siphonophora List), with most specimens coming again from submersible dives in the Bahamas region (Pugh and Harbison 1986). *L. utricularia* shares certain characters with Agalmatidae *sensu stricto* species, including nectophores with paired ridges and the tentilla which are involucrate with a long coiled cnidoband, but differs in having a ventral nectosome. Unusually for a physonect, it is completely non-bioluminescent, and the mature tentillum is also exceptionally large, reaching up to 7.5 mm in length (see Mapstone 2014, Fig. 16c), with a large central ampulla and eight terminal filaments. These pulsate like a swimming medusa and form an intriguing lure which may perhaps attract small fish, although so far no prey has been found in any of the gastrozooids collected from *L. utricularia*.

## Family Prayidae

The Calyophorae is a monophyletic clade (Fig. 3) which is monoecious, has lost the pneumatophore (Fig. 5), and retained reduced larval cormidia (Dunn and Wagner 2006). Species in the six calyophoran families (Table 3) have only two nectophores (sometimes one and occasionally four or more) which are alike and apposed in prayomorphs (Fig. 14b, e) and different and linearly aligned in diphyomorphs; they also lack the axial wings and thrust block of physonect nectophores. A single larval nectophore develops from the calyconula larva, before the first definitive nectophore appears. Prayidae is one of the largest calyophoran families, including 27 species (Fig. 4), and systematic changes since 1987 are summarized in Table 3. In life prayomorph nectophores attach at the anterior end of a typically very long siphosome bearing hundreds of cormidia (Fig. 14a). When feeding a “sit and wait” strategy is employed, when the stem relaxes and the extended tentacles hang down in a long feeding curtain.

The largest of the three subfamilies is the Prayinae, which undergo nectophore replacement, probably throughout life. The first definitive nectophore develops inside a long proximal groove in the larval nectophore (termed the hydroecium) and matures (Pugh 1992), and then a second definitive nectophore may start to form before the larval nectophore is shed. Buds for third and fourth nectophores are often also visible inside the hydroecium, and these will enlarge and replace earlier definitive nectophores over time, as summarized by Mapstone (2009). Stem cormidia are retained throughout life in prayines and comprise a single rounded bract (except *Gymnopræia*) with typically six bracteal canals enclosing a gastrozoid, tentacle, and gonophore (Fig. 14c). Prayine tentilla are all alike (Fig. 14da) with a swollen sinker at the distal end of the terminal filament to act as a weight (Fig. 14db). Unlike physonects, tentilla are not useful for species or genus diagnosis in calyophorans, and prayine species are separated on nectophore and bract characters. These include the relative size of nectosac to nectophore (small in *Praya* and *Rosacea* species (see Fig. 14b) and large in *Lilyopsis* (see Fig. 14e)), presence or absence of a disjunct pedicular canal (see Mapstone 2009, Fig. 5), the type and branching of the somatocyst when present, the branching and courses of the lateral radial canals of the nectophore, and the number and arrangement of canals in the bract (all summarized in Mapstone 2009).

Prayine nectophores vary in size, with some species reaching as much as 6 or 10 cm in length (*Praya* species and *Rosacea cymbiformis*), although most are shorter (circa 3–4 cm) and others diminutive (*Mistoprayina fragosa*, *Prayola* species, *Rosacea arabiana*, 3–6 mm in length (WoRMS Siphonophora List)). Prayines with large nectosacs are very fragile and hence rarely successfully collected (*Lilyopsis*

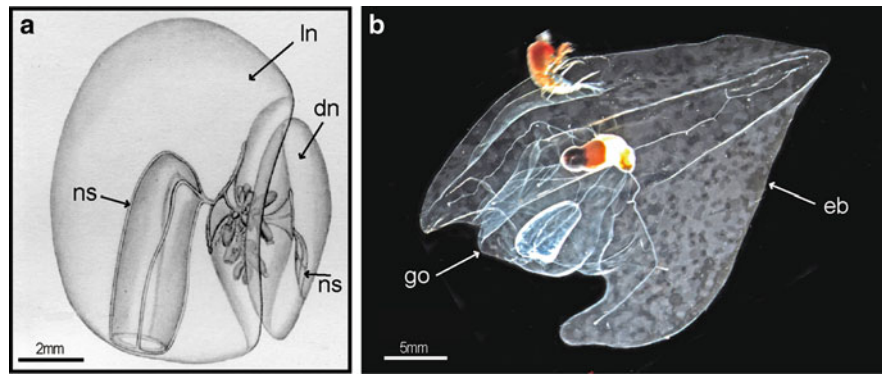


**Fig. 14 Prayine prayomorph morphology.** (a) Typical prayomorph *Praya* sp. feeding, with two rounded bells and a very long siphosome bearing over 100 cormidia; tentacles extended for feeding, each bearing 80–90 nematocyst batteries, giving <9,000+ batteries in all (Steven Haddock © MBARI). (b) *Rosacea* sp. feeding (© Jessica Luo/Cowen Lab); (c, d) *Rosacea cymbiformis*; (c) cormidium enlarged; (d) a tentillum, b sinker (© Gillian Mapstone 2014, Figs. 8A and 14A); (e) *Lilyopsis rosea* swimming (© Jessica Luo/Cowen Lab). Labels: ani anisorhizas, b bract, bc bracteal canal, c cormidium, dl large desmoneme, ds small desmoneme, go gonophore, gz gastrozoid, mm microbasic mastigophore, n nectophore, ns nectosac, rh rhopalomes, pe pedicel, sk sinker, st stem, t tentacle, te tentilla, tf terminal filament

Fig. 14e), while others with more mesogloea are robust (*Praya* and *Rosacea* Fig. 14a, b) and collected periodically in epi- and mesopelagic waters of most seas (*Praya dubia* and *Rosacea plicata*; see Mapstone 2014, Table 1; also *R. cymbiformis* Mapstone 2009).

The two much smaller prayid subfamilies Amphicaryoninae and Nectopyramidinae have only four species apiece and are probably derived from the prayines, although only two species were included in the molecular analysis of Dunn et al. (see Fig. 3). Amphicaryonines are small, rounded, and composed of two unequal-sized nectophores: a larger retained larval nectophore and a smaller reduced definitive nectophore (see summary in Mapstone 2009). The nectosac is functional in both nectophores of the largest amphicaryonine *Maresearsia praeclara* (20 mm diameter), but only in the larval nectophore of the





**Fig. 15 Amphicaryonine and nectopyramidine prayomorph morphology.** (a) *Amphicaryon acaule* colony (Bigelow 1911, pl. 4 Fig. 1); (b) *Nectadamas diomedae* eudoxid (© Russ Hopcroft UAF). Labels: *dn* definitive nectophore, *eb* eudoxid bract, *go* gonophore, *ln* larval nectophore, *ns* nectosac

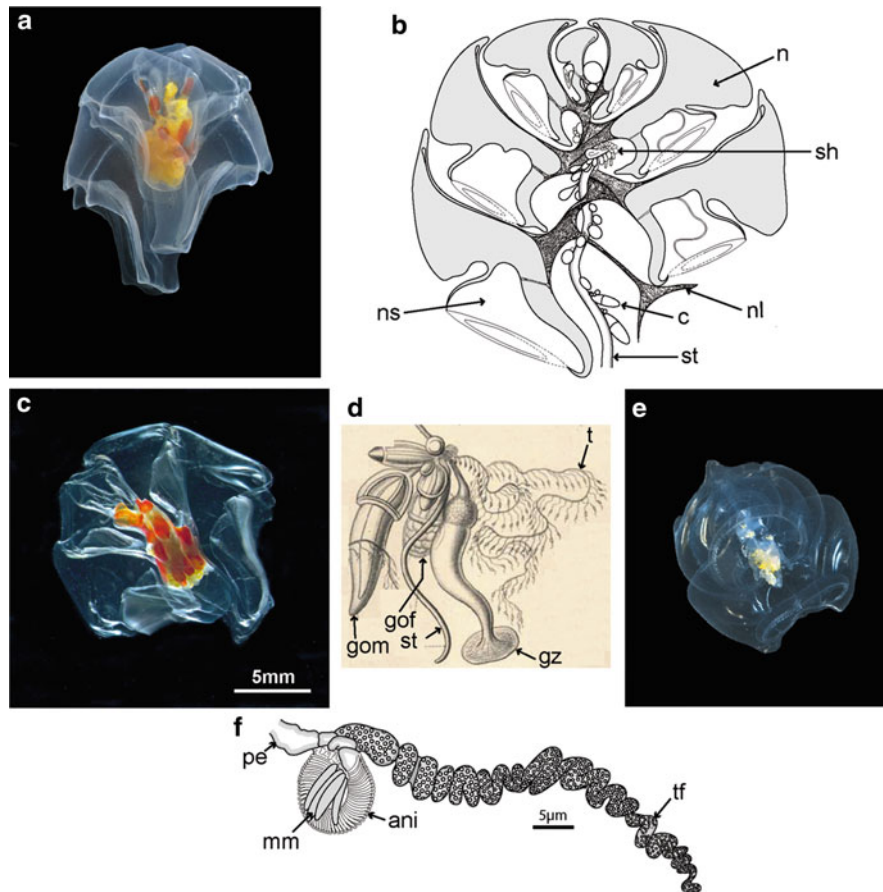
three smaller *Amphicaryon* species (WoRMS Siphonophora List). The best known amphicaryonine is *A. acaule* (8 mm diameter) (Fig. 15a), which inhabits epi- and mesopelagic layers of warmer waters worldwide (see Mapstone 2014, Table 1). All amphicaryonines release small free-living eudoxids with only two canals in the bract, for species dispersal.

Nectopyramidine prayids develop only one ridged asymmetric definitive nectophore, from a smaller ridged larval nectophore, and also release a free-living eudoxid (Fig. 15b) (reviewed by Mapstone 2009). Definitive nectophores vary from pyramidal to rhomboidal or bow-shaped, with a penetrating somatocyst of one or several branches and a hydroecium of varied shape. This subfamily is rare worldwide, being mainly mesopelagic with a greater latitudinal range than amphicaryonines (though absent from the Mediterranean) (Mapstone 2009, 2014). Nectophores and eudoxids of three of the four species are large, reaching up to 36 mm or more in length.

### Family Hippopodiidae

Hippopodiidae is a small and unusual calycophoran family of five species each with up to 12 nectophores (Fig. 16a–c, e) and found to be nested with the family Prayidae by Dunn et al. (2005b) (Fig. 3, Table 3). Like prayine prayids, the first definitive nectophore develops inside the hydroecium of a small rounded larval nectophore (see Mapstone 2009, Fig. 42), which is later shed and more definitive nectophores formed, each from the pedicel of its predecessor. Thus, the largest nectophore, and the only one with a functional nectosac, occurs at the base (or posterior end) of the colony (Fig. 16b). There are no bracts in the siphosomal cornidia (Fig. 16d), and this allows the stem to be more easily withdrawn into the chamber created by the nectophores (Fig. 16a, c, e). Buoyancy for the colony is instead provided by the thick and typically robust nectophores, which are either rounded with two or more protuberances on the distal side of the nectosac (*Hippopodius hippopus* and *Vogtia glabra*; see Mapstone 2009, Fig. 2f and g for nectophore axes) or angular and pentagonal, often with ridges and cusps (Mapstone 2009). Buoyancy in hippopodiids is likely controlled by active transport of lighter and heavier ions across the covering epithelium (Mackie and Mackie 1967).

Although two genera are included within the family Hippopodiidae, *Hippopodius* and *Vogtia* (WoRMS Siphonophora List), the differences between them are small. Both genus names are very old and are still retained only to avoid confusion in the literature (Totton 1965). All five species have nectophores of similar dimensions (<21 mm along upper-lower axis) and a widespread cosmopolitan distribution. However, they occur at varied latitudes and depth horizons, and all feed selectively on ostracods (Table 3), unlike all other calycophorans.



**Fig. 16 Hippopodiid prayomorph morphology.** (a) *Hippopodius hippopus* colony (© Sonke Johnsen, Duke); (b) section through *Hippopodius* (© Gillian Mapstone 2014, Fig. 8B; see figure legend for original reference); (c) *Hippopodius hippopus* colony (© Russ Hopcroft UAF); (d) *Hippopodius hippopus* cormidium; note, no bracts (© Mapstone 2014, Fig. 8D; see figure legend for original reference); (e) *Vogtia glabra* colony (© Sonke Johnsen, Duke); (f) *Hippopodius hippopus* tentillum (© Gillian Mapstone 2014, Fig. 14C; see figure legend for original reference). Labels: *ani* anisorhizas, *c* bractless cormidium, *gom* male gonophore, *gz* gastrozoid, *mm* microbasic mastigophore, *n* nectophore, *nl* nectophoral lamella, *ns* nectosac, *pe* pedicel, *sh* siphosomal horn, *st* stem, *t* tentacle, *tf* terminal filament

*Hippopodius hippopus* is the most abundant and best known species. It has tentilla with a very long terminal filament for feeding (Fig. 16f) and is a robust and epipelagic species, which lives in warmer waters worldwide (Mapstone 2014), often occurring nearer the coast than the four *Vogtia* species. It undergoes blanching, and this, together with nerve/epithelial conduction, has been studied in detail by Mackie (reviewed in Mackie et al. 1987). *Vogtia glabra* is the only rounded *Vogtia* species (Fig. 16e), with just two prominences distal of the ostium when mature (Pugh 1999b). *V. glabra* also prefers, like *H. hippopus*, tropical and temperate waters, but differs in inhabiting mainly the mesopelagic zone, with many fewer and sporadic records from the world's oceans.

Of the three pentagonal *Vogtia* species, *V. serrata* is the largest and the most abundant (Mapstone 2009), with an extensive latitudinal range in both hemispheres (Mapstone 2014, Table 1), inhabiting shallow depths in the Antarctic, and deeper layers in temperate seas, where it is typically the dominant hippopodiid of mesopelagic assemblages, and also the deepest living (reviewed by Mapstone 2009). *V. pentacantha* is a smaller and less frequently encountered *Vogtia*, with cusped ridges but smooth facets on the nectophores, and is also mainly mesopelagic. In contrast, nectophores of *V. spinosa* have cusps on both



the facets and the ridges, and this species is epipelagic at lower latitudes and mesopelagic at higher latitudes (Mapstone 2009).

### Family Clausophyidae

The remaining four calycophoran families in Table 3 are all diphyomorphs, which typically have two dissimilar angular and also often streamlined nectophores strengthened with longitudinal ridges and containing a relatively large powerful nectosac and little mesogloea; they also contain a swollen blind-ending diverticulum from the gastrovascular canal system termed the somatocyst (Fig. 2c) which is mirrored in the canal system of the eudoxid bract as a swollen phyllocyst. These structures might act as food stores and/or increase buoyancy (Mapstone 2009).

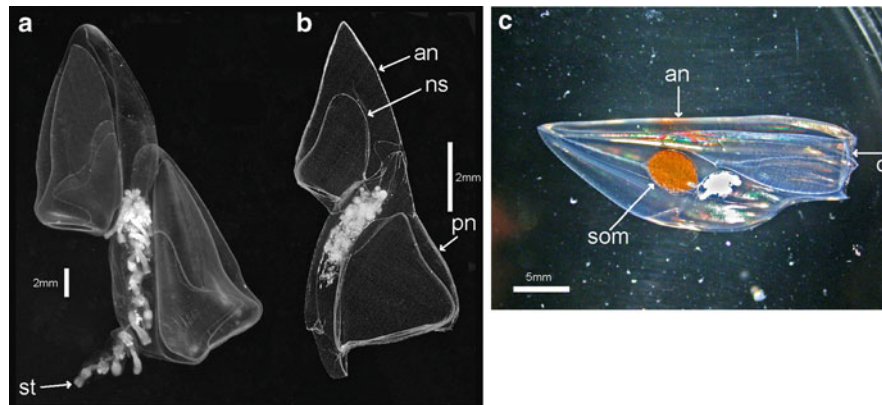
Clausophyidae is a small family of ten species which are mostly meso- and bathypelagic and hard to sample. They were poorly understood for many years until the advent of modern sampling methods. Clausophyids were only raised to family status in 1965, in contrast to the other calycophoran families which are much older (Mapstone 2009, 2014; Totton 1965, WoRMS Siphonophora List). Distinctive family characters include typically two nectophores, both containing somatocysts and with the posterior larger than the anterior, aligned partially linearly, and partially in apposition (Mapstone 2009, Fig. 4). This latter character suggests that they may represent the ancestors of the other diphyomorph families, as noted in Table 3. Cormidia are released as free eudoxids in three of the five genera (*Chuniphyes*, *Kephyes*, and *Heteropyramis*), but bracts are absent in *Clausophyes* species, and each bract is fused with a gonophore in the monotypic genus *Crystallophyes* (Table 3). Few clausophyid species were sampled in the molecular analysis of Dunn et al. (2005b) (Fig. 3), and, although the results indicate that this family might be paraphyletic, the nodes are poorly supported and further sampling is needed.

There is considerable size variation among clausophyid genera, with anterior nectophores of *Chuniphyes* growing up to 30 mm in length, while those of *Heteropyramis* (which does not develop a posterior nectophore) reaching only 5 mm; nectophores of *Clausophyes* and *Kephyes* are of intermediate size (Fig. 1; see Pugh (2006b) and Mapstone (2009) for further details and other references). The somatocyst reaches to the anterior end of both nectophores when mature, and in the anterior nectophore the nectosac typically extends to only half its length (Fig. 17b, c; *K. ovata* in Fig. 17a is an exception). The stem attaches to the hydroecial wall of the anterior nectophore some distance anterior of the ostium (Fig. 17b), suggesting that clausophyids might be an intermediate stage in the migration of the posterior nectophore from the apposed position in prayids to the superimposed, or linearly aligned, position in most Diphyidae and Abylidae (see Mapstone 2009, Fig. 4). The many nomenclatural problems among some species of the family Clausophyidae have been resolved in recent years, as discussed by Mapstone (2009).

Clausophyids are mostly cosmopolitan worldwide (see Mapstone 2014, Table 2), but none are common, and, indeed, species such as *Clausophyes laetmata*, *C. galeata*, and *C. tropica* are rare to very rare (WoRMS Siphonophora List). Perhaps the most successful clausophyid is the large species *Chuniphyes multidentata* which has a considerable latitudinal range worldwide and produces a large number of small eudoxids when breeding (Mapstone 2009). Although it inhabits the same depth horizons as its congener *C. moserae*, Mackie et al. (1987) conclude that these two species are allopatric in the North Atlantic at least, with *C. moserae* being more prevalent below 40°N and *C. multidentata* more abundant above this latitude; where the two species coexist, their population nuclei are spread over different depth zones (summarized in Mapstone 2009).

### Family Sphaeronectidae

Sphaeronectidae is a small and distinctive family of ten valid species and one *species inquirenda* (WoRMS Siphonophora List), in which a rounded larval nectophore is retained into adulthood (paedomorphy), producing cormidia on the elongate siphosomal stem which are released into the

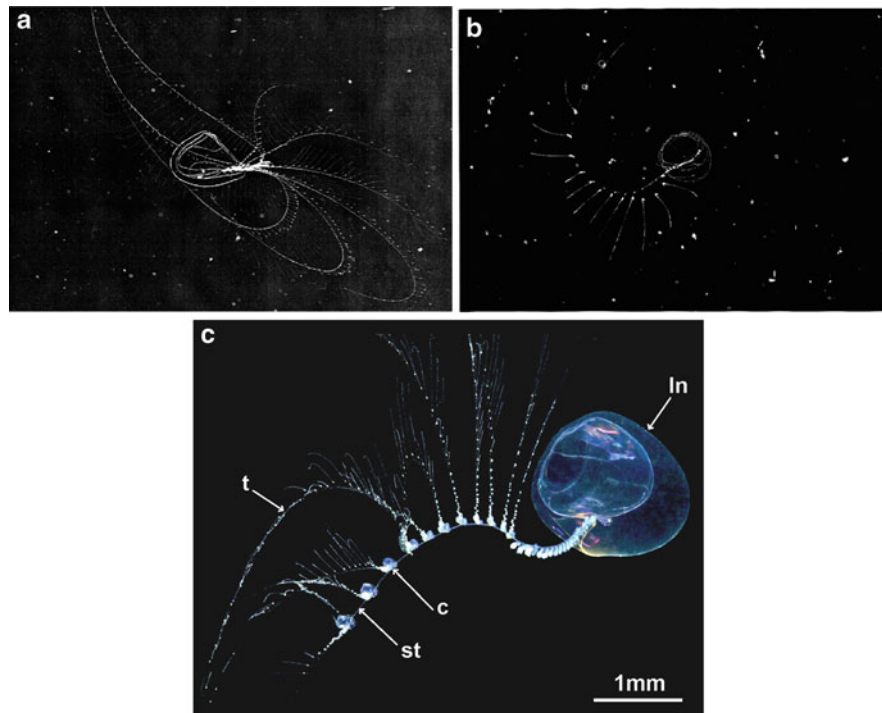


**Fig. 17 Clausophyid diphyomorph morphology.** (a) *Kephyes ovata* and (b) *Clausophyes moserae* (both © JMBA Plymouth, from Pugh 2006b); (c) *Chuniphyes multidentata* anterior nectophore only (posterior nectophore detached during capture) (© Casey Dunn). Labels: *an* anterior nectophore, *ns* nectosac, *o* ostium, *pn* posterior nectophore, *som* somatocyst, *st* stem

plankton as free-living eudoxids, like diphyids and abyliids (Mapstone 2009). No definitive nectophores are formed. Only one species was sequenced by Dunn et al. (2005b), appearing in their molecular phylogeny as *Sphaeronectes gracilis* (Fig. 3); this species has since been referred to *S. koellikeri* (Mapstone 2009; Pugh 2009). The species is firmly nested within the diphyomorph clade of calycophorans (Fig. 3), dispelling some earlier ideas about affinities of sphaeronectids. All sphaeronectid species are small, with a single rounded or ovoid nectophore that is very fragile and varies in size from 1.5 to 11.5 mm (Pugh 2009). As a result, most plankton nets miss these small calycophorans, and several new species have been discovered recently by SCUBA divers and using fine-meshed nets deployed in the surface layers of coastal waters around various continents. Despite this, two of the newly introduced species are meso- and bathypelagic, found only so far in Monterey Bay (Pugh 2009, Fig. 18).

Axes for nectophores of *Sphaeronectes koellikeri* are given by Mapstone (2009, Fig. 3g), and all species have a small hydroecial opening on the lower nectophore surface, since no second nectophore has to be accommodated (Fig. 18a–c). All species except *S. koellikeri* also have a small and very short hydroecium which originates on the lower side of the nectosac; in *S. koellikeri*, the hydroecium uniquely extends over the top of the nectosac on the anterior side (Mapstone 2009, Fig. 65a). Species differ in the ratio of nectosac to nectophore length, position of origin of the four radial canals on the nectosac, and the courses of the lateral radial canals over the nectosac to the ostial ring canal. Size, shape, color, extent, and position of the somatocyst are also important for species identification, with some having an elongate tubular somatocyst, most having a pyriform one, and one species having a stalked somatocyst. In *S. tiburonae* from Monterey Bay, the somatocyst is minute, and in *S. christiansonae*, also from this location, the somatocyst is red (Pugh 2009). Eudoxids are so far known for only three of the ten valid species, and all differ in phyllocyst shape and bract to gonophore ratios.

Only one sphaeronectid species, *Sphaeronectes koellikeri*, is well known and its distribution, together with those of five of the other species, is summarized by Pugh (2009). Two species more recently introduced are noted in Table 3, and their distributions are limited so far to Japanese waters and subantarctic waters off Australia (see Mapstone 2014 for references). The identity of another small species originally referred to the genus *Sphaeronectes* is now likely a calyconula of *Lilyopsis medusa* (Table 3).



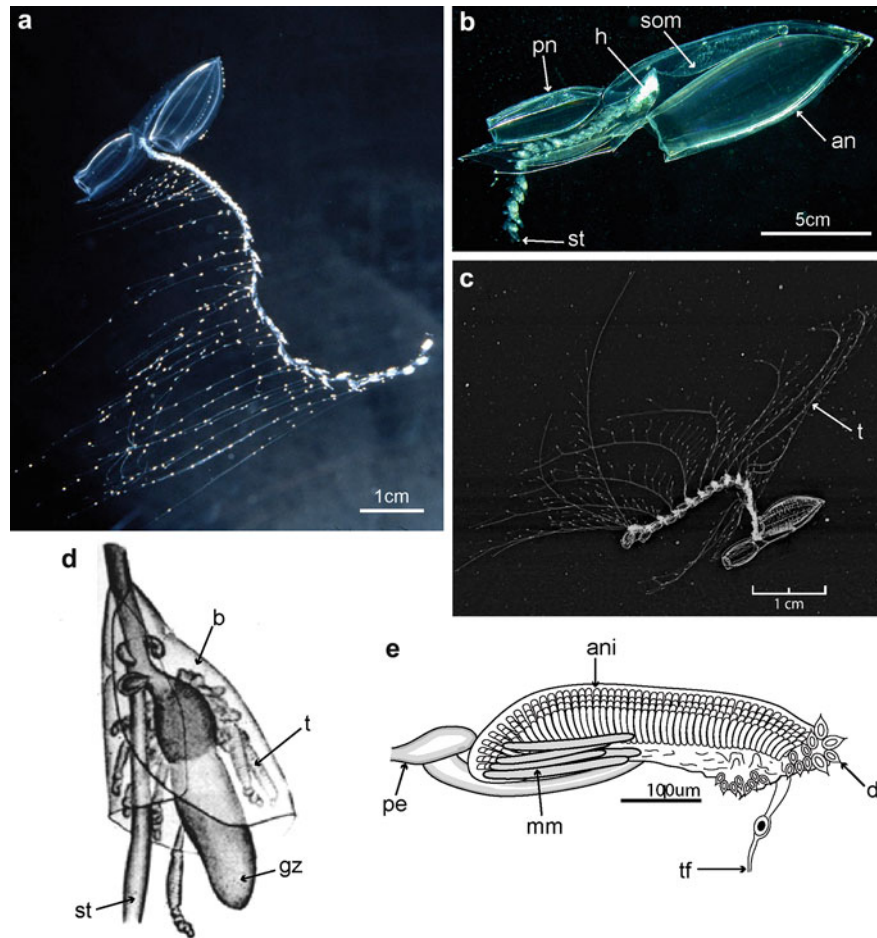
**Fig. 18 Sphaeronectidae diphyomorph morphology.** (a, b) *Sphaeronectes* spp. feeding (© Jessica Luo/Cowen Lab); (c) *Sphaeronectes pagesi* feeding (© D. Lindsay, R. Minemizu, JAMSTEC). Labels: *c* cormidium, *ln* larval nectophore, *st* stem, *t* tentacle

## Family Diphyidae

Diphyidae are the most successful and speciose siphonophore family (Fig. 4), currently comprising 45 species considered valid ([WoRMS Siphonophora List](#)). Diphyidae dominate surface layers in the ocean, and their systematics is very stable because most species were introduced many years ago. Recent changes are summarized in Table 3, and Fig. 3 shows that in the molecular phylogeny, abyloids (represented by *Abylopsis tetragona*) are nested within the five diphyid species tested.

Diphyids typically have two linearly aligned nectophores, led by a pointed streamlined anterior nectophore, and followed by a smaller posterior nectophore (Fig. 19a–c). The stem is completely withdrawn into the elongate hydroecium of the posterior nectophore for swimming, which alternates with a motionless phase during which the stem and tentacles relax and form a fishing net for feeding (Mapstone 2009, p. 30) (Fig. 19a, c). Nectophores are typically ridged and have a nectosac which fills the nectophore, a mouthplate adjacent to the ostium, and, in the anterior nectophore only, a discrete somatocyst food storage/buoyancy organ (Mapstone 2009, Fig. 3d). The stem bears numerous cormidia which each comprise a bract, gastrozoid and tentacle (Fig. 19d), and, when mature, a gonophore for reproduction. The structure of diphyid-type tentilla and their nematocyst compliments are summarized by Mapstone (2014, Table 8, Fig. 14d, e), and tentillum structure is shown for three diphyomorph species in Figs. 19e and 20c, f. The typical bract is typically helmet shaped (Fig. 20b) with a food storage equivalent of the somatocyst, the phyllocyst, and no bracteal canals. The gonophore has a large nectosac for propulsion, and, when released into the plankton as a free-living eudoxid from the posterior end of the stem, can live for several months and release a large number of gonophores for sexual reproduction.

The family includes three subfamilies: the Sulculeolariinae (five species) in which the stem is very long because cormidia are never released and nectophores can be replaced up to four times during life, the



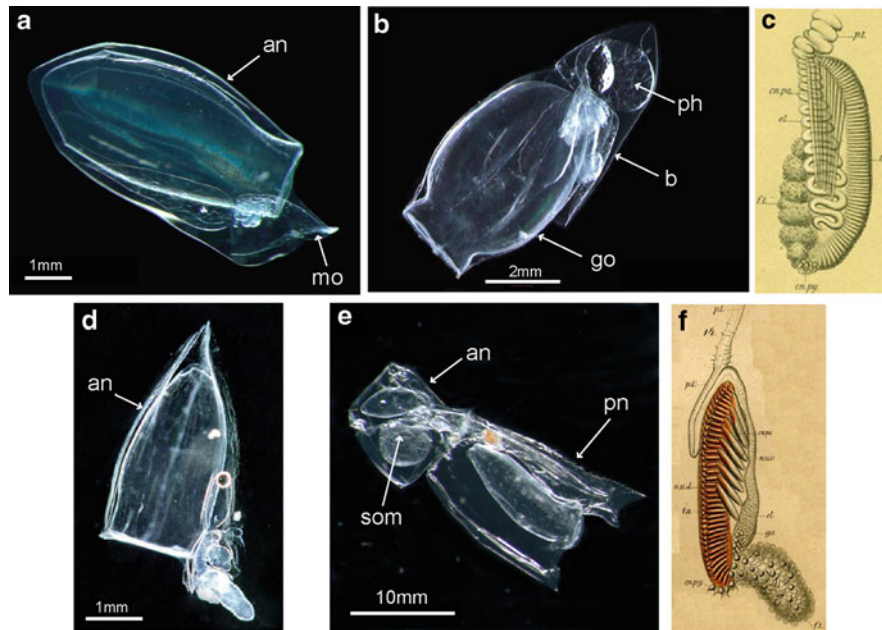
**Fig. 19 Diphyid diphymorph morphology.** (a) *Lensia conoidea* feeding (Rob Sherlock © MBARI); (b) *Chelophyes appendiculata* (© Peter Schuchert MHNG); (c) *Lensia multicristata* feeding (© Inter-Research, revised from Luo et al. 2014); (d) *C. appendiculata* corium; and (e) *Diphyes dispar* tentillum (© Gillian Mapstone 2014, Figs. 8C and 14D; see figure legends for original references from which these figures were derived). Labels: an anterior nectophore, ani anisorhizas, b bract, dl large desmonemes, gz gastrozoid, h hydroecium, mm microbasic mastigophores, pe pedicel, pn posterior nectophore, som somatocyst, st stem, t tentacle, tf terminal filament

Diphyinae (39 species) with typically two ridged nectophores which cannot be replaced and a shorter stem from which eudoxids are released when mature, and the Giliinae (summarized in Table 3).

Sulculeolariines are warm-water epipelagic and cosmopolitan species (Mapstone 2014, Table 2), separated on the length of the somatocyst, the presence or absence of teeth around the ostium and small swellings on the upper sides of the mouthplate (Mapstone 2009, Fig. 44). Anterior nectophores vary in size from 8 to 26 mm, with *S. quadrivalvis* being the largest and probably most abundant species worldwide (Totton 1965).

Diphyines include 39 valid species in five genera (WoRMS Siphonophora List), which are separated on characters of the anterior nectophore, and in a few species a posterior nectophore does not develop (Fig. 20d). The genus *Chelophyes* comprises two distinctive warm-water 5-ridged epipelagic species with a claw-shaped hydroecium (Fig. 19b) and allopatric distribution. *C. appendiculata* is the most abundant siphonophore species worldwide, with an anterior nectophore more than twice the size of *C. contorta* and a much broader latitudinal range (Mapstone 2009, 2014; Pugh 1999b). *Dimophyes arctica* is monotypic for the genus *Dimophyes*, has a smooth anterior nectophore with a prominent undivided mouthplate





**Fig. 20 Diphyid and abyloid diphyomorph morphology.** (a, b) *Dimophyes arctica* polygastric colony (a) and eudoxid (b) (© Russ Hopcroft UAF); (c) *D. arctica* tentillum (Chun 1897, pl. 1 Fig. 9); (d) *Muggiaea kochi* (© Peter Schuchert MHNG); (e) *Abylopsis tetragona* (© Russ Hopcroft UAF); (f) *Enneagonum hyalinum* tentillum (Chun 1892, pl. 12 Fig. 14). Labels: an anterior nectophore, b bract, go gonophore, mo mouthplate, ph phyllocyst, pn posterior nectophore, som somatocyst

(Fig. 20a), a very small posterior nectophore rarely collected, and a particularly broad cosmopolitan distribution, occupying deeper layers at lower latitudes and surface layers at higher ones (Mapstone 2009, 2014, Table 2). *Diphyes* anterior nectophores have a deep hydroecium, prominent teeth around the ostium, are all epipelagic, and include the largest of all diphyid species, *D. dispar* (<36 mm long, Pugh 1999b). Three of the four species are tropical, with two common worldwide (*D. dispar* and the much smaller *D. bojani*) and the third, which lacks a posterior nectophore, inhabiting only the Indo-Pacific region (*D. chamissonis*) (Totton 1965). The fourth *Diphyes* species, *D. antarctica*, is also large (<30 mm long) and common, but only in the cold waters of the Southern Ocean (Pugh 1999b).

Two more small tropical diphyines are referable to the genus *Eudoxoides* and have an anterior nectophore with five serrated ridges, a hydroecium reaching 1/3 nectophore length (from the ostium), and a prominent mouthplate (Pugh 1999b). *E. mitra* is common and epipelagic in all oceans except the Mediterranean (Mapstone 2014, Table 2), while *E. spiralis*, which lacks a posterior nectophore, has a slightly more extended vertical and latitudinal distribution (Pugh 1999b). The genus *Muggiaea* (Fig. 20d) includes four small species (4–10 mm long) without a posterior nectophore, so the stem is accommodated during swimming inside a deep hydroecium in the anterior nectophore. Three species are neritic, restricted to the shallow shelf waters fringing continents, with *M. atlantica* occupying temperate waters worldwide, *M. kochi* replacing it in tropical Atlantic waters, and *M. delsmanni* in tropical Indo-Pacific waters; these temperate/tropical pairs can also coexist, for example, in the English Channel (Mapstone 2009) and Sagami Bay (Grossmann and Lindsay 2013). The fourth species, *M. bargmannae*, is a bipolar species living only at very high latitudes in epi- and mesopelagic layers (Mapstone 2014). *M. delsmanni* from the South China Sea was unfortunately misidentified by Lo et al. (2012) as *M. kochi*.

*Lensia* is a catch-all diphyine genus of circa 26 diverse valid species (WoRMS Siphonophora List) with most species ridged (from five to multiridged or multistriate) and some unridged. In the anterior nectophore, the hydroecium is typically very shallow, and the size, shape and position of the somatocyst, and the divided mouthplate are specifically diagnostic. Many species are rare to very rare, and their

posterior nectophores and eudoxids unknown. A few have very small anterior nectophores (3–4 mm long), but most are intermediate (8–12 mm long), with some (*L. achilles*, *L. conoidea*, *L. fowleri*, *L. hardy*, *L. havock*, *L. hostile*, and *L. multicristata*) reaching from 15 to 25 mm in length. Forty-two percent of species inhabit epipelagic layers offshore, and several species make significant contributions to mid-water siphonophore assemblages (*L. conoidea*, *L. multicristata*, Mackie et al. 1987). A number of small fragile and rare multistriate species inhabit the deeper and calmer meso- and bathypelagic layers of temperate waters (*L. lelouveteau*, *L. quadriculata*, *L. grimaldii*, *L. exeter*).

## Family Abylidae

This is another well-known and successful diphyomorph family of ten species, which are most abundant in tropical surface waters and differ from diphyids in having more prismatic and faceted nectophores, with serrated ridges and teeth and a posterior nectophore larger than the anterior one (Fig. 20e). This large nectophore provides the main propulsive force for abyloid locomotion (Totton 1932) and also protects the contracted stem in a long hydroecium enclosed by a serrated longitudinal flap on the inner surface of the left hydroecial wing. Several aspects of the family are summarized in Table 3. Abylids are a stable and long-known group, like the diphyids, with seven of the ten species already introduced by 1860 and the remaining three by 1925 (WoRMS Siphonophora List). Species diagnoses are based on the characters of the anterior nectophore, and are well summarized by Pugh (1999b), who also lists often used synonyms for five of the ten valid species.

Two subfamilies are recognized. The Abylinae include six species in two genera (*Abyla* and *Ceratocymba*), with a small facet at the anterior end of the anterior nectophore which leads the colony during locomotion. The Abylopsinae includes four species in three genera (*Abylopsis*, *Bassia*, and *Enneagonum*), with a small leading ridge at the anterior end of the anterior nectophore instead of a facet in *Abylopsis* and *Bassia* and a very differently shaped pyramidal anterior nectophore in *Enneagonum hyalinum*, which never develops a posterior nectophore.

Abyline species are all epipelagic and rare worldwide except for *Ceratocymba sagittata*, which is common and mainly epipelagic, with a slightly broader latitudinal range than other abylines, although this subfamily is absent from the Mediterranean. The anterior nectophore of most abylines is only 8–13 mm in length, but in *C. sagittata* it can reach 25 mm (Pugh 1999b). This species also has a pointed anterior extension beyond the small leading facet, and whole colonies of *C. sagittata* can reach 45 mm in length (Totton 1965, Fig. 140), which is very long for a diphyomorph species. *Abyla* species have anterior nectophores which are rectangular in lateral view, variable in width, and with a long hydroecium into which fits the prominent apophysis of the posterior nectophore. The latter are larger when mature in abylines, as noted above, and differ in width and number of teeth on the internal flap of the left hydroecial wing (Pugh 1999b). *Ceratocymba* comprises three species, which, in addition to *C. sagittata*, include the conspicuous but smaller opaque, rare, and sturdy species *C. dentata* and a third rare species *C. leuckarti*.

Abylopsines include three mainly epipelagic and common tropical and subtropical species: *Abylopsis eschscholtzii*, *A. tetragona*, and *Bassia bassensis*, which all occur worldwide and in the Mediterranean (Mapstone 2014 Table 2; Pugh 1999b). Anterior nectophores of *Abylopsis* and *Bassia* are similar, but can be distinguished by their somatocysts, which in *Abylopsis* terminate in a thin diverticulum. *A. tetragona* has a relatively longer posterior nectophore than *A. eschscholtzii*, although that shown in Fig. 20e has not yet reached its maximum length (see Totton 1965, Fig. 149, for a mature colony). These three species are often abundant in tropical siphonophore assemblages, together with certain tropical diphyid species (Lo et al. 2012), and *Bassia bassensis* is distributed throughout tropical and subtropical latitudes of all oceans and is also particularly tolerant of the varied environmental conditions found in neritic habitats (Lo et al. 2012); the ridges of this species are also tinged blue in life. *Enneagonum hyalinum*, in contrast, is a large and relatively uncommon abylopsine, from both tropical and temperate latitudes, with a pyramidal

nectophore having nine points, a slim anteriorly directed somatocyst, and a relatively small nectosac. This shape is unwieldy, suggesting that this species is an ineffectual swimmer with a nectosac that can do little more than simply counteract the pull of gravity while floating in the water column (Totton 1932).

## Conclusions and Future Directions

Forty three morphological siphonophore taxa have so far been successfully sampled for two genes, a comprehensive molecular consensus generated, and some interesting new characters and relationships revealed. More such characters and relationships might be found if further taxa are sampled (particularly for calycophorans and also for other physonects) and wider suite of genes investigated, although CO1 should be omitted, as this gene is unsuitable for detecting interspecific differences in Siphonophora. Investigation of mechanisms of tentillum discharge in different species and prey consumption in a wider range of taxa might also produce interesting new findings. Sampling of siphonophores and other zooplankton in areas not so far well studied worldwide (there are many) would also be informative, particularly if specimens of further species with gastrozooids containing prey items are collected, and might show further connections between siphonophores and other taxa in mid-water food webs, such as that recently discovered by Burford et al. (2014).

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