

BOOK 3: THE SIPHONOPHORES



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The intent of this report is to be used as a field guide for the identification of midwater invertebrates of South-eastern Australia. It is envisioned that this report will lead to further editions as a published field guide; comments toward improving the presentation and usability are appreciated. This work was supported by CSIRO Wealth from Oceans Flagship.

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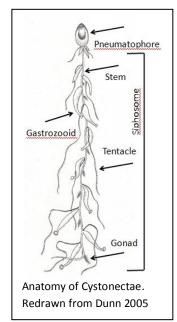
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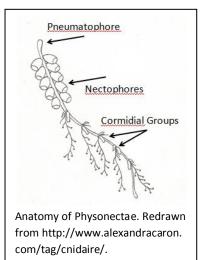
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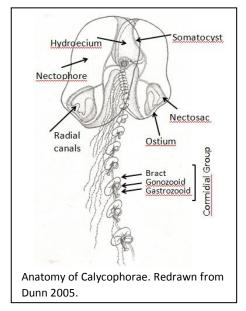
Clockwise, from upper left: *Sphaeronectes* n. sp. (copyright L. Gershwin), *Abylopsis tetragona* (copyright R. Hopcroft), *Eudoxoides spiralis* (copyright A. Slotwinski), *Rhizophysa* sp. (copyright L. Madin/WHOI), *Forskalia edwardsi* (copyright D. Riek), *Physophora hydrostatica* (copyright L. Gershwin).

GENERAL INFORMATION ABOUT THE SIPHONOPHORES

Siphonophores are a highly modified type of jellyfish. They evolved from within the hydrozoan order Anthomedusae, but they are so strange in their morphology and behaviour that they have long been regarded as a separate group altogether.





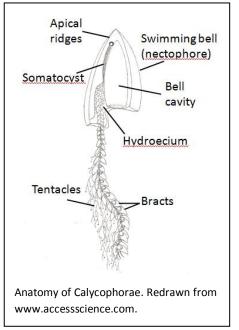


Unlike regular jellyfish, with

siphonophores each specimen is actually a colony made up of numerous small connected individuals, each with a specific function, such as feeding, attack and defence. The different colony members are called 'persons', thus there are feeding persons, stinging persons, swimming persons, etc.

Siphonophores are classified into three main groups depending on their possession of a gas-filled float (called a pneumatophore) or swimming bells (called nectophores), or both. The most familiar siphonophore is the Blue Bottle or Portuguese Man-o-war in the group Cystonectae, which is characterised by having a float but no swimming bells. The Calycophorae, in contrast, have one or two swimming bells but no float. Members of the third group, the Physonectae, have a float and many swimming bells.

Siphonophores are highly active organisms that jet through the water column at relatively high speed. They are



voracious predators on smaller organisms such as crustaceans, molluscs, small fish, and larvae, which many species are able to catch by setting a sheet-like wall of tentacles from a number of persons in a row. At times, siphonophores may bloom so densely as to clog up fishermen's nets or even give false sonar readings.

Identification of the higher groupings is based on size and shape of the float and shape and arrangement of the swimming bells. Finer taxonomy is based on characters such as ridges and radial

canal patterns in calycophoran nectophores, nectophore shape and internal features in physonects, and microscopic features in cystonects. None of the features are difficult to observe, they just have unfamiliar names and forms, and so can seem daunting.

ANNOTATED CLASSIFICATION

Subclass Siphonophora: strangely shaped pelagic colonies
Order Cystonectae: with a float but no swimming bells
Rhyzophysa: a round or oblong float with a long rope of spikes and frills
Order Physonectae: with a float and numerous swimming bells
Agalma: a long clear baton with scattered red flecks
Forskalia: a long clear baton with red sections in a row on one side of the central stem
Nanomia: a small ovoid float with a cylindrical region of nectophores and long trailing stem 7
Physophora: a long slender float with a midregion of nectophores and a whorl of pink palpons 9
Order Calycophora: with one or two swimming bells but no float
Abylopsis: anterior nectophore strongly cuboid; somatocyst ovoid
Amphicaryon: small spheres of clear jelly with a yellow stem inside, like tiny marbles
Bassia: anterior nectophore strongly cuboid; ridges tinged in blue; somatocyst spherical 17
Chelophyes : two bullet-shaped nectophores articulated end-to-end; hydroecium claw-shaped14
Diphyes : two bullet-shaped nectophores articulated end-to-end; with undivided mouthplate 14
Eudoxoides: small bullet-shaped colony, with the whole body distinctly twisted
<u>Sulculeolaria</u> : anterior nectophore resembles a boot; lacks gelatinous ridges
Hippopodius: a rounded colony of about 10 horseshoe-shaped prism-like nectophores
Lensia: one or two nectophores; anterior with very shallow stem-niche (hydroecium)
Muggiaea: one nectophore with complete dorsal ridge and very deep, rounded hydroecium14
<u>Praya</u> : two large, smoothly rounded, opposing nectophores with a stem up to 40 metres long12
Rosacea: similar to Praya (above) but much smaller; the nectophores are more rounded 13
Sphaeronectes : a single sub-spherical nectophore, with a massive cavity inside
Vogtia: a globular colony of 6 or more pentagonal prisms

The best identification resources for siphonophores include the following:

- Haeckel, E. 1888. Report on the scientific results of the voyage of H.M.S. Challenger ... Siphonophorae. *Challenger Reports* 35:1–380, 50 Plates.
- Kirkpatrick, P. A., and P. R. Pugh. 1984. Siphonophores and Velellids: Keys and notes for the identification of the species, Synopses of the British Fauna, no. 29. Leiden: E.J. Brill/ Backhuys.
- Mapstone, G. M. 2009. Siphonophora (Cnidaria, Hydrozoa) of Canadian Pacific waters. Ottawa, Ontario, Canada, NRC Research Press.
- Pagès, F. and J. M. Gili. 1992. Siphonophores Cnidaria Hydrozoa of the Benguela Current Southeastern Atlantic. Scientia Marina 56(SUPPL. 1): 65–112.
- Pugh, P. R. 1999. Siphonophorae. In *South Atlantic Zooplankton I*. Edited by D Boltovskoy. Backhuys Publishers, Leiden, The Netherlands. pp 467-511.
- Totton, A. K. 1965. A Synopsis of the Siphonophora. London: British Museum of Nat. Hist.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CYSTONECTAE

Rhizophysa filiformis (Forskål, 1775) (a.k.a. "Long Stingy Stringy Thingy") CAAB 11 098002

FIELD MORPHOLOGY:

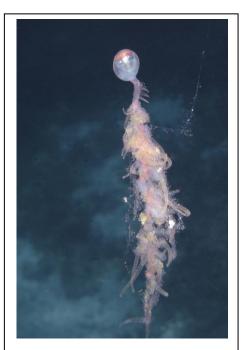
Rhizophysa looks like a small round bubble with a long string hanging from it, on which are attached long gelatinous 'spikes' and some frilly bits. The float may be round or oblong, and is typically plum-coloured on top. Colony can relax to several meters or contract to several centimetres.

The differences between the two known species

are microscopic and generally require expert identification. Specific morphological descriptions are widely available in most texts that describe siphonophores.



Rhizophysa filiformis, preserved, Tasmania. Copyright L. Gershwin



Rhizophysa sp., in life, ©2013 Guido & Philippe Poppe - www.poppe-images.com

MAY BE CONFUSED WITH: *Rhizophysa* is superficially similar to the other 'vertical' siphonophore species, e.g., *Physophora*, *Halistemma*, but those other species have a zone of swimming bells under the float, whereas *Rhizophysa* lacks the swimming bells.

NOTES: Two species have been confirmed in Australian waters, namely *R. filiformis* and *R. eysenhardti*. Both are considered cosmopolitan. Only *R. filiformis* has been confirmed from SE Australian waters, but both species likely occur here.

Rhizophysa has a relatively large spherical pneumatocyst (air bladder) that can lead to confusing signals with acoustic or sonar equipment.

The stings of *Rhizophysa*, like those of many siphonophores, are painful. They are often encountered by fishermen when handling their lines (Cooke and Halstead, 1970). If stung, the affected area should be rinsed well with seawater to wash away any remaining microscopic nematocysts (stinging cells) remaining on the skin: freshwater or tap water should not be used, as it will aggravate the sting. After rinsing with seawater, ice may be used to relieve pain. If systemic symptoms such as difficulty breathing occur, prompt medical attention should be sought.

CNIDARIA: HYDROZOA: SIPHONOPHORA: PHYSONECTAE: AGALMATIDAE

Agalma new species CAAB 11 100901

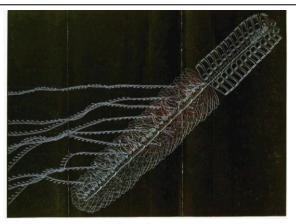
baton with scattered red flecks. Like other physonects, *Agalma* has small float at the extreme anterior end, a mid region of many nectophores or swimming bells, followed by a long stem containing many bracts, tentacles, and stinging palpons. The nectophores are diagnostic: roughly heart-shaped they are longer than broad; the shape of the cavity is broadly Y-shaped or T-shaped, resembling a whale's tail, with a broad opening; and the canals form M-shaped patterns at the ends of the cavity. The nectophores reach about 35mm wide; the colony may be up to a metre long.

MAY BE CONFUSED WITH: Most similar to *Forskalia* in overall appearance but readily separated on their nectophore morphology.

NOTES: Species of *Agalma* are found worldwide in temperate and sub-tropical waters, particularly over continental shelves and at depths down to 400m. This is the first record from Australia.

Their abundance has made them easy targets for research, and as a consequence we know more about the behaviour of *Agalma* than most other siphonophores.

Agalma drifts or swims to position itself in the water column. When feeding, the stem coils into loose arcs above the rest of the colony, and the tentacles and side branches (tentilla) spread out into a formidable invisible feeding net. Only the orange-red tentilla are visible. Agalma uses its tentilla as lures to attract prey, both in their structural appearance and by jiggling the tentilla mimicking the swimming motion of zooplankton (Purcell, 1980).



Agalma clausi - Copyright Bedot, 1888



Agalma nectophore from Tasmania - Copyright L. Gershwin



Agalma sp., New Caledonia - copyright L. Gershwin/SPC

CNIDARIA: HYDROZOA: SIPHONOPHORA: PHYSONECTAE: AGALMATIDAE

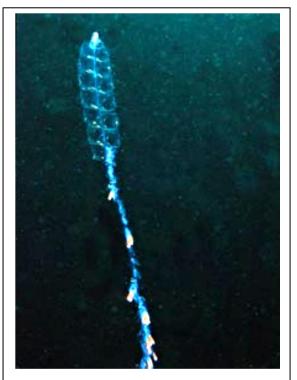
Nanomia bijuga (Delle Chiaje, 1841)

CAAB 11 100001



physonects, *Nanomia* colonies consist of a small ovoid, red-pigmented apical float, followed by a more or less cylindrical region of nectophores, with a long trailing stem. The nectophores are arranged in two rows in an interlocking way. The stem bears numerous groups of organs,

often accented with red or yellow pigmented flecks.



Nanomia bijuga – Copyright Dave Wrobel

The whole colony can reach up to 45cm long, but in Australian waters is more often 3-5cm long at the most; Australian nectophores are typically about 1-2mm wide, of a rounded-boxy form with a voluminous internal cavity.

MAY BE CONFUSED WITH: Similar in general morphology to other physonects, but much more dainty and lacking heavy gelatinous bracts on the stem (such as found in *Agalma* and *Forskalia*) and large palpons (such as those of *Physophora*).

NOTES: *Nanomia* is episodically very common in eastern Australian waters, as it is elsewhere in the world, particularly in the Oxygen Minimum Zone of the open ocean (Purcell et al., 2001b). In fact, its abundance can be so great as to disrupt commercial fishing by clogging the nets (Rogers et al., 1978) or even shoaling in a deep scattering layer that mimics a false bottom on sonar readings (Barham, 1963). In quiescent water the stem of living colonies hangs at about a 45° angle, such that the tentacles all hang down evenly spaced, creating essentially a wall of sting (Berrill, 1930).

The gas in *Nanomia*'s float comprises more than 90% carbon monoxide (Pickwell et al., 1964), although how the animal is not poisoned by this is unclear.

CNIDARIA: HYDROZOA: SIPHONOPHORA: PHYSONECTAE: FORSKALIIDAE

Forskalia edwardsi Kölliker, 1853

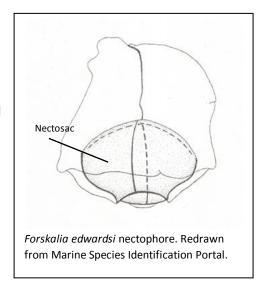
CAAB 11 103001



Forskalia edwardsi – Copyright Denis Riek

FIELD MORPHOLOGY: The anterior portion of the colony consists of a small float, almost completely dwarfed by a cylindrical region of numerous nectophores arranged in multiple rows, followed by the stem which may be several metres long. The nectophores are oddly-shaped, almost boxy, and completely transparent.

MAY BE CONFUSED WITH: Similar in overall appearance to *Agalma* but differentiated as follows: the nectophores and their internal cavities are of completely different shapes, and while the red pigment flecks in *Agalma* are scattered throughout, they are arranged in a row along one side of the stem in *Forskalia*.



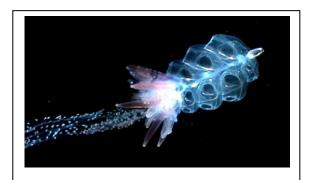
NOTES: When disturbed, the palpons (the reddish stinging batons) may eject a plum or orange coloured drop of bioluminescent liquid from their tips.

This is the first record of Forskalia in Australian waters.

CNIDARIA: HYDROZOA: SIPHONOPHORA: PHYSONECTAE: PHYSOPHORIDAE

Physophora hydrostatica Forskål, 1775

CAAB 11 104001



Physophora hydrostatica - Copyright L. Gershwin/CSIRO.



Physophora hydrostatica -- MIDOC SS2011_T02 -OP25 MIDOC4 Net5

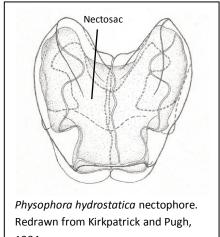
FIELD MORPHOLOGY: This is one of the more

beautiful siphonophores, with a whorl of conspicuous shimmery-orange-pink palpons (stinging batons) protecting the more delicate members of the colony. The apical float is up to 5mm long and quite slender, with the cap pigmented deep-red. The midsection of the colony contains the nectophores in two rows of about 12 each, spiralling down the stem; the nectophores are up to 20mm long, with a Y-shaped central cavity.

MAY BE CONFUSED WITH: The pink palpons make Physophora hard to confuse with others.



Preserved. Photo L. Gershwin



1984.

NOTES: Physophora is found in all the world's oceans and seas, commoner in the Atlantic and in more temperate waters. It is found regularly in SE Australian waters, sometimes quite close in to shore. It has even been reported from a rock pool.

For many years only a single species was recognised, namely P. hydrostatica. However, a second species was discovered in 2004, so it is possible that specific differences may be found in Southern Hemisphere material.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: HIPPOPODIIDAE

Hippopodius hippopus (Forskal, 1776)

CAAB 11 094001



Hippopodius nectophores – 2009 Noumea-Hobart 8/1



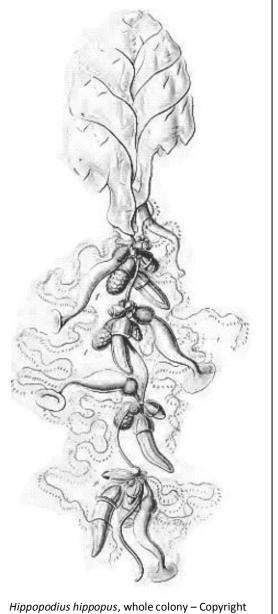
Hippopodius hippopus – Copyright Greg Dellavalle

FIELD MORPHOLOGY:

Up to about ten horseshoe-shaped nectophores fit together alternating on opposite

sides around the stem to form a rounded, somewhat bullet-shaped colony. The colony is very delicate and does not usually hold together in a plankton sample, and it is therefore much more common to find separated nectophores than a whole colony. Transparent in life, with a yellowish stem. Individual nectophores to about 1cm diameter, 3-4mm thick.

MAY BE CONFUSED WITH: Species in the genus *Vogtia* also have numerous nectophores that fit together in a similar manner; however, in *Vogtia* the nectophores are pentagonal to star-shaped, whereas in *Hippopodius* they are horseshoeshaped.



Hippopodius hippopus, whole colony – Copyrigh Haeckel, 1888

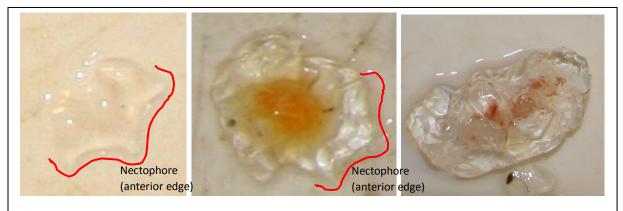
NOTES: The nectophores are brilliantly bioluminescent in life and tend to turn cloudy whitish as they die. Very little is currently known about the biology or ecology of this species.

While most siphonophores feed primarily on copepods and, *Hippopodius* is known to feed exclusively on ostracods and this is probably true for *Vogtia* as well (Pugh, 1991).

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: HIPPOPODIIDAE

Vogtia pentacantha Kölliker, 1853 Voqtia spinosa Keferstein & Ehlers, 1860

CAAB 11 094002 CAAB 11 094003



 $Vogtia\ spp.:\ single\ nectophore\ (left)\ and\ two\ whole\ colonies\ -\ SS2009_TO2-MIDOC2\ //\ Net1\ SS2011\ TO2\ OP53,\ MIDOC8\ Net5\ //\ 2009\ Noumea-Hobart\ 7/31$

FIELD MORPHOLOGY: Six or more pentagonal starshaped nectophores fit together spirally around the stem to form a three-dimensional strangelyshaped many-pointed globular colony. The colony rarely holds together in a plankton sample, and it is therefore much more common to find separated nectophores than a whole colony. The nectophores are more or less pentagonal, smooth or spined, extremely flattened prisms that are utterly transparent and colourless in life, becoming milky whitish when preserved; the stem is yellowish to reddish in life and can be seen through the nectophores.

MAY BE CONFUSED WITH: Species in the genus Hippopodius also have numerous nectophores that fit together in a similar manner. However, in Vogtia the nectophores are pentagonal to starshaped, whereas in Hippopodius they are horseshoe-shaped.

Vogtia spinosa: single nectophore above; whole colony, below – Copyright Bigelow, 1911

NOTES: The nectophores are highly luminescent in

life, even when separated from the colony. This is the first record for both of these species, and indeed for the genus *Voqtia*, in Australian waters.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: PRAYIDAE

Praya reticulata (Bigelow, 1911)

CAAB 11 095001

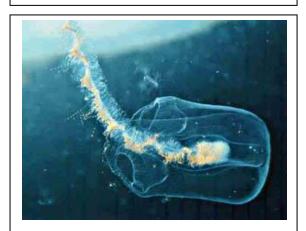


Praya sp. - SS2011_T02 - OP4_MIDOC1



Praya sp. - SS2011 TO2 OP53, MIDOC8 Net1

FIELD MORPHOLOGY: Praya is one of the spectacular pelagics often featured in documentaries on deep sea life: the colony is one the largest invertebrates known, and can grow to more than 40m long; the transparent 'main body' is made of two opposing asymmetrical swimming bells (i.e., nectophores) that can reach 10cm long,



Praya dubia, a closely related species – Copyright Dave Wrobel.

and the transparent and yellow stem is typically about 2.5cm in diameter.

MAY BE CONFUSED WITH: See notes below for Rosacea.

NOTES: *Praya* delivers a powerful sting that can result in a strange cottage cheese-like mottling of the skin followed by peeling of the skin in the sting area in one large layer (similar to that from a bad sunburn or like a snake shedding its skin). While the sting can be painful or even medically worrying to humans, it is often lethal to fish and other invertebrates.

Praya hunts its prey by 'setting its net' of tentacles: with the stem portion of the colony trailing over quite some distance, the animal stops and hangs in the water like a cloud in the sky, and the tentacles are then relaxed into a curtain of sting.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: PRAYIDAE

Rosacea plicata sensu Bigelow, 1911

CAAB 11 095002



Roseacea plicata -- SS2011 TO2 OP11, MIDOC 2 Net1

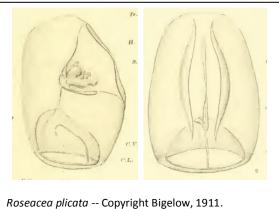


Roseacea plicata -- SS2011 TO2 OP11, MIDOC 2 Net1

FIELD MORPHOLOGY: The nectophores are smooth, more or less rounded-rectangular in outline, with thick, stiff jelly and a hollowed cavity in the posterior portion of each nectophore. The two opposing nectophores are generally separated during collection and sorting. Colour: transparent with a yellow to orange stem. Size typically about 15-20mm long (known to 60mm), 10-15mm wide, 5-10mm thick.

MAY BE CONFUSED WITH: Rosacea superficially resembles Praya, except that Praya is generally much larger, and more rectangular in shape.

NOTES: Rosacea can be incredibly abundant in SE Australian waters at times, with several litres being taken in each sample. This much biomass probably exerts heavy predation pressure during the growth phase and a pulse of organic matter as the bloom dies off, in an ecosystem that is otherwise characterised by





Roseacea plicata -- SS2011 TO2 OP17, MIDOC 3 Net4

low biomass. However, the ecology of these Rosacea blooms and their impact has not been studied.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: DIPHYIDAE

 Chelophyes spp.
 CAAB 11 093902

 Lensia spp.
 CAAB 11 093901

Diphyes spp. CAAB 11 093903 Muggiaea spp. CAAB 11 093904

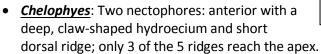


2009 Noumea-Hobart 7/31



Diphyes sp., anterior nectophore – Copyright L. Gershwin. Note gelatinous 'teeth' (arrow).

FIELD MORPHOLOGY: The body resembles a bullet in shape and size. Some species have a 'double bullet' body, i.e., with two nectophores articulated end-on, while other species have only a 'single-bullet' form. The nectophores are of a stiff gelatinous consistency, usually with well developed longitudinal ridges, and are conical and closed at the anterior end; the posterior opening may be surrounded by gelatinous 'ostial teeth'.





Chelophyes sp. – Copyright L. Gershwin. Note claw-shaped hydroecium (arrow).

- <u>Diphyes</u>: Two nectophores: anterior with a complete dorsal ridge and very deep, rounded hydroecium; three large ostial teeth and undivided mouthplate.
- Lensia: One or two nectophores: anterior with very shallow hydroecium and no ostial teeth.
- <u>Muggiaea</u>: One nectophore, with a complete dorsal ridge and very deep, rounded hydroecium; no conspicuous ostial teeth and divided mouthplate.

MAY BE CONFUSED WITH: May be quite easily mistaken for the pseudoconch (gelatinous shell) of the pteropod mollusc *Cymbulia*, in that both have the long, pointy, angular, tough gelatinous nature. However, in *Cymbulia* the surface is covered with tubercles and there is a well in the dorsal side where the visceral mass sits; in contrast, the diphyid siphonophores are hollow from one end, and their surface is smooth.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: DIPHYIDAE

Eudoxoides spiralis (Bigelow, 1911)

CAAB 11 093007



FIELD MORPHOLOGY: The body resembles a bullet in shape and size, but with the whole body distinctly 'twisted'. Only the anterior nectophore is present. The nectophore is of a stiff gelatinous consistency, with five well developed longitudinal ridges twisted along almost their entire length; conical and closed at the anterior end, with the posterior opening bearing small gelatinous 'teeth' and a long rectangular protrusion on one side, in which is contained the stem. The hollow cavity of the body, called a 'nectosac', is voluminous and also twisted. Length to about 15mm.

MAY BE CONFUSED WITH: There is some question as to whether this is truly *Eudoxoides spiralis*, or a closely related separate species. In *E. spiralis*, the lip around the opening of the nectosac contains no spines or teeth, whereas conspicuous teeth are present at the base of each longitudinal ridge in the Australian form. Furthermore, the local form has a relatively longer 'nosecone' and is considerably larger than is typical for the species (i.e., to 11mm). More research should be done on this form to identify whether additional differences exist and what they mean in terms of species recognition criteria.

NOTES: *Eudoxoides* is one of the most abundant siphonophores in the Eastern Mediterranean, Gulf of Mexico, eastern South Africa, and southern Western Australia (Gasca, 1993; Gamulin and Krsinic, 1993b; Gaughan and Fletcher, 1997; Thibault-Botha et al., 2004).

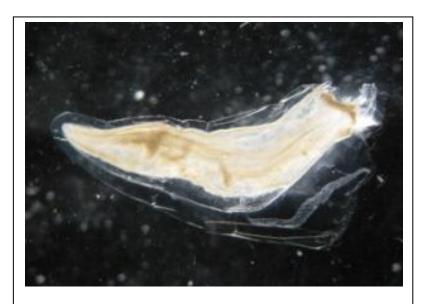
Its presence has not been quantified in SE Australian waters, nor, surprisingly given its prevalence, is much known about its general biology or ecology.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: DIPHYIDAE

Sulculeolaria quadrivalvis de Blainville, 1834

CAAB 11 093010

FIELD MORPHOLOGY: The anterior nectophore resembles a boot in general shape, albeit a small one! The posterior nectophore is more cylindrical. The nectophores are of a stiff gelatinous consistency, lacking longitudinal ridges as are found in other diphyids, conical and closed at the anterior end, with the posterior opening surrounded by gelatinous 'ostial teeth'. The anterior and posterior nectophores are each to about 20mm long.



Sulculeolaria quadrivalvis – Copyright L. Gershwin.

MAY BE CONFUSED WITH: The conspicuous bootlike shape of the anterior nectophore makes this species unlikely to be mistaken for any other.

NOTES: This species has been taken at all times of the year in samples from northern and southern Queensland and is likely to be found in samples from New South Wales.

op Op

Sulculeolaria quadrivalvis – Copyright Totton, 1932: Fig. 19.

Sulculeolaria quadrivalvis is widely distributed in epipelagic waters of the tropical and subtropical regions of the world.

When feeding, the tentacles spread out in what is called a 'Veronica array': the animal swims in an arc to spread the tentacles in a three-dimensional array; drag acting on the stem and tentacles helps to set the pattern (Mackie et al., 1987). The result is 2 to 3 helices of fishing lines appearing as strings of dots (the dots are the nematocyst batteries) spreading in all directions (see photo in Purcell (1984)). In general, *Sulculeolaria* are fast-swimming, active species.

Sulculeolaria species are often infested with the hyperiid amphipod *Paralycaea* spp. (Mackie et al., 1987); for the most part, this association appears to be mutually species-specific.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: ABYLIDAE

Abylopsis tetragona Otto, 1823 Bassia bassensis (Quoy & Gaimard, 1833) CAAB 11 091002 CAAB 11 093901



Abylopsis tetragona – Copyright L. Gershwin.



Abylopsis tetragona – Copyright R. Hopcroft.

FIELD MORPHOLOGY: These are delightfully boxy and angular animals. The anterior nectophore is more or less cuboid; the posterior nectophore is rectangular with one side projecting lower and with bigger 'teeth' than the other side. Total length to 5cm, more typically 1cm.

- Abylopsis: Somatocyst ovoid; posterior nectophore tough, short stalk is to one side
- Bassia: Somatocyst spherical; posterior nectophore delicate; ridges of the nectophores are tinged in blue

MAY BE CONFUSED WITH: *Abylopsis* and *Bassia* might be superficially confused with the diphyid siphonophores (e.g., *Diphyes*, *Chelophyes*) based on their possession of double nectophores; however, confusion seems unlikely because both nectophores of *Abylopsis* and *Bassia* are very boxshaped, whereas those of the diphyids are very streamlined, pointy and bullet-shaped.

NOTES: As the name suggests, *Bassia bassensis* was originally discovered in Bass Strait by early French explorers aboard the ship *Astrolabe* in the 1820s.

Long-term research in the Mediterranean demonstrated that *Abylopsis* abundance is constant through the year and greatest below the thermocline (Buecher, 1999). It is also greatest during less rainy periods, i.e., when the water is warmer and hypersaline.

Both species are considered cosmopolitan, but it seems likely that specific regional differences will be found with closer examination. Like so many other small, inconspicuous pelagic invertebrates, not even their global taxonomy has been studied, let alone their biology and ecology.

This is the first record of *Abylopsis* in Australian waters.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: PRAYIDAE

Amphicaryon acaule Chun, 1888

CAAB 11 095003



Amphicaryon acaule -- 2009 Noumea-Hobart 8/1

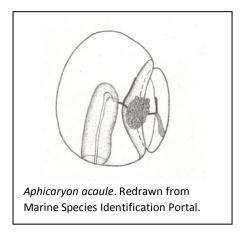
FIELD MORPHOLOGY: These are unmistakable little spheres of clear jelly with yellow in the middle. Upon closer examination, the sphere is comprised of two parts, one much larger and partially enclosing the smaller. The yellow bit inside is the stem. Diameter to 10mm, but often smaller.

MAY BE CONFUSED WITH: These might be mistaken for the small spherical siphonophore *Sphaeronectes*, but *Sphaeronectes* is essentially a sphere with a big hollow middle, wheres *Amphicaryon* is more like a solid sphere with the two parts articulated.

It is also possible that one might confuse *Amphicaryon* with cydippid ctenophores (the small, nearly spherical comb jellies, e.g., *Euplokamis* and *Pukia*), but they can be instantly distinguished in several ways: (1) ctenophores have 8 'comb rows' of cilia on the body, whereas *Amphicaryon* does not; (2) *Amphicaryon* has two parts that can be separated, whereas ctenophores do not; (3) the stem inside of *Amphicaryon* is almost always yellow, whereas the internal organs of ctenophores are generally whitish unless they have



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recently eaten something pigmented; and (4) *Euplokamis* and *Pukia* are about 20mm long, whereas *Amphicaryon* is about one-fourth that size.

NOTES: Common worldwide in warmer waters except, curiously, not often found in the Mediterranean. This is the first record for *Amphicaryon* in Australian waters.

CNIDARIA: HYDROZOA: SIPHONOPHORA: CALYCOPHORA: SPHAERONECTIDAE

Sphaeronectes tasmanica, new species

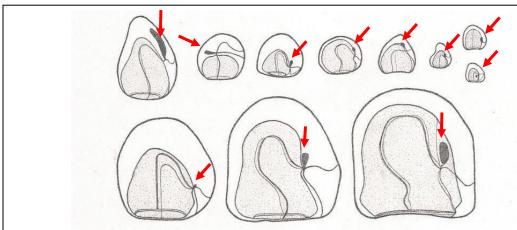
CAAB 11 096901



Sphaeronectes tasmanica, holotype SAMA H1945, preserved – copyright L. Gershwin.



Sphaeronectes tasmanica, in life – copyright L. Gershwin.



Illustrations of the eleven described *Sphaeronectes* species. Arrows indicate position of somatocyst. Top row, from left: *S. brevitruncata* Chun, 1892; *S. koellikeri* Huxley, 1859; *S. irregularis* Claus, 1874; *S. fragilis* Carré, 1968; *S. pughi*; *S. pagesi* Lindsay et al., 2011; *S. bougisi* Carré, 1968; *S. gamulini* Carré, 1966; Bottom row, from left: *S. tiburonae* Pugh, 2009; *S. christiansonae* Pugh, 2009; *S. haddocki* Pugh, 2009. All redrawn from Grossmann et al. 2011.

FIELD MORPHOLOGY: Body sub-spherical and of soft gelatinous consistency. The majority of the body is a large cavity (nectosac), with a separate narrower cavity (hydroecium) next to it and arching over it containing the retractile stem. In this new species, the somatocyst attaches apically relative to the nectosac as in *S. koellikeri*, but the hydroecium opens orally, as in most other species. The body is transparent and the stem is pale yellowish. Total diameter to about 1cm.

MAY BE CONFUSED WITH: See Amphicaryon and the ctenophores Pukia and Euplokamis.

NOTES: A key to the world species of <i>Sphaeronectes</i> is presented in Grossmann et al. (2011). This new species will be more thoroughly described in an upcoming publication.		

GLOSSARY TO THE SIPHONOPHORES

Aboral – literally, 'away from the mouth', or in siphonophores, "away from the ostium"; the term is used for orientation. See also 'oral'.

Anterior – the forward end.

Anterior nectophore – in diphyids with two nectophores, the front one.

Apical ridges – the external ridges of the nectophore reaching the apex, or summit.

Basal lamella – mesogleal element of the mouthplate.

Bioluminescence – biological light, made by organisms in a chemical reaction inside their tissues.

Blastostyle – the cormidial element that bears the gonophores.

Bract – mesogleal elements of the cormidia with a protective or buoyancy function.

Colony – a genetically identical group, usually physically connected; siphonophores are variably interpreted as an individual or as a colony.

Cormidium – an organised group of 'persons' in the colony, usually containing one or more of the following: gastrozooids, gonozooids, bracts, tentacles, palpons (in Physonects), and a blastostyle.

Deep Scattering Layer – a layer of animals in the ocean detectable by acoustics as a 'false bottom'.

Diphyids – members of the family Diphyidae, the bullet-shaped species.

Dorsal – the orientation direction relating to the longest edge in diphyids; opposite of ventral.

Dorsal ridge – the longitudinal ridge running down the long side of diphyid nectophores; features of the dorsal ridge are often diagnostic.

Epipelagic – the upper 200m of the open ocean water column, where enough light penetrates to drive photosynthesis; about 90% of all ocean life lives in this layer, and siphonophores are common here. Also called the 'euphotic zone' or 'sunlit zone'.

Eudoxid – detached, free-swimming reproductive stage of calycophorans.

Float – see 'pneumatophore'.

Gastrozooid – feeding 'person', located on the siphosome as a member of a cormidial group.

Gonad – reproductive organ.

Gonozooid – reproductive 'person', located on the siphosome as a member of a cormidial group.

Hydroecium – the 'stem niche': a cavity in the anterior nectophore of calycophorans from which the stem emerges.

Mesopelagic – the layer of the open ocean water column from 200m to 1000m, where an insufficient amount of light penetrates for photosynthesis; siphonophores are one of the primary predators in this zone. Also called the 'twilight zone' because of its low light.

Mouthplate – an extension of one side of the nectophore below the ostium, comprising one or more basal lamella; whether the mouthplate is divided or undivided is highly diagnostic.

Morphology – the anatomical or structural features of a species.

Nectophore – the swimming bell of a siphonophore, the muscular contractions of which give the animal its jet propulsion capabilities.

Nectosac – the open space in a nectophore where water used in jet propulsion is pumped from; believed to be homologous to the subumbrellar cavity of medusae.

Nectosome – the portion of the stem which bears nectophores.

Nematocyst – stinging cell, found in all members of the phylum Cnidaria (e.g., jellyfish, corals, sea anemones).

Oral – the mouth-end of the animal or nectophore; see also 'aboral'.

Ostial teeth – gelatinous 'spike-like' or 'tooth-like' protrusions around the ostium (opening) of the nectosac in some genera of calycophoran siphonophores.

Ostium – literally 'opening'; in siphonophores, the opening of the nectosac.

Oxygen Minimum Zone – a zone in the water column of the open ocean where the oxygen is permanently reduced; some species use this zone for feeding or refuge.

Palpon – a cormidial element with a sensory, excretory, or stinging function.

Pelagic - drifting.

'Persons' – the cormidial elements such as gonozooids, gastrozooids, dactylozooids, etc.

Pneumatophore – the gas-filled float in cystonect and physonect species.

Posterior – the back end.

Posterior nectophore – in diphyids with two nectophores, the back one.

Radial canals – fine extensions of the gastrovascular system, the shape of which are diagnostic.

Siphosome – the portion of a colony without swimming bells or a float, i.e., the main portion with the stinging and other pigmented bits.

Somatocyst – in calycophoran nectophores, a prominent extension of the gastrovascular system; the length, shape, and position of the somatocyst are highly diagnostic.

Stem – the central cord of the colony onto which all the other bits are connected.

Swimming bell – see 'nectophore'.

Tentacles – highly extensile filaments used in feeding and defence.

Tentilla (singular tentillum) – side branches of tentacles, may be used as lures in feeding.

Thermocline – a layer in the ocean where temperature changes more rapidly than above or below.

Ventral – orientation of a diphyid nectophore relating to the short side opposite the longest side.

CHECKLIST FOR THE SIPHONOPHORES







<u>Rhyzophysa</u>

Agalma/ Forskalia

<u>Nanomia</u>









Physophora

Hippopodius

Vogtia

<u>Praya</u>







<u>Rosacea</u>

Lensia / Muggiaea / Chelophyes / Diphyes

Eudoxoides









<u>Sulculeolaria</u>

Abylopsis / Bassia

<u>Amphicaryon</u>

Sphaeronectes

REFERENCES ON THE SIPHONOPHORES

The following references may be of use across a broad field of interests including biology, ecology, taxonomy, physiology, evolution, bloom dynamics, and faunistics. Many are available online through Google, Biodiversity Heritage Library, the journals of publication, or the authors.

- Alvariño, A. 1971. Siphonophores of the Pacific with a review of the world distribution. Bull. Scripps Inst. Oceanogr. 16: 1-432.
- Båmstedt, U., J. H. Fosså, M. B. Martinussen and A. Fosshagen. 1998. Mass occurrence of the physonect siphonophore *Apolemia uvaria* (Lesueur) in Norwegian waters. Sarsia 83: 79-85.
- Barham, E. G. 1963. Siphonophores and the deep scattering layer. Science (Washington DC) 140: 826-828.
- Bedot, M. 1896. Les Siphonophores de la baie d'Amboine. Etude suivie d'une Revision de la famille des Agalmidae. Revue Suisse de Zoologie et Annales du Mus. d'Hist. Nat. de Genève 3: 367-414, Tafel 12.
- Benfield, M. C., A. C. Lavery, P. H. Wiebe, C. H. Greene, T. K. Stanton and N. J. Copley. 2003. Distributions of physonect siphonulae in the Gulf of Maine and their potential as important sources of acoustic scattering. Can. J. Fish. Aquat. Sci. 60(7): 759-772.
- Berrill, N. J. 1930. On the occurrence and habits of the siphonophore *Stephanomia bijuga* (Delle Chiaje). Journal of the Marine Biological Association of the United Kingdom 16: 753-755.
- Bigelow, H. B. 1911a. Biscayan plankton collected during a cruise of H.M.S. 'Research', 1900. Part XIII, The Siphonophora. Transactions of the Linnean Society of London, 2d Series. Zoology 10: 337–358, 1 plate.
- Bigelow, H. B. 1911b. The Siphonophorae. Reports of the scientific research expedition to the tropical Pacific. Albatross XXIII. Memoirs of the Museum of Comparative Zoology, Harvard 38(2): 173–401, 32 plates.
- Bigelow, H. B. and M. Sears. 1937. Siphonophorae. Report on the Danish Oceanographical Expeditions 1908–1910 to the Mediterranean and adjacent seas 2. Biology(2): 1–144, 83 figs.
- Biggs, D. C. 1977. Field studies of fishing, feeding, and digestion in siphonophores. Marine Behaviour and Physiology 4(4): 261-274.
- Biggs, D. C., P. R. Pugh and C. Carré. 1978. *Rosacea flaccida* n. sp., a new species of siphonophore (Calycophorae Prayinae) from the North Atlantic Ocean. Beaufortia 27(340): 207–218.
- Bone, Q. and E. R. Trueman. 1982. Jet propulsion of the calycophoran siphonophores *Chelophyes* and *Abylopsis*. Journal of the Marine Biological Association of the United Kingdom 62: 263-276.
- Browne, E. T. 1926. Siphonophorae from the Indian Ocean. Trans. Linn. Soc. Lond. (Zool.). (2) 19: 55-86.
- Buecher, E. 1999. Appearance of *Chelophyes appendiculata* and *Abylopsis tetragona* (Cnidaria, Siphonophora) in the Bay of Villefranche, northwestern Mediterranean. Journal of Sea Research 41(4): 295-307.
- Burnett, J. W. and W. D. Gable. 1989. A fatal jellyfish envenomation by the Portuguese man-o'war. Toxicon 27(7): 823-824.
- Carré, C. 1979. Sur le genre *Sulculeolaria* Blainville, 1834 (Siphonophora, Calycophorae, Diphyidae). Annales de l'Institut Oceanographique 55(1): 27–48.
- Carré, C. and D. Carré. 1991. A complete life cycle of the calycophoran siphonophore *Muggiaea kochi* (Will) in the laboratory, under different temperature conditions: Ecological

- implications. Philosophical Transactions of the Royal Society of London B Biological Sciences 334(1269): 27-32.
- Caster, K. E. 1942. Two siphonophores from the Paleozoic. Palaeontographica Americana 3(no.14): ca 31 pp + 2 pls.
- Chun, C. 1897. Die Siphonophoren der Plankton-expedition. Kiel, Lipsius & Tischer.
- Claus, C. 1889. On the organism of the Siphonophora and their phylogenetic derivation: a criticism upon E. Haeckel's so-called Medusome-theory. Ann. & Mag. N. Hist. Ser. 6 4: 185-198.
- Cooke, T. S. and B. W. Halstead. 1970. Report of stingings by the coelenterate *Rhizophysa eysenhardti* Gegenbaur in California waters. Clinical Toxicology 3(4): 589-595.
- Daniel, R. 1974. Siphonophora of the Indian Ocean. Memoirs of the Zoological Survey of India 15(4): 1–242.
- Dunn, C. W., P. R. Pugh and S. H. D. Haddock. 2005. Molecular phylogenetics of the Siphonophora (Cnidaria), with implications for the evolution of functional specialization. Syst. Biol. 54(6): 916–935.
- Dunn, C. W. and G. P. Wagner. 2006. The evolution of colony-level development in the Siphonophora (Cnidaria:Hydrozoa). Development, Genes, and Evolution 216: 743–754.
- Gamulin, T. and F. Krsinic. 1993. Distribution and abundance of calycophores (Siphonophora, Calycophorae) in the Mediterranean and Adriatic Sea. Marine Ecology 14(2): 97-111.
- Garstang, W. 1946. The morphology and relations of the Siphonophora. Quarterly Journal of Microscopical Science 87(2): 103-195, 57 text figs.
- Gasca, R. 1993. Species and abundance of siphonophores (Cnidaria: Hydrozoa) in the southern region of the Gulf of Mexico. Caribbean Journal of Science 29(3-4): 220-225.
- Gasca, R. 2009. Diversity of Siphonophora (Cnidaria: Hydrozoa) in the Western Caribbean Sea: new records from deep-water trawls. Zootaxa 2095: 60-68.
- Gaughan, D. J. and W. J. Fletcher. 1997. Effects of the Leeuwin current on the distribution of carnivorous macrozooplankton in the shelf waters off southern Western Australia. Estuarine Coastal and Shelf Science 45(1): 89-97.
- Gough, L. H. 1905. On the distribution and migration of *Muggiaea atlantica* Cunningham. Pub. Circ. Cons. Explor. Mer. 29: 13 pp., 3 charts.
- Gould, S. J. 1984. A most ingenious paradox: When is an organism a person; when is it a colony? Natural History 93(Dec): 20-30.
- Greve, W. 1994. The 1989 German Bight invasion of *Muggiaea atlantica*. ICES Journal of Marine Science 51(4): 355-358.
- Grossmann, M. M., D. J. Lindsay and V. Fuentes. 2011. *Sphaeronectes pughi* sp. nov., a new species of sphaeronectid calycophoran siphonophore from the subantarctic zone. Polar Science 6(2): 196–199.
- Haddock, S. H. D. 2005. The complex world of siphonophores. JMBA Global Marine Environment Summer 2005(2): cover + 24-25.
- Haddock, S. H. D., C. W. Dunn and P. R. Pugh. 2005. A reexamination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable biooptical properties. J. Mar. Biol. Assoc. U.K. 85: 695-707.
- Haddock, S. H. D., C. W. Dunn, P. R. Pugh and C. E. Schnitzler. 2005. Bioluminescent and redfluorescent lures in a deep-sea siphonophore. Science 309: 263.
- Haeckel, E. 1874. System der Siphonophoren. Jenaische Zeitschrift für Naturwissenschaft Band 22: 1-46.
- Hissmann, K. 2005. In situ observations on benthic siphonophores (Physonectae: Rhodaliidae) and descriptions of three new species from Indonesia and South Africa. Systematics and Biodiversity 2(3): 223–249.

- Huxley, T. H. 1859. The Oceanic Hydrozoa: A description of the Calycophoridae and Physophoridae observed during the voyage of the H.M.S. "Rattlesnake" in the years 1846–1850. London, Ray Society.
- Kirkpatrick, P. A. and P. R. Pugh. 1984. Siphonophores and Velellids: Keys and notes for the identification of the species. Leiden, E.J. Brill/Dr. W. Backhuys.
- Leloup, E. 1955. Siphonophores. Rep. Scient. Results Michael Sars N. Atlant. Deep Sea Exped. 5(11): 1-24.
- Lens, A. D. and T. van Riemsdijk. 1908. The Siphonophora of the Siboga expedition. Siboga-Expeditie Monograph 9: 1–130.
- Mackie, G. O. 1963. Siphonophores, bud colonies, and superorganisms. The lower Metazoa. E. C. Dougherty. Berkeley, University of California: 329-337.
- Mackie, G. O. 1964. Analysis of locomotion in a siphonophore colony. Proc. Royal Soc. London, B 159(No. 975): 366-391, 9 text-figs.
- Mackie, G. O. 1973. Report on giant nerve fibres in *Nanomia*. Publ. Seto Mar. Biol. Lab. 20 (Proc. Second Internat. Symp. Cnidaria): 745-756.
- Mackie, G. O. 1978. Coordination in Physonectid Siphonophores. Mar. Behav. Physiol. 5: 325-346.
- Mackie, G. O. and D. A. Boag. 1963. Fishing, feeding and digestion in siphonophores. Pubblicazione della Stazione zoologica di Napoli 33: 178-196.
- Mackie, G. O., P. R. Pugh and J. E. Purcell. 1987. Siphonophore biology. Advances in Marine Biology 24: 97-262.
- Mapstone, G. M. 2009. Siphonophora (Cnidaria, Hydrozoa) of Canadian Pacific waters. Ottawa, Ontario, Canada, NRC Research Press.
- Margulis, R. Y. 1987. Siphonophora of the South Pacific Coelenterata Hydrozoa. Vestnik Moskovskogo Universiteta Seriya XVI Biologiya(2): 24-28.
- Margulis, R. Y. 1988. Revision of the Subfamily Clausophyinae Siphonophora Diphyidae. Zoologicheskii Zhurnal 67(9): 1269–1281.
- Margulis, R. Y. 1994. Revision of the genus *Rosacea* (Cnidaria, Siphonophora, Calycophorae, Prayidae, Prayinae). Zoologicheskii Zhurnal 73(11): 15–28.
- Margulis, R. Y. and D. O. Alekseev. 1985. On the genus *Lensia* (Siphonophora, Calycophorae). Zoologicheskii Zhurnal 64(1): 5–15 [In Russian, with English summary].
- Musayeva, E. I. 1976. Distribution of siphonophores in the eastern part of the Indian Ocean. Trudy Instituta Okeanologii 105: 171-197. (in Russian).
- Neppi, V. 1921. Sifonofori del Golfo di Napoli. Publ. Staz. Zool. Napoli, Milano 3: 223-228.
- Pagès, F. and J. M. Gili. 1992. Siphonophores Cnidaria Hydrozoa of the Benguela Current Southeastern Atlantic. Scientia Marina 56(SUPPL. 1): 65–112.
- Pagès, F., J. M. Gili and J. Bouillon. 1989. The siphonophores (Cnidaria, Hydrozoa) of Hansa Bay, Papua New Guinea. Indo-Malayan Zoology 6: 133-140.
- Pickwell, G. V. 1966. Physiological dynamics of siphonophores from deep scattering layers: size of gas-filled floats and rate of gas production, U.S. Navy Electronics Laboratory: 50 pp.
- Pickwell, G. V. 1967. Gas and bubble production by Siphonophores. Dept. of the Navy, Naval Undersea Warfare Centre, NUWC TP. San Diego, California, Marine Environment Division. 8: 1-87.
- Pickwell, G. V. 1970. The physiology of carbon monoxide production by deep-sea coelenterates: causes and consequences. Annals of the New York Academy of Sciences 174: 102-115.
- Pickwell, G. V., E. G. Barham and J. W. Wilton. 1964. Carbon monoxide production by a bathypelagic siphonophore. Science 144(1620): 860-862.
- Pugh, P. R. 1983. Benthic Siphonophores: A review of the family Rhodaliidae. (Siphonophora, Physonectae). Philosophical Transactions of the Royal Society of London B Biological Sciences 301(1105): 165-300, pls.

- Pugh, P. R. 1991. Co-occurrence of hippopodiid siphonophores and their potential prey. Hydrobiologia 216/217: 327-334.
- Pugh, P. R. 1992. A Revision of the Subfamily Nectopyramidinae (Siphonophora, Prayidae).

 Philosophical Transactions of the Royal Society of London B Biological Sciences 335(1274): 281-322.
- Pugh, P. R. 1999. Siphonophorae. South Atlantic Zooplankton. D. Boltovskoy. Leiden, Backhuys: 467-511.
- Pugh, P. R. 2002. A new species of *Rosacea* (Siphonophora: Calycophorae: Prayidae) from the Gulf of Oman. Journal of the Marine Biological Association of the United Kingdom 82: 171-172.
- Pugh, P. R. 2003. A revision of the family Forskaliidae (Siphonophora, Physonectae). Journal of Natural History 37: 1281-1327.
- Pugh, P. R. 2005. A new species of *Physophora* (Siphonophora: Physonectae: Physophoridae) from the North Atlantic, with comments on related species. Systematics and Biodiversity 2(3): 251–270.
- Pugh, P. R. 2009. A review of the family Sphaeronectidae (Class Hydrozoa, Order Siphonophora), with the description of three new species. Zootaxa 2147: 1-48.
- Pugh, P. R., F. Pagés and B. Boorman. 1997. Vertical distribution and abundance of pelagic cnidarians in the eastern Weddell Sea, Antarctica. Journal of the Marine Biological Association of the United Kingdom 77: 341-360.
- Pugh, P. R. and M. J. Youngbluth. 1988. Two new species of prayine siphonophore (Calycophorae, Prayidae) collected by the submersibles *Johnson-Sea-Link I* and *II*. Journal of Plankton Research 10(4): 637-657.
- Purcell, J. E. 1980. Influence of siphonophore behavior upon their natural diets: evidence for agressive mimicry. Science, N.Y. 209: 1045-1047.
- Purcell, J. E. 1981a. Selective predation and caloric consumption by the siphonophore *Rosacea cymbiformis* in nature. Marine Biology 63: 283-294.
- Purcell, J. E. 1981b. Feeding ecology of *Rhyzophysa eysenhardti*, a siphonophore predator of fish larvae. Limnology and Oceanography 26: 424-432.
- Purcell, J. E. 1981c. Dietary Composition and Diel Feeding Patterns of Epipelagic Siphonophores. Marine Biology 65(1): 83-90.
- Purcell, J. E. 1982. Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham, 1893). J. Exp. Mar. Biol. Ecol. 62: 39-54.
- Purcell, J. E. 1983. Digestion rates and assimilation efficiencies of siphonophores fed zooplankton prey. Marine Biology 73: 257-261.
- Purcell, J. E. 1984. The functions of nematocysts in prey capture by epipelagic siphonophores (Coelenterata, Hydrozoa). Biological Bulletin (Woods Hole) 166(2): 310-327.
- Purcell, J. E. and P. Kremer. 1983. Feeding and metabolism of the siphonophore *Sphaeronectes gracilis*. J. Plankton Res. 5: 95-106.
- Purcell, J. E. and C. E. Mills. 1988. The correlation between nematocyst types and diets in pelagic Hydrozoa. The Biology of Nematocysts. D. A. Hessinger and H. M. Lenhoff. San Diego, Academic Press, Inc.: Chapter 24 (463-485).
- Purcell, J. E., D. L. Breitburg, M. B. Decker, W. M. Graham, M. J. Youngbluth and K. A. Raskoff. 2001. Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. Coastal Hypoxia: consequences for living resources and ecosystems. N. N. Rabalais and R. E. Turner, American Geophysical Union: Coastal and Estuarine Studies Series 58: 77-100.
- Robison, B. H., K. R. Reisenbichler, R. E. Sherlock, J. M. B. Silguero and F. P. Chavez. 1998. Seasonal abundance of the siphonophore, Nanomia bijuga, in Monterey Bay. Deep-Sea Res. II, 45: 1741-1751. need -
- Rogers, C. A. 1976. Impact of autumn-winter swarming of a siphonophore ("Lipo") on fishing in coastal waters of New England.

- Rogers, C. A., D. C. Biggs and R. A. Cooper. 1978. Aggregations of the siphonophore *Nanomia cara* Agassiz 1865 in the Gulf of Maine: observations from a submersible. Fishery Bulletin (Washington, D.C.) 76(1): 281-284.
- Russell, F. S. 1938. On the development of *Muggiaea atlantica* Cunningham. Journal of the Marine Biological Association of the United Kingdom 22: 441-446, 6 figs.
- Sears, M. 1953. Notes on siphonophores 2. A revision of the Abylinae. Bulletin of the Museum of Comparative Zoology at Harvard College 109(1): 1-119.
- Sherlock, R. E. and B. H. Robison. 2000. Effects of temperature on the development and survival of *Nanomia bijuga* (Hydrozoa, Siphonophora). Invertebrate Biology 119(4): 379-385.
- Spencer, A. N. 1971. Myoid conduction in the siphonophore *Nanomia bijuga*. Nature, London 233(5320): 490-491.
- Thibault-Botha, D., J. R. E. Lutjeharms and M. J. Gibbons. 2004. Siphonophore assemblages along the east coast of South Africa; mesoscale distribution and temporal variations. Journal of Plankton Research 26(9): 1115-1128.
- Totton, A. K. 1932. Siphonophora. Scientific reports / Great Barrier Reef Expedition, 1928-29 4(10): 317-374, text-figs. 1-36.
- Totton, A. K. 1936. Plankton of the Bermuda Oceanographic Expeditions. VII. Siphonophora taken during the year 1931. Zoologica, N. Y. 21(4): 231-240.
- Totton, A. K. 1954. Siphonophora of the Indian Ocean, together with systematic and biological notes on related specimens from other oceans. "Discovery" Report 27: 1-162, 12 pls., 83 text-figs.
- Totton, A. K. 1965. A Synopsis of the Siphonophora. London, British Museum of Nat. Hist.
- Vanhöffen, E. 1906a. Siphonophoren. Nordisches Plankton 6(11): 9-39.