

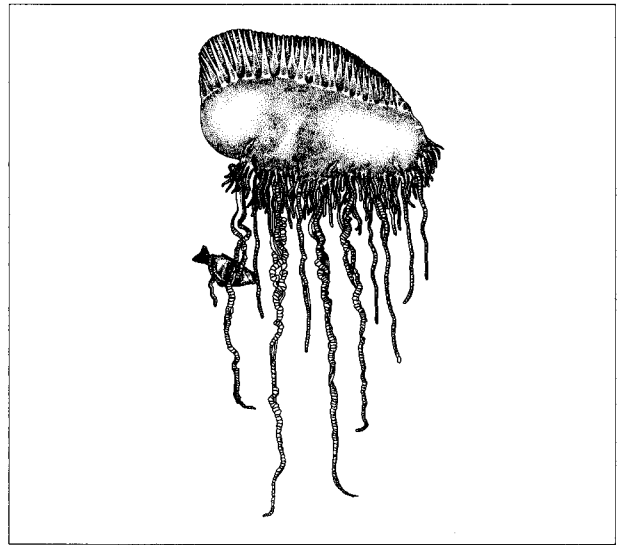
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Siphonophorae (Cnidaria) of the Gulf of Mexico

Philip R. Pugh and Rebeca Gasca

The siphonophorae are a subclass of the class Hydrozoa, phylum Cnidaria. They are highly polymorphic and complex animals, and their zooids, both medusoid and polypoid, have become specialized to carry out various functions, such as swimming, feeding, reproduction, and protection. Although phylogenetically they originated as colonies, structurally, physiologically, and embryologically they qualify as an organism (Wilson 1975), and they are sometimes referred to as “superorganisms” (Mackie 1963). They are exclusively marine, and the vast majority of species are pelagic. The only exceptions are a family of physonect siphonophores, the Rhodaliidae, that use their tentacles to attach themselves to the bottom substrate, and the only well-known species, the Portuguese Man o’ War *Physalia physalis*, which is pleustonic, floating at the surface with its tentacles hanging down many tens of meters into the water below. Siphonophores occur in a bewildering array of shapes and sizes, and can vary in length from a few millimeters to several tens of meters; some are undoubtedly the longest animals in the world (Robison 2004). They can be found throughout the world’s oceans, and throughout the water column down to a depth of at least 4500 m, although individual species are restricted in their geographical and depth distributions to a lesser or greater extent.

Classically, siphonophores have been split into 3 orders, based first on the presence (Cystonectae and Physonectae) or absence (Calycophorae) of an apical, gas-filled float (pneumatophore). The orders whose species possess a pneumatophore are split according to whether



Siphonophora. After Brusca and Brusca 2003, modified by F. Moretzsohn.

asexual swimming bells (nectophores), arranged in a biserial or spiral series immediately below the float, are present (Physonectae) or absent (Cystonectae). However, recent molecular studies (Dunn, Pugh, and Haddock 2005) have shown that although the Cystonectae are monophyletic and sister to all other siphonophores, the Physonectae are paraphyletic and gave rise to the Calycophorae. Dunn, Pugh, and Haddock (2005) suggested that these 2 latter groups should be collectively called the Codonophora. The consequence of this study is that the traditional taxonomy of the Physonectae will have to be

substantially altered, particularly with regard to the families Agalmatidae and Athorybiidae. However, because we do not yet know the phylogenetic relations of all the physonect genera, for the present review the classical systematic arrangement, as summarized by Totton (1965), will be maintained, with the addition of the recently established family Erennidae (Pugh 2001).

The best text for the systematics and morphology of siphonophores remains *A Synopsis of the Siphonophora* by Totton (1965), although 7 of the species presently recorded in the Gulf of Mexico have been described since then. Other useful, well-illustrated texts on the siphonophores of certain areas are Bouillon et al. (2004, Mediterranean); Gasca (1990b, Gulf of Mexico); Kirkpatrick and Pugh (1984, British Isles); Pagès and Gili (1992, South West Africa); and Pugh (1999a, South Atlantic); the last includes a key to the species occurring in that region, with illustrations of all but 13 of the species now known to be present in the Gulf of Mexico. Mackie, Pugh, and Purcell (1987) have summarized our knowledge regarding their biology, evolution, distribution, and ecology, and Carré and Carré (1995) have considered their anatomy and reproduction.

Phillips (1972) considered that, for the original list of siphonophores from the Gulf of Mexico, Sears (1954) "presents a hypothetical list of siphonophores, none based on actual records." In actuality this is not the case, as her list of 24 species appears to be almost exclusively based on Bigelow (1918), although some of the species Bigelow listed were actually caught in the western Atlantic and not in the Gulf of Mexico. Nonetheless, there were some species that had previously been found in the Gulf of Mexico that Sears did not include. In recent years, there have been many studies on the siphonophores of the Gulf of Mexico, as summarized by Gasca (2002). The vast majority of these have reported on net collections in the top 200–500 m of the water column, and there are very few records from greater depths (Stepanjants 1975). However, judging by the number of species new to the Gulf of Mexico that have been collected recently by submersibles (e.g., Pugh 2001), there is probably still a large number to add to the present list of 82. This number represents almost half of the total number of about 175 siphonophore species that are currently recognized as valid. None of the species found in the Gulf are endemic to the area.

Although only 24 siphonophore species were found in all 4 quadrants of the Gulf of Mexico, with the largest number of species being found in the 2 southern ones, this

is largely a reflection of sampling effort, and one would expect to find all the species throughout the area. Most of the 13 species found exclusively in the SE quadrant were recently collected by the submersible *Johnson-Sea-Link*, and the only quadrant where net sampling took place at depths greater than 500 m was the SW one, where 9 species were exclusively found.

Abbreviations

In the checklist, the families, and the genera and species within each, are listed in alphabetical order for each of the orders—Cystonectae, Physonectae, and Calycophorae, respectively. Under the heading of Habitat-Biology, each species is considered to be either neritic (ner) or deep-sea (dps), and, for the pelagic species, their depth distribution is categorized as epipelagic (epp = 0–ca. 300 m), mesopelagic (mep = ca. 300–1000 m), and/or bathypelagic (bap = >1000 m). The latter categories refer the usual depth ranges where the species occur (Pugh, unpublished data), which may not be reflected in the records from the Gulf of Mexico itself. One species is pleustonic (ple). Under the heading Overall Geographic Range, the geographical distribution of a species is considered in 3 ways. First, whether the species has a widespread distribution in the world's oceans (world) or is restricted to either the Atlantic (Atl), Indian (Ind), or Pacific (Pac) Oceans, or to the Mediterranean (Med) Sea. For rarer species, where there is no clear-cut pattern of distribution, they are considered to have sporadic occurrences. Second, within these distributional zones, the waters where the species is most abundant, when known, are considered broadly as either tropical (trop), subtropical (subtrop), temperate (temp), or boreal. It should be recognized, however, that these are very coarse categories and that their boundaries vary spatially. Third, the relative abundance of each species is indicated by the categories: v. common, common, uncommon, rare, and v. rare.

The specimens from which the new records for the Gulf of Mexico are derived are currently housed in the National Oceanography Centre Collections (NOCC). The numbers refer to the *Johnson-Sea-Link* dives during which the specimens were collected. At some time in the future, once the specimens have been fully examined and described, it is intended to transfer them to the U.S. National Museum of Natural History (Smithsonian Institution).

Abbreviations used in the Habitat-Biology column of the checklist include bap = bathypelagic; dps = deep sea;

epp = epibenthic/planktonic; mep = mesopelagic; ner = neritic; ple = pleustonic; plg = pelagic.

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Taxonomic summary for Siphonophora of the Gulf of Mexico.

Order	Total species	Number endemic species	Number nonindigenous species
Cystonectae	3	0	0
Physonectae	21	0	0
Calycophorae	58	0	0
Total	82	0	0

Checklist of Siphonophora from the Gulf of Mexico.

Taxon	Habitat-Biology	Depth (m)	Overall geographic range	GMx range	References/Endnotes
Order: Cystonectae					
Family: Physaliidae					
<i>Physalia physalis</i> (Linnaeus, 1758)	ple	Surface	World, trop-temp, common	entire	10, 18, 24
Family: Rhizophysidae					
<i>Rhizophysa eysenhardti</i> Gegenbaur, 1859	dps, epp, mep	0–10	World, trop-temp, sporadic	se	22
<i>Rhizophysa filiformis</i> (Forskål, 1775)	dps, epp, mep	0–200	World, trop-temp, sporadic	nw, ne, sw	5, 8, 24
Order: Physonectae					
Family: Agalmatidae					
<i>Agalma elegans</i> (Sars, 1846)	dps, epp, mep	0–200	World, trop-temp, common	sw, se	10, 13, 18
<i>Agalma okeni</i> Eschscholtz, 1825	dps, epp	0–200	World, trop-temp, common	entire	2, 5, 10, 13, 14, 24
<i>Cordagalma cordiforme</i> Totton, 1936	dps, epp	0–200	World, trop-temp, common	nw, ne, sw	3, 5, 12, 24
<i>Frillagalma vityazi</i> Daniel, 1966	dps, mep	500–1500	World, trop-temp, uncommon	se	¹
<i>Halistemma cupulifera</i> Lens & van Riemsdijk, 1908	dps, mep	683	Sporadic, rare	se	¹
<i>Halistemma rubrum</i> (Vogt, 1852)	dps, epp, mep	0–200	World, trop-temp, common	ne, sw, se	2, 12, 24 ²
<i>Halistemma striata</i> Totton, 1965	dps, mep	814	Sporadic, rare	ne	³
<i>Lychnagalma utricularia</i> (Claus, 1879)	dps, mep	700–800	World, trop-temp, uncommon	ne, se	⁴
<i>Marrus orthocannoides</i> Totton, 1954	dps, plg	0–1410	Sporadic, rare	se	24 ⁵
<i>Nanomia bijuga</i> (delle Chiaje, 1841)	dps, epp, mep	0–200	World, trop-temp, common	entire	14, 24, 33
<i>Stephanomia amphitridis</i> Lesueur & Petit, 1807	dps, mep	750–850	Atl/Ind, ?Pac, trop-temp, rare	ne, se	⁶
Family: Apolemiidae					
<i>Apolemia</i> spp.	dps, plg	490–920	World, trop-temp, common	ne, se	⁷
Family: Athorybiidae					
<i>Athorybia rosacea</i> (Forskål, 1775)	dps, epp	0–200	World, trop-temp, uncommon	nw, sw, se	8, 14, 30

(continued)

Checklist of Siphonophora from the Gulf of Mexico. (continued)

Taxon	Habitat-Biology	Depth (m)	Overall geographic range	GMx range	References/Endnotes
Family: Erennidae					
<i>Erenna cornuta</i> Pugh, 2001	dps, mep, bap	896	Sporadic, rare	se	26
<i>Erenna laciniata</i> Pugh, 2001	dps, mep, bap	811	Sporadic, rare	se	26
<i>Erenna richardi</i> Bedot, 1904	dps, mep, bap	0–2400	World, trop-temp, rare	se	24, 26
Family: Forskaliidae					
<i>Forskalia asymmetrica</i> Pugh, 2003	dps, epp, mep	191–823	Atl, Med, trop-temp	ne	⁸
<i>Forskalia edwardsi</i> Kölliker, 1853	dps, epp	0–200	World, trop-temp, uncommon	se	8 ⁹
Family: Physophoridae					
<i>Physophora hydrostatica</i> Forskål, 1775	dps, epp	0–200	World, trop-temp, rare	sw	12, 24
Family: Pyrostephidae					
<i>Bargmannia amoena</i> Pugh, 1999	dps, mep	831–914	World, trop-temp, uncommon	ne, se	25
<i>Bargmannia elongata</i> Totton, 1954 (<i>partim</i>)	dps, mep	0–1000	World, trop-temp, uncommon	ne	23 ¹⁰
Order: Calycophorae					
Family: Abylidae					
Subfamily: Abylinae					
<i>Abyla haeckeli</i> Lens & van Riemsdijk, 1908	dps, epp	0–200	World, trop-subtrop, uncommon	sw, se	12, 16
<i>Abyla trigona</i> Quoy & Gaimard, 1827	dps, epp	0–200	World, trop-subtrop, common	nw, sw	13 ¹¹
<i>Ceratocymba dentata</i> (Bigelow, 1918)	dps, epp	0–200	World, trop-subtrop, uncommon	sw, se	24, 31
<i>Ceratocymba leuckarti</i> (Huxley, 1859)	dps, epp	0–200	World, trop-subtrop, uncommon	entire	14, 24, 31
<i>Ceratocymba sagittata</i> (Quoy & Gaimard, 1827)	dps, epp	0–200	World, trop-subtrop, common	nw, ne, sw	13, 24, 31 ¹¹
Subfamily: Abylopsinae					
<i>Abylopsis eschscholtzi</i> (Huxley, 1859)	dps, epp	0–200	World, trop-temp, common	entire	2, 14, 24, 33
<i>Abylopsis tetragona</i> (Otto, 1823)	dps, epp	0–200	World, trop-temp, common	entire	2, 14, 24, 31, 33
<i>Bassia bassensis</i> (Quoy & Gaimard, (1833) 1834)	dps, epp	0–200	World, trop-temp, common	entire	14, 24, 31, 33 ¹¹
<i>Enneagonum hyalinum</i> Quoy & Gaimard, 1827	dps, epp, mep	0–200	World, trop-temp, uncommon	ne, sw, se	2, 14, 24, 33
Family: Clausophyidae					
<i>Chuniphyes moserae</i> Totton, 1954	dps, bap	1000–3000	World, uncommon	sw	29
<i>Chuniphyes multidentata</i> Lens & van Riemsdijk, 1908	dps, mep, bap	0–2500	World, uncommon	ne, se	24
<i>Clausophyes moserae</i> (Keferstein & Ehlers, 1860)	dps, mep, bap	0–1875	World, common	se	24 ¹²
<i>Crystallophyes amygdalina</i> Moser, 1925	dps, mep, bap	1000–2000	World, uncommon	sw	29
Family: Diphyidae					
Subfamily: Diphyinae					
<i>Chelophyes appendiculata</i> (Eschscholtz, 1829)	dps, epp	0–500	World, trop-temp, v. common	entire	2, 13, 29, 33
<i>Dimophyes arctica</i> (Chun, 1897)	dps, plg	0–500	World, various depths, common	nw, sw, se	13, 29, 33
<i>Diphyes bojani</i> (Eschscholtz, 1829)	dps, epp	0–500	World, trop-temp, common	entire	2, 13, 29, 33

Checklist of Siphonophora from the Gulf of Mexico. (continued)

Taxon	Habitat-Biology	Depth (m)	Overall geographic range	GMx range	References/Endnotes
<i>Diphyes dispar</i> Chamisso & Eysenhardt, 1821	dps, epp	0–500	World, trop-temp, common	entire	2, 14, 29, 33
<i>Eudoxoides mitra</i> (Huxley, 1859)	dps, epp	0–200	World, trop-temp, common	entire	2, 13, 29, 33
<i>Eudoxoides spiralis</i> (Bigelow, 1911)	dps, epp	0–200	World, trop-temp, common	entire	14, 29, 33 ¹¹
<i>Lensia achilles</i> Totton, 1941	dps, plg	0–200	World, trop-temp, uncommon	ne, sw	33
<i>Lensia campanella</i> (Moser, 1925)	dps, plg, epp	0–200	World, trop-subtrop, uncommon	entire	14, 29, 33
<i>Lensia canopusi</i> Stepanjants, 1977	dps, plg, epp	0–200	Sporadic, v. rare	sw	12, 17 ⁴
<i>Lensia challengerii</i> Totton, 1954	ner, plg, epp	0–500	E Pac, ?GMx, rare	nw, ne, sw	24, 29 ⁴
<i>Lensia conoidea</i> (Keferstein & Ehlers, 1860)	dps, epp, mep	0–200	World, mainly temp, common	nw, ne, sw	33 ⁴
<i>Lensia cossack</i> Totton, 1941	dps, epp, mep	0–200	World, trop-subtrop, uncommon	entire	14, 33
<i>Lensia exeter</i> Totton, 1941	dps, mep	200–500	Atl, trop-temp, uncommon	sw	28
<i>Lensia fowleri</i> (Bigelow, 1911)	dps, epp	0–200	World, trop-temp, common	nw, sw, se	14, 29 ¹¹
<i>Lensia havock</i> Totton, 1941	dps, mep, bap	1000–3000	World, trop-temp, rare	sw	29 ¹³
<i>Lensia hostile</i> Totton, 1941	dps, mep, bap	500–3000	World, trop-temp, rare	sw	29
<i>Lensia hotspur</i> Totton, 1941	dps, epp, mep	0–200	World, trop-subtrop, rare	entire	13, 29, 33
<i>Lensia lelouveteau</i> Totton, 1941	dps, mep	200–500	World, trop-temp, rare	sw	29
<i>Lensia meteori</i> (Leloup, 1934)	dps, epp, mep	0–500	World, trop-temp, uncommon	nw, sw, se	14, 33
<i>Lensia multicristata</i> (Moser, 1925)	dps, mep	0–200	World, trop-temp, common	ne, sw	14, 33
<i>Lensia subtilis</i> (Chun, 1886)	dps, epp, mep	0–200	World, trop-subtrop, common	entire	14, 29, 33 ¹⁴
<i>Muggiaea kochi</i> (Will, 1844)	ner, epp	0–200	World, trop-temp, common	entire	9, 14, 33
Subfamily: Giliinae					
<i>Gilia reticulata</i> (Totton, 1954)	dps, bap	0–200	World, temp-boreal, rare	sw	1
Subfamily: Sulculeolariinae					
<i>Sulculeolaria biloba</i> (Sars, 1846)	dps, epp	0–200	World, trop-subtrop, uncommon	entire	14, 24, 29
<i>Sulculeolaria chuni</i> (Lens & van Riemsdijk, 1908)	dps, epp	0–200	World, trop-subtrop, uncommon	entire	14, 24, 29, 33
<i>Sulculeolaria monoica</i> (Chun, 1888)	dps, epp	0–200	World, trop-subtrop, uncommon	entire	2, 14, 29, 33
<i>Sulculeolaria quadrivalvis</i> Blainville, 1834	dps, epp	0–200	World, trop-subtrop, uncommon	ne, sw, se	2, 13, 29 ¹⁵
<i>Sulculeolaria turgida</i> (Gegenbaur, 1843)	dps, epp	0–200	World, trop-subtrop, uncommon	entire	2, 14, 29 ¹⁶
Family: Hippopodiidae					
<i>Hippopodius hippopus</i> (Forskål, 1776)	dps, epp	0–200	World, trop-subtrop, common	entire	2, 14, 24, 29
<i>Vogtia glabra</i> Bigelow, 1918	dps, epp, mep	0–200	World, trop-temp, common	entire	5, 14, 24 ¹¹

(continued)

Checklist of Siphonophora from the Gulf of Mexico. (continued)

Taxon	Habitat-Biology	Depth (m)	Overall geographic range	GMx range	References Endnotes
<i>Vogtia pentacantha</i> Haeckel, 1888	dps, mep	0–200	World, trop-temp, uncommon	sw	13 ¹¹
<i>Vogtia serrata</i> (Moser, 1925)	dps, mep	0–675	World, trop-temp, uncommon	se	24
<i>Vogtia spinosa</i> Keferstein & Ehlers, 1861	dps, epp, mep	0–1000	World, trop-temp, uncommon	nw, sw, se	13, 24, 29, 33
Family: Prayidae					
Subfamily: Amphicaryoninae					
<i>Amphicaryon acaule</i> Chun, 1888	dps, epp	0–200	World, trop-subtrop, uncommon	ne, sw, se	2, 13, 24
<i>Amphicaryon ernesti</i> Totton, 1954	dps, epp	0–200	World, trop-subtrop, rare	entire	14, 24
<i>Amphicaryon peltifera</i> (Haeckel, 1888)	dps, epp	0–100	World, trop-subtrop, rare	ne	24
<i>Maresearsia praeclara</i> Totton, 1954	dps, mep	0–2500	Atl, Ind, trop-temp, rare	se	24
Subfamily: Nectopyramidinae					
<i>Nectadamas diomedae</i> (Bigelow, 1911)	dps, mep, bap	0–1600	World, trop-temp, rare	sw	24
<i>Nectopyramis natans</i> (Bigelow, 1911)	dps, mep, bap	0–675	World, trop-subtrop, rare	se	24
Subfamily: Prayinae					
<i>Desmophyes annectens</i> Haeckel, 1888	dps, epp	0–200	Sporadic, v. rare	sw	14
<i>Praya dubia</i> (Quoy & Gaimard, (1833) 1834)	dps, epp, mep	0–1000	Sporadic, rare	se	24
<i>Rosacea cymbiformis</i> (delle Chiaje, 1822)	dps, epp	0–675	Sporadic, uncommon	nw, ne, sw	3, 24
<i>Rosacea flaccida</i> Biggs, Pugh & Carré, 1978	dps, epp	0–50	Sporadic, rare	nw	3
<i>Stephanophyes superba</i> Chun, 1888	dps, epp	0–50	Sporadic, rare	nw, ne	3 ¹⁷
Family: Sphaeronectidae					
<i>Sphaeronectes gracilis</i> (Claus, 1873; 1874)	dps, plg	0–10	Sporadic, uncommon	se	22 ¹⁸

¹ New records for GMx; from region of Dry Tortugas: NOCC 1450-DS5 (*Frillagalma vityazi*), 1450-CG4 (*Halistemma cupulifera*).² Sears (1954) recorded this species under the name *Stephanomia rubra*.³ New record for GMx; from north of Dry Tortugas: NOCC 2664-DS8.⁴ New records for GMx; from region of Dry Tortugas: NOCC 1450-CG7, 1458-CG1, 2665-DS7, 2668-DS2, 2679-DS2, 2681-DS2.⁵ We have some doubts as to the validity of this identification.⁶ New records for GMx; from region of Dry Tortugas: NOCC 1457-DS8, 2666-DS7, 2667-DS8, 2677-DS4.⁷ New records for GMx; from region of Dry Tortugas: NOCC 1449-CG2, 1450CG2, 1450-CG3, 1450-CG5, 1453-DS8, 1455-DS2, 1455-FS7, 1456-DS4, 1457-DS4, 1458-CG7, 2664-DS3, 2670-DS1, 2670-DS8, 2674-DS4, 2678-CG8. At least 8 different undescribed species.⁸ New record for GMx; from region of Dry Tortugas: NOCC 2678-DS2.⁹ Recorded from region of Dry Tortugas by Fewkes (1882), under the name *Stephanomia Atlantica* sp. nov.¹⁰ The specific identity of Phillips' specimen may be in doubt. Additional records from north of Dry Tortugas: NOCC 2673-DS6, 2676-DS2.¹¹ It is assumed that the GMx record for this species given by Sears (1954) is derived from that of Bigelow (1918). However, Bigelow's specimen was not collected within the present GMx area.¹² Phillips (1972) refers to *Clausophyes ovata* but, with more recent taxonomic changes, we assume he was referring to *C. moserae*.¹³ Stepanjants (1975) recorded this species under the name *Muggiaea havock*.¹⁴ Stepanjants (1975) includes, in the southeast region, a record for *L. subtilis* var. *chuni* Totton, 1965, which has a much shorter pedicle to its somatocyst.¹⁵ Bigelow (1918) recorded this species under the name *Galeolaria quadridentata*, which Sears (1954) changed to *S. quadridentata*.¹⁶ Bigelow (1918) recorded this species under its junior synonym *Galetta australis*, as did Stepanjants (1975). Sears (1954) used the name *Galeolaria australis*.¹⁷ New record for GMx; from north of Dry Tortugas: NOCC 2678-DS4.¹⁸ Sears (1954) included this species under the name *Sphaeronectes truncata*.