Cnidaria

(Plates 38–71)

Cnidarians, like sponges, are an ancient group, relatively simple in structural organization, wholly aquatic, and most greatly developed in the sea, where they occur from the shore to abyssal depths, both in the plankton and the benthos. At the seashore, cnidarians are confined with few exceptions to lower tidal levels or below because, like the sponges, bryozoans, and ascidians, they are not adapted to withstand exposure. But in contrast to these latter groups, which are mostly all filter feeders, cnidarians are primarily predators. Their success seems to be explained by two devices for food-getting and defense—tentacles and cnidocysts, by an effective means of distribution, the ciliated planula larva, and in many cases (most Scyphozoa, many Hydrozoa) by a free-swimming sexual medusa.

Hydrozoa: Polyps, Hydromedusae, and Siphonophora

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(Plates 38–60)

Hydrozoa, of which there are roughly 3,000 species (Schuchert 1998), are abundantly represented in the intertidal zone by "hydroids," the sessile polypoid stages of these cnidarians. Hydroids vary tremendously in form, from tiny individuals to large and showy colonies. The life cycles of hydrozoans (plate 38) often include a sexual **MEDUSA** stage, which exists free in the plankton, but even some hydroid colonies exist free-living in the plankton. In the intertidal, the medusa stage is more commonly retained upon the polypoid generation as an attached **MEDUSOID** or as an even more reduced **SPOROSAC**.

The existence of free-living medusa stages in some life cycles has led to difficult problems in taxonomy. In many cases, the polyp and the medusa of a single species have been described under different genus and species names, some of which have persisted in common usage even after the two forms have been recognized as stages in the life cycle of one species. We provide separate keys for the attached polypoid, or "hydroid" forms, for the hydromedusae, and for the siphonophores. The polyp phase is chiefly encountered in intertidal collecting, while medusae and siphonophores are generally taken in plankton tows or by dip-netting in pools, in harbors around floats, or among *Zostera* or macroalgae, and all might be collected by snorkeling or scuba diving.

The hydroids, apparently a nonmonophyletic group, include representatives of the subclasses **ANTHOATHECATA** (also known as **ANTHOMEDUSAE**), **LEPTOTHECATA** (also known as **LEPTOMEDUSAE**), and **LIMNOMEDUSAE**, which account for almost all local species of hydroids and their medusae. Also included among the hydroids are the calcareous "hydrocorals," which are represented intertidally on this coast by one species of the family Stylasteridae, namely the lavender, encrusting *Stylantheca porphyra*. Subtidally, species of the stylasterid genus *Stylaster* occur as pink, encrusting and branching growths.

The anthoathecate family Porpitidae is often abundantly represented on our beaches by the blue "by-the-wind sailor" *Velella* (plate 43A), which may be blown ashore in vast numbers. Its floating hydroid colonies are composed of a series of gastrozooids, gonozooids bearing medusa buds, and dactylozooids surrounding a central mouth.

The pelagic colonial **SIPHONOPHORA** are now placed in the pelagic hydromedusae (Bouillon and Boero 2000; Collins 2000, 2002; Marques 2001; Marques and Collins 2004), but they receive their own key here for ease of identification. Hydromedusan affinities were earlier suggested by Petersen (1979, 1990) and Schuchert (1996). Siphonophores have a much more complex organization than other hydromedusae (Totton 1965, Kirkpatrick and Pugh 1984, Pugh 1999, Bouillon et al. 2004). Each colony has a distinct form, size, and arrangement of its members. The colony, which may be supported by a float, forms a complex array of polyps and medusoids specialized for feeding, swimming, reproduction, or other functions. When collected in plankton tows and preserved in formalin, these colonies fragment into bits, on which much of the identification has traditionally been based. Onshore currents and winds carry the floating hydroid *Velella,* as well as some siphonophores, to our coast, but both are more characteristic of oceanic waters.

The subclasses **NARCOMEDUSAE** and **TRACHYMEDUSAE** consist of hydromedusae that lack a polyp stage in the life cycle; these medusae are occasionally taken in our plankton, but most are essentially oceanic forms. Many of the holoplanktonic siphonophores, narcomedusae, and trachymedusae are considered to be cosmopolitan species. Molecular studies will eventually reveal the amounts of gene flow between animals

presently bearing the same names in widely separated oceans. The subclass **ACTINULIDAE**, considered a near-relative of the **NARCOMEDUSAE**, is composed of highly reduced interstitial medusae; one actinulid species of *Halammohydra* has been found on California beaches.

Hydroids include many local intertidal species of such varied form and structure that a detailed account is desirable. Certain terms are widely used for the parts of the hydroid colony. Unfortunately, they by no means always have the same meaning nor are they always consistently applied. The only monographic treatment for the West Coast is that of Fraser (1937), but the distinctions he makes are often obscure, his terminology complex, his illustrations sketchy at best, and in his work little or no attention was paid to the medusoid stages.

The hydroid colony (plate 38) is a continuous, often branching, cellular tube—the **COENOSARC**. The coenosarc consists of a layer of ectoderm separated by a thin layer of noncellular **MESOGLEA** from an inner layer of endoderm that surrounds a continuous central cavity, the **COELENTERON**, or gastrovascular cavity. Partly or completely surrounding the coenosarc is a thin, chitinous, noncellular, nonliving layer, the **PERISARC**.

Hydroid polyps show considerable polymorphism, and the zooids may be of several different types, named according to their specialized function: nutritive **GASTROZOOIDS**, generative **GONOZOOIDS**, or defensive **DACTYLOZOOIDS**. The term **HYDRANTH** is used to designate the terminal part of a nutritive zooid but does not include associated perisarcal structures such as the **HYDROTHECA**. The hydranth is therefore entirely coenosarcal, consisting of the body, hypostome, mouth, and tentacles.

The term **GONOSOME** is used to include all the specialized generative zooids of the colony and the perisarcal structures associated with them; the term **TROPHOSOME** refers to the rest of the colony. In thecate hydroids (such as *Obelia*), the gonosome includes the asexual generative zooids or **BLASTOSTYLES**, which produce sexual zooids—**MEDUSAE**, **MEDUSOIDS**, or **SPOROSACS**—by budding, together with the **GONOTHECAE** or cases enclosing the whole set.

The sexual zooids are termed **GONOPHORES** by some, or are referred to in general as the "medusoid" stage or generation, in contrast to the "hydroid" or polyp(oid) stage. However, Fraser (1937) uses gonophore as a synonym of blastostyle, but often includes the budding sexual zooids and the protective theca as well. We and others call this assemblage a **GONANGIUM**, a term Fraser uses to mean gonotheca. Such a reproductive element of a colony (blastostyle with buds and protective covering, if any) is occasionally still spoken of as a "fruiting body." The term "gonophore" is used, therefore, with the most diverse meanings, and we need to know with which of these meanings it is used in each case. Dr. Light remarked that, "This necessity of using terms whose meanings differ with the author, while annoying for the moment, affords very excellent intellectual experience."

The sexual zooids produce gametes from which, by fertilization, arise zygotes that develop into **PLANULA LARVAE**. Each larva can give rise to a new individual polyp or hydroid colony (or, in the case of species that do not produce polyps, will develop directly into a new medusa). All the zooids of a given colony are derived from a single zygote; hence the sexual zooids of a colony are clones, all of the same sex, and we speak of the colony as being male or female (in a few cases, colonies are hermaphroditic).

The generalized hydromedusa (plate 39) is a free-swimming animal consisting of a gelatinous **BELL** that can range from bell- to saucer-shaped with all gradations between. The outer surface of the umbrella is known as the **EXUMBRELLAR SURFACE**, the inner as the **SUBUMBRELLAR SURFACE**. From the center of the subumbrellar surface hangs the **MANUBRIUM**, which can be of various lengths and, in some species, is mounted upon a gelatinous **PEDUNCLE**. The oral opening is terminal on the manubrium. It frequently carries lobes (often spoken of as "lips"), frills, or tentacles, all of which are liberally provided with cnidocysts. Where the manubrium joins the bell or peduncle there is usually a gastric cavity. **RADIAL CANALS** arise from the gastric cavity and course along the bell to the margin, where they join the ring canal. There are usually four radial canals, but other numbers commonly occur (e.g., six, eight, numerous). In a few species the radial canals are branched, while in others **CENTRIPETAL CANALS** rise upward from the **RING CANAL** but may not reach the stomach.

Hydromedusae and siphonophores are typically "craspedote"—that is, they possess a **VELUM** or membrane that partly closes off the subumbrellar space at the level of the bell margin (plate 39). The velum is occasionally lacking, as in *Obelia* (plate 38B–38D).

The bell margin is usually simple and unscalloped. Tentacles usually arise from the bell margin and may be simple, few, or many in number, occurring singly or in groups, or they may be branched (e.g., *Cladonema,* plate 54F–54I) or rudimentary. The margin may also be provided with specialized sense organs. Chief among these are **OCELLI** and **STATOCYSTS**. Ocelli occur as dark pigmented spots, usually one on each tentacle bulb, if present. Statocysts are **MARGINAL VESICLES**, or open pits, or dangling marginal clubs containing one or more concretions known as **STATOLITHS**.

Medusae are almost always of separate sexes, although most siphonophores are hermaphrodites. The gonads are epidermal structures on the radial canals, peduncle, or manubrium.

Many of the characteristics customarily used in the classification of hydrozoans are now recognized as varying markedly with environmental conditions and developmental stage, the result of which means that many species should be reexamined and their validity established (e.g., Boero 1987, Widmer 2004). In addition, for many species the complete life cycle is still not known, resulting, as noted above, in a curious double taxonomy in which polyp and medusa of the same animal have been described under separate names. Thus, the polyp originally named *Lar* is now known to give rise to the hydromedusa *Proboscidactyla,* and when such life cycles are established, the older name takes precedence. For many species, the polyp is known, but not the medusa, or vice versa.

Positive identification of many hydrozoan polyps cannot be made unless the fixed gonophores or sexually mature medusae associated with them are known. Specimens such as these are presently best keyed out only to genus. Some hydroids, including *Proboscidactyla* spp. and *Cladonema* spp., can be identified to species only if their medusae are raised to maturity because the species-distinguishing features lie only in the medusan portion of the life cycle (see both keys in this case for positive identification). Russell (1953), Naumov (1969), Kramp (1961), Millard (1975), Calder (1988, 1991, 1997), Cornelius (1995a, b), and Vervoort and Watson (2003) are of particular help for those who wish to pursue the taxonomy of the group.

For hydromedusae that cannot be identified by the following key, the most useful single reference is Russell (1953). The serious student will also find Kramp (1961) of great assistance because that monograph defines all families and genera of medusae known through 1960 and gives a brief diagnosis of each species. Kramp's *Dana Reports for the Pacific Ocean* (1965,

1968) are a little less inclusive, but they provide illustrations and keys not found in the 1961 synopsis. Totton (1965), Kirkpatrick and Pugh (1984), and Pugh (1999) are indispensable for detailed study of siphonophores. Although it covers a different geographic region, a monograph on hydrozoa of the Mediterranean by Bouillon et al. (2004) has extensive descriptions of hydroid, hydromedusa, and siphonophore morphology (including a few species present or introduced on the West Coast) and good illustrations; this monograph includes descriptions of many families described in the past 50 years and not in Kramp (1961). Some of these important monographs are now available online at no cost (see "References" at the end of this section).

Hydrozoans are best examined alive, but it is frequently necessary to anesthetize them. To do so, a solution of magnesium chloride (73.2 g of $MgCl_2 \bullet 6\ H_2O$ per liter of fresh water) is recommended in the proportion of 10–40% added to the water containing the animals. Relaxation will take several minutes. Preservation for general morphological studies should be in 5–10% formalin, which tends to dissolve the statoliths of medusae but leaves the structure of the statocyst intact. For histological work, Bouin's fixative is recommended. Specimens for molecular studies should be preserved in 95% ethanol.

Following is a combined glossary containing terms used for hydroid polyps, hydromedusae, and siphonophores. The hydroid polyps selected for inclusion in this key are those species found in the intertidal or the shallow subtidal in our area, or those raised from their medusae in the lab, whose field distribution is unknown. Hydromedusae and siphonophores selected for inclusion in the keys are those found near shore over the same geographic range—note that a few of these species are oceanic but may occasionally drift in from the high seas and have previously been collected in the study area.

In the unified annotated species list that follows the three keys, we have attempted to integrate the separate taxonomies of hydroid polyps and their medusae. Families used in the species list are a composite, found mostly in Kramp (1961), Totton (1965), Bouillon (1994), Bouillon et al. (2004), and adopted by Cairns et al. (2002).

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Glossary of Hydrozoa

See text above for additional definitions. For additional discussion of terms, see Millard (1975), Cornelius (1995a), and Bouillon et al. (2004). Schuchert (2004–present) provides an extensive online, illustrated hydrozoan glossary at http://www.ville-ge.ch/musinfo/mhng/hydrozoa/glossary/glossary.htm.

P: refers to polypoid terminology.

M: refers to medusoid terminology.

S: refers to siphonophore terminology.

ABCAULINE (P) facing away from the stem or branch.

ABCAULINE CAECUM (P) a digit-shaped "blind sac" appearing on the abcauline wall of the contracted hydranth of some sertulariids; also known as the "abcauline diverticulum."

ABORAL (P/M) opposite to the location of the mouth.

ACTINULA (P/M) a larva resembling a polyp and typically having two whorls of tentacles.

ADCAULINE (P) facing towards the stem or branch.

ADNATE (P/M) in contact with (i.e., having one side of a structure adjoining that of another).

ANNULATION (P) ringed constriction of the perisarc, frequently in series.

APICAL PROJECTION (M) a glob or particularly thick portion of the umbrellar mesogloea at the top of the bell and often pinched off to some extent with a constriction.

BELL MARGIN (M) the broad or open edge of the umbrella, or bell-shaped jellyfish body.

BIMUCRONATE (P) with two sharp points; hydrothecal cusps each having two lateral points.

BRACT (S) a transparent protective, gelatinous structure covering other parts attached to the stem of siphonophores.

CAMPANULATE (P) bell-shaped.

CAPITATE (P/M) bulbous; having an enlarged tip (e.g., a tentacle or nematophore).

CENTRIPETAL CANAL (M) an outpocketing of the ring canal extending upward toward the manubrium.

CIRRI (M) small, solid tentaclelike organs situated on the umbrella margin between true tentacles and always without a basal bulb.

CLASPERS (P) tentaclelike structures supporting the gonophores in some candelabrid hydroids.

CNIDOCYST (=**NEMATOCYST**) (P/M/S) stinging organelle characteristic of the Cnidaria that consists of a double-walled capsule containing a fluid and a long tubule that everts and straightens when the capsule discharges upon stimulation; used for prey capture, defense, and attachment (also called "stinging cell"). Cnidocyst morphology, particularly of the everted tubule and its spines, is often used for taxonomic determinations.

CNIDOCYST RING (M) cnidocysts organized in such a way to form a distinct ringlike or annular structure on the tentacles of some hydromedusae.

COENOSARC (P) a living cellular tube of ectoderm and endoderm connecting polyps of a hydroid colony; usually covered by chitinous perisarc.

CORBULA (P) a protective basketlike structure that encloses several gonothecae and is composed of modified hydrocladia.

CORDYLI (M) minute, marginal club-shaped structures present instead of marginal vesicles in some Leptomedusae (Laodiceidae).

CRENULATE (P) scalloped or weakly notched.

CUSP (P) a toothlike projection; usually occurring as a series of prominences on the margin of a hydrotheca or gonotheca.

DACTYLOZOOIDS (P) elongate, slender, atentaculate polyps in some polymorphic hydroids; believed to be either defensive or chemosensory.

DESMONEME (P/M) a type of cnidocyst having a tightly coiled thread when discharged.

DISTO-LATERAL SPINE (P) a spine located to one side near the end of a structure, such as a gonotheca.

DIVERTICULA (singular diverticulum) (M) outpocketings (e.g., the blind sidebranches of some radial canals).

ERECT COLONY (P) a colony in which upright stems bearing multiple hydranths arise from the stolons (see "stolonal colony" for contrast).

EXUMBRELLA (M) the upper, or outer (aboral), surface of a jellyfish "bell."

FILIFORM (P/M) threadlike (e.g., a filiform tentacle is uniform in diameter throughout, or gradually tapering from end to end, without knoblike or beadlike concentrations of cnidocysts).

GASTROZOOID (P/S) a feeding polyp, with mouth and usually with oral tentacles (see "hydranth") in a hydroid; with basal tentacle in a siphonophore.

GONOPHORE (P/S) a reproductive structure bearing the gonads; gonophores may remain fixed or may be liberated as a medusa.

GONOTHECA (P) a capsule of perisarc enclosing and protecting a gonophore.

GONOZOOID (P) a reproductive polyp, capable of forming gonophores; sometimes derived from a gastrozooid.

HOLOPLANKTONIC (M/S) describes species whose entire life cycle takes place in the water column (without any benthic component of the life cycle).

HYDRANTH (P) a feeding polyp, usually with a mouth and tentacles (see "gastrozooid").

HYDROCAULUS (P) main stem of a hydroid.

HYDROCLADIUM (P) an ultimate branchlet, arising from a stem or a branch and usually bearing one or more hydranths.

HYDROECIUM (S) gutterlike furrow on a swimming bell; the stem is attached within the hydroecium and may retract partially or wholly into it.

HYDRORHIZA (P) a structure anchoring a hydroid to its substrate, varying from a system of stolons to an encrusting mat.

HYDROTHECA (P) a cuplike capsule of perisarc, usually capable of enclosing and protecting a hydranth.

HYPOSTOME (P) a part of the hydranth surrounding the mouth.

INTERNODE (P) a segment of a stem or branch, delimited at either end by a constriction or node, more appropriately called a segment.

LATERAL NEMATOTHECA (P) a nematotheca occurring lateral to the hydrothecal aperture; usually occurs in one or more pairs (see "nematotheca").

MANTLE CANALS (S) superficial canals present on the apex of sexual medusoid (gonophore).

MANUBRIUM (M) saclike feeding structure that hangs down from the subumbrellar apex or sometimes from a gastric peduncle, containing the stomach, the mouth, and often distinct lips of the mouth that may be ornamented in varying ways.

MARGINAL SENSORY CLUB (M) pendant, microscopic, statocyst structure located at the bell margin, containing one or more spherical statoliths, which are usually stacked vertically within it.

MARGINAL VESICLE (M) a microscopic statocyst structure located at the bell margin, composed of a cavity and one or more statoliths inside the cavity.

MESENTERIES (M) colorless tissue connections in a few species of hydromedusae connecting the wall of the manubrium to the upper portions of the radial canals.

MESOGLOEA (P/M/S) noncellular substance (e.g., the "jelly") lying between the ectoderm and endoderm of a hydrozoan. This forms the gelatinous bulk of the umbrella of a hydromedusa and a lamellalike layer in hydroids.

MONILIFORM (P/M) beadlike (e.g., a moniliform tentacle bears a series of annular swellings, armed with cnidocysts, along its length).

MONOSIPHONIC (P) single hydroid stem, not bundled with others (see "polysiphonic" for contrast).

MOUTHPLATE (S) process extending below the subumbrella opening of a swimming bell on the side where the stem is attached.

NEMATOCYST (P/M/S) a stinging capsule (see "cnidocyst").

NEMATOPHORE (P) a highly modified defensive zooid armed with cnidocysts.

NEMATOTHECA (P) a perisarcal sheath protecting a nematophore.

OCELLUS (plural ocelli) (M) a small dark spot at the bell margin, usually located on a tentacle bulb, or occasionally associated with a marginal vesicle.

ORAL (P/M) referring to the mouth.

ORAL TENTACLES (P/M) short, sometimes dichotomously branched tentacles located around or just above the mouth rim in some hydromedusae; also refers to tentacles immediately below the hypostome of hydroids.

OPERCULUM (P) a chitinous lid that closes the aperture of a hydrotheca or gonotheca; usually composed of one or more valves.

OTOPORPAE (M) elongate vertical tracks with bristles and cnidocysts, running upward from each marginal sensory club, only found in some Narcomedusae.

PALPON (S) a polyp, with or without a basal tentacle, that serves a defensive, excretory, or food-handling function; appears to be a reduced gastrozooid.

PEDICEL (P) a stalk that supports a hydranth (or a hydrotheca) or a gonophore (or a gonotheca).

PEDICELLATE (P) stalked; having a stalk or pedicel.

PEDUNCLE (M) a round to cone-shaped extension of the mesogloea down from the apex of the subumbrella, bearing the manubrium terminally; the radial canals run down the peduncle to reach the manubrium.

PERISARC (P) the chitinous exoskeleton enclosing and protecting the living tissues of a hydroid.

PLANKTONIC (P/M/S) free-living within the water column and being a sufficiently weak swimmer to be at the general mercy of the ocean currents.

PLANULA (P/M/S) a usually ciliated, embryonic, dispersal stage.

PLEUSTONIC (P/M/S) floating at the sea surface.

PODOCYST (P) a resting body, covered by perisarc.

POLYSIPHONIC (P) composed of two or more united tubes; a composite stem or branch (synonymous with "fascicled").

PSEUDOHYDROTHECA (P) a filmy covering of perisarc at the base of a hydranth resembling a hydrotheca, varying in shape and often with transverse wrinkles.

RADIAL CANALS (M/S) circulatory tubes running from the manubrium or apex of the bell to (usually) a ring canal circling the bell margin. In hydromedusae, the radial canals attach at the manubrium and usually are straight and narrow, but they may be broad, have wavy or even diverticulated walls; in a few species the radial canals branch one or more times before reaching the bell margin, particularly in siphonophores.

RUDIMENTARY TENTACLE OR BULB (M) a permanently minute or undeveloped marginal tentacle and its bulb; in some species there are a number of rudimentary tentacles or tentacle bulbs that never develop into the normal size and length of the other tentacles and bulbs.

SOMATOCYST (S) tubular or bulblike structure running up through the jelly in a calycophoran siphonophore from its origin at the base of the hydroecium; probably a caecal extension of the original, larval gastrovascular cavity.

STATOCYST (M) microscopic structure apparently used for orientation; always in symmetrical multiple arrangement and

located around the bell margin, containing one or more hard concretions, or statoliths. Hydromedusan statocysts take the form of either marginal vesicles or marginal sensory clubs.

STATOLITH (M) spheroidal or polygonal concretion in a statocyst structure; the marginal vesicles or marginal sensory clubs.

STEM (P) see "hydrocaulus."

STOLON (P) a tube of coenosarc, covered with perisarc; basal stolons usually grow over the substrate and anchor the hydroid to its substrate.

STOLONAL COLONY (P) a colony in which hydranths arise singly from stolons, either with or without a pedicel, and without an upright stem.

STOMACH POUCH (M) well-defined and symmetrical outpocketing of the stomach surface, in some Narcomedusae.

SUBUMBRELLA (M/S) the concave underside of a jellyfish, which in siphonophores and most hydromedusae forms a distinct cavity with a small opening.

SWIMMING BELL (S) asexual medusoid present at or close to the apex of a siphonophore colony that propels the colony through the water; often arranged in a series with species- or genus-specific arrangement (also called nectophore).

TENTACLE BULB (M) swelling at the bell margin that forms the base of the hollow marginal tentacles of many species of hydromedusae. The bulb usually forms before the tentacle, and thus in a developing medusa there may be more bulbs than tentacles.

TENTACULA (singular tentaculum) (M) small solid marginal tentacles, usually without marginal bulbs, located between normal hollow tentacles.

TENTACULAR RUDIMENT (M) see "rudimentary tentacle."

VALVE (P) see "operculum."

ZOOXANTHELLAE symbiotic, photosynthetic single-celled organisms that live within the tissues of a number of cnidarians, including corals, some sea anemones, and some medusae.

Key to the Polypoid Stages of Hydrozoa

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Plates refer to polyp plates 40–49.

1. Hydranths enclosed by a distinct hydrotheca of definite shape; gonophores protected by gonothecae or similar structures . . . . . Leptothecata 42
— Hydranths not enclosed by a hydrotheca; gonophores not protected by a gonotheca or thin perisarc sheath . . . . . Anthoathecata, Limnomedusae 2
2. Exoskeleton a calcareous encrustation, vivid purple in color . . . . . *Stylantheca porphyra*
— Exoskeleton not a calcareous encrustation 3
3. Polyps planktonic or pleustonic, with no vestige of stem 4
— Polyps benthic, sedentary, with or without stems and/or pedicels 5
4. Polyps pleustonic (floating at the sea surface), deep blue or purple, with oval float and upright triangular sail; colonies polymorphic, with central gastrozooid (plate 43A) . . . . . *Velella velella*
— Polyps planktonic and solitary, with no float or sail; tentacles arranged more or less in definite circlets (plate 42I) . . . . . *Climacocodon ikarii*
5. Polyps without tentacles and with mouth surrounded by cnidocysts; minute, fairly transparent and very cryptic 6
— Polyps with tentacles; of various sizes 8
6. Solitary; elongate and wormlike, with nematocysts sprinkled over the body surface as well as concentrated near the mouth; interstitial in fine sediment or in intertidal algal mats (plate 49R, 49S) . . . . . *Protohydra leuckarti*
— Solitary or in small clusters; not wormlike in character 7
7. In fresh water (plate 49O) . . . . . *Craspedacusta sowerbii*
— In estuarine to full salinity water (plate 49P, 49N) . . . . . *Maeotias marginata* and *Aglauropsis aeora*
8. Hydranths with one to two tentacles 9
— Hydranths with three or more tentacles 10
9. Gastrozooids with two filiform tentacles; gonozooids without mouth or tentacles; colonies commensal on tubes of sabellid polychaetes; budding off medusae (see key to hydromedusae, couplets 34–36) (plate 41A) . . . . . *Proboscidactyla* spp.
— Gastrozooids with one or rarely two capitate tentacles; dactylozooids lacking tentacles but with distal cnidocyst cluster; hydrorhizae mostly covered by bryozoan skeleton; polyps arising at intersection of bryozoan zooecia, or directly in front of zooecial openings (plate 43I, 43J) . . . . . *Zanclella bryozoophila*
10. Mature hydranths with at least some capitate tentacles 11
— Mature hydranths with all tentacles filiform or appearing essentially filiform, or in a few cases moniliform 21
11. Hydroids solitary or with two to three interconnected polyps only 12
— Hydroids colonial 13
12. Hydranths large (ca. 10 mm or more), with numerous (up to 500) irregularly arranged tentacles; gonophores fixed; perisarcal spines absent; with clasper tentacles attaching to developing embryos in the blastostyle-bearing region, at least during the reproductive season (plate 43O) . . . . . *Candelabrum fritchmanii*
— Hydranths small (0.15–0.2 mm), commonly with four tentacles (exceptionally with three to eight tentacles), fingerlike perisarcal projection (spine), protecting zooid, present on a circular thecal base (plate 42J) . . . . . *Halimedusa typus*
13. Hydranths with both capitate and filiform tentacles (the filiform tentacles may be difficult to see) 14
— Hydranths with capitate tentacles only 16
14. Hydranths with an oral whorl of (usually) four capitate tentacles and an aboral whorl of four filiform tentacles (sometimes rudimentary) (plate 41H, 41I) . . . . . *Cladonema californicum* and *Cladonema radiatum*
— Hydranths with about 10–20 capitate tentacles, arranged in two whorls or scattered along hydranth body, and an aboral whorl of four filiform tentacles (sometimes rudimentary) 15
15. Capitate tentacles eight to 10, in two whorls (plate 42E) . . . . . *Dipurena bicircella*
— Capitate tentacles four to five in an oral whorl, plus three to four additional whorls of ca. four tentacles each (plate 42A) . . . . . *Coryne japonica*
16. Capitate tentacles (usually) four, in a single oral whorl (plate 41E–41G) . . . . . *Cladonema myersi* and *Cladonema pacificum*
— Capitate tentacles 15 to as many as 70, on hydranth body (although some hydranths in a colony may have only four capitate tentacles, around the mouth) 17
17. Hydranths large (generally more than 1 cm when extended); tentacles 30–70, arranged in five to six tight distal circlets (plate 42H) . . . . . *Hydrocoryne bodegensis*

87. With marginal sensory clubs and otoporpae (bristly tracks of ectodermal cells running up the exumbrella from the bell margin) (rare) (plate 57K) . . . . . *Cunina* spp.
— With marginal sensory clubs, but without otoporpae 88
88. With eight to 20 (usually 16) tentacles and stomach pouches; each marginal lappet with up to 20 marginal sensory clubs (plate 51J) . . . . . *Solmissus marshalli*
— With 20–40 tentacles and stomach pouches; each marginal lappet with two to five marginal sensory clubs . . . . . *Solmissus incisa*
89. Without peripheral canal system, without otoporpae (bristly tracks of ectodermal cells running up the exumbrella from the bell margin); with simple annular gonad (plate 51I) . . . . . *Solmaris* spp.
— With peripheral canal system, with otoporpae (bristly tracks of ectodermal cells running up the exumbrella from the bell margin); gonads forming diverticula of the margin of the oral wall of the stomach (rare) (plate 57M) . . . . . *Pegantha* spp.

Key to the Siphonophora

CLAUDIA E. MILLS, STEVEN H. D. HADDOCK, CASEY W. DUNN, AND PHILIP R. PUGH

Plates refer to siphonophore plates 58–60.

This key covers the life stages of some siphonophore species most likely to be encountered near shore, where they might be dipped from harbors and marinas or observed by snorkellers or scuba divers.

1. With a gas-filled float, and with numerous swimming bells arranged below this, followed by a stem region bearing groups of feeding, reproductive, and buoyant zooids (see supplementary key for stem pieces of *Apolemia* species) 2
— Without a gas-filled float, and usually with only one or two swimming bells (see supplementary key for stem pieces of *Rosacea* and *Praya* species) 6
2. Stem elongate with feeding and reproductive zooids along the entire length 3
— Stem reduced and laterally expanded into a bulbous structure, with zooids arranged spirally around it (plate 58C) . . . . . *Physophora hydrostatica*
3. Swimming bells arranged in two rows along opposite sides of stem 4
— Swimming bells numerous and whorled (not in two rows), packed into a characteristic cone-shaped or cylindrical arrangement (plate 58F, 58G) . . . . . *Forskalia* spp.
4. Elongate polyps present between swimming bells; stem with "woolly" appearance; tentacles without side branches (plates 58E, 59A) . . . . . *Apolemia* spp.
— Polyps not present between swimming bells; tentacles with side branches 5
5. Stem densely covered with bracts (most noticeable when removed from the water); gastrozooids few and far between; tentacles all hanging down along one side of stem; stem cannot contract (plates 58A, 59B) . . . . . *Agalma elegans*
— Stem with small inconspicuous bracts; gastrozooids relatively numerous; tentacles emerge from anywhere along the stem (not all from one side); stem can contract when the colony is disturbed (plates 58B, 59D) . . . . . *Nanomia bijuga*
6. Swimming bells rounded, without ridges, without coming to a point; if two bells, then attached side by side 7
— Swimming bells elongate, pointed or faceted; if two bells, then not attached side by side, but slightly offset along the stem 10
7. Single, soft, spherical, colorless, and very transparent swimming bell, up to 8 mm in length; gastrozooids minute (plate 60A) . . . . . *Sphaeronectes gracilis*
— Usually with two robust swimming bells; gastrozooids and tentacles yellow 8
8. Swimming bells with a simple, slender, tubular somatocyst; pair of deeply sinusoidal radial canals on subumbrella (plate 59G, 59H) . . . . . *Rosacea* spp.
— Swimming bells with a complexly branched somatocyst; radial canals on subumbrella branch many times 9
9. No cross-links between branches of radial canals (plates 58D, 58H, 59E) . . . . . *Praya dubia*
— Cross-links between branches of radial canals, forming a meshlike pattern (plate 59F) . . . . . *Praya reticulata*
10. Anterior (upper) swimming bell roughly conical and larger than or approximately equal in size to posterior (lower) one 11
— Anterior (upper) swimming bell polyhedral; posterior (lower) bell considerably larger, with two prominent basal teeth (plate 60B) . . . . . *Abylopsis tetragona*
11. Anterior swimming bell without ridges, with rounded apex 12
— Anterior swimming bell with ridges, with pointed apex 13
12. Anterior swimming bell with divided mouthplate and with four "teeth" on opening of subumbrella; with slender tubular somatocyst about one-third the length of the nectosac; posterior bell with characteristic constriction in middle of subumbrella (plate 60D) . . . . . *Sulculeolaria quadrivalvis*
— Anterior swimming bell with undivided mouthplate and without "teeth" on opening of subumbrella, with carrot-shaped somatocyst about two-thirds the length of the subumbrella; posterior bell reduced, but rarely present (plate 60E) . . . . . *Dimophyes arctica*
13. Ridges on swimming bells spirally twisted and prominently serrated (plate 60F) . . . . . *Eudoxoides spiralis*
— Ridges on swimming bells straight or slightly curved, may or may not show serrations 14
14. Anterior swimming bell very stiff, with five or six ridges at base and only three or four ridges at apex 15
— Anterior swimming bells not as above 16
15. Anterior swimming bell to 20 mm long; somatocyst swollen and fusiform; small claw-shaped hydroecium only open at base (plate 60G) . . . . . *Chelophyes appendiculata*
— Anterior swimming bell to 35 mm long; somatocyst with two prominent lateral swellings, forming a T shape; rounded hydroecium to half bell length, open at base and along one side (plate 60P) . . . . . *Chuniphyes multidentata*
16. Somatocyst of anterior swimming bell extending to at least one-half of its length 17
— Somatocyst of the anterior swimming bell substantially less than one-quarter its length 20
17. Hydroecium one-third to one-half the length of the anterior swimming bell 18
— Hydroecium very shallow; anterior swimming bell to 20 mm long with fusiform somatocyst extending to over one-half its length (plate 60L) . . . . . *Lensia conoidea*

18. None of the ridges of the anterior swimming bell serrated, without teeth on the opening of the subumbrella; mouthplate divided; hydroecium one-third the length of the bell; somatocyst long and slender, reaching to the apex of the subumbrella (plate 60I) . . . . . *Muggiaea atlantica*
— At least some of the ridges of the anterior swimming bell serrated; with three conspicuous teeth around the opening of the subumbrella; mouthplate undivided 19
19. Anterior swimming bell to 35 mm in length, hydroecium extends one-half the length of the bell, somatocyst long and slender, subumbrella with distinct fingerlike extension at its apex (plate 60J) . . . . . *Diphyes dispar*
— Anterior swimming bell to 14 mm in length, hydroecium extends nearly one-third the length of the bell, somatocyst fusiform, subumbrella tapering apically, without distinct extension (plate 60K) . . . . . *Diphyes bojani*
20. Anterior swimming bell with five ridges and no obvious hydroecium 21
— Anterior swimming bell with numerous ridges; hydroecium relatively deep; inverted heart-shaped somatocyst (plate 60M) . . . . . *Lensia hostile*
21. Anterior swimming bell with spherical, egg-shaped, or flattened somatocyst; shallow hydroecial cavity (plate 60O) . . . . . *Lensia challengeri*
— Anterior swimming bell with oblique, ovate somatocyst; hydroecial cavity reduced to only a slight depression (plate 60N) . . . . . *Lensia hotspur*

Supplementary Key to Some Stem Fragments of Siphonophores

1. Stem with overall "woolly" appearance, with numerous gastrozooids, palpons and bracts; gastrozooids red or white (plates 58E, 59A) . . . . . *Apolemia* spp.
— Stem with distinct and repetitive groups of zooids (called "cormidia"), each with a single bract and gastrozooid; gastrozooids and tentacles yellow 2
2. Bracts hemispherical, gonophores with two mantle canals (plate 59G, 59H) . . . . . *Rosacea* spp.
— Bracts somewhat flattened, gonophores with three mantle canals (plates 58D, 58H, 59E, 59F) . . . . . *Praya* spp.

Note: The characters distinguishing the bracts of *Praya* species are often difficult to make out and are omitted here.

Combined Species List of Hydroids, Hydromedusae, and Siphonophores

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HYDROZOA SUBCLASS ANTHOATHECATA (also known as ANTHOMEDUSAE and ATHECATA)

ORDER FILIFERA

BOUGAINVILLIIDAE

Bougainvillia muscus (Allman, 1863). Hydroid and medusa. Synonyms in Calder, (1988, pp. 24–25). The name replaces *B. ramosa* (van Beneden, 1844), which is an invalid junior homonym. Probably introduced, present in bays and harbors. Remarkable color illustration of hydroid and medusa from Naples in Brinckmann-Voss 1970, plate 9.

*****_Bougainvillia_ spp. Hydroid and medusa. Unidentified hydroids of *Bougainvillia* occur in San Francisco Bay, and may be introduced species. Other *Bougainvillia,* of the same or different species in Bodega Harbor, have been collected and raised by J. T. Rees and C. E. Mills.

Garveia annulata Nutting, 1901. Hydroid. Hydroids conspicuous, with bright orange to yellow colonies and deeper orange gonophores (Torrey 1902; Fraser 1937; Haderlie et al. 1980—color photograph 3.6, plate 15). Rocky intertidal zones of the open coast, especially in late winter and spring, frequent on sponges and coralline algae; also reported subtidally to 117 m; Alaska to the Channel Islands (Fraser 1937, 1946).

Garveia franciscana (Torrey, 1902) (=*Bimeria franciscana*). Hydroid. A robust and conspicuous fouling species, abundant on floats and pilings in areas of low salinity in the San Francisco Bay area. Female gonophores a distinctive blue-purple, with a red-orange spadix. Lower intertidal and shallow subtidal. Reported in harbors from San Francisco Bay to San Diego (Torrey 1902; Fraser 1937, 1948). Introduced, but original provenance unknown.

Rhizorhagium formosum (Fewkes, 1889). Hydroid. Synonyms in Hochberg and Ljubenkov (1998, p. 9). A small and poorly known species, growing on gastropod shells and other hard substrates. Intertidal to 550 m; San Francisco Bay to Baja California (Fraser 1937, 1946; Hochberg and Ljubenkov 1998).

*****Unidentified bougainvillioid(?). Hydroid and possibly medusa. Hand and Jones (see below) described and illustrated a light, flesh-pink, translucent hydroid collected from 10 m off Point Richmond in San Francisco Bay that underwent curious asexual reproduction involving changes in polarity. The tiny polyps (1–1.5 mm in length) supported four to 12 filiform tentacles inserted in a single cycle at the base of the proboscis. Bavestrello et al. (see below) observed a similar hydroid in the Genoa Aquarium that underwent both asexual reproduction and sexual reproduction with medusae and which they placed in the superfamily Bougainvillioidea; see Hand and Jones 1957, Biol. Bull. 112: 349–357; Bavestrello et al. 2000, Sci. Mar. 64 (Suppl. 1): 147–150.

BYTHOTIARIDAE (=CALYCOPSIDAE, a junior synonym)

Bythotiara stilbosa Mills and Rees, 1979. Medusa (hydroid unknown). Known only from newly released medusae collected off docks in Mason's Marina, Bodega Harbor, and raised in the laboratory. Some bythotiarid polyps are symbiotic in tunicates, including *Bythotiara huntsmani* (Fraser, 1911) in Washington and British Columbia. See Mills and Rees 1979, J. Nat. Hist. 13; 285–293. Color photograph in Wrobel and Mills 1998 and 2003, p. 25.

Calycopsis nematophora Bigelow, 1913. Medusa (hydroid unknown). Apparently a Pacific oceanic species that is occasionally found near shore (illustration in Arai and Brinckmann-Voss 1980, p. 68).

Calycopsis simulans (Bigelow, 1909). Medusa (hydroid unknown). Apparently a Pacific oceanic species that is occasionally found near shore. Color photograph in Wrobel and Mills 1998 and 2003, p. 25.

Heterotiara anonyma Maas, 1905. Medusa (hydroid unknown). An oceanic species of the Pacific, Atlantic, and Indian Oceans that is occasionally found near shore (illustration in Arai and Brinckmann-Voss 1980, p. 70).

Sibogita geometrica Maas, 1905. Medusa (hydroid unknown). An oceanic species of the Pacific, Atlantic, and Indian Oceans that is occasionally found near shore.

***** = Not in key.

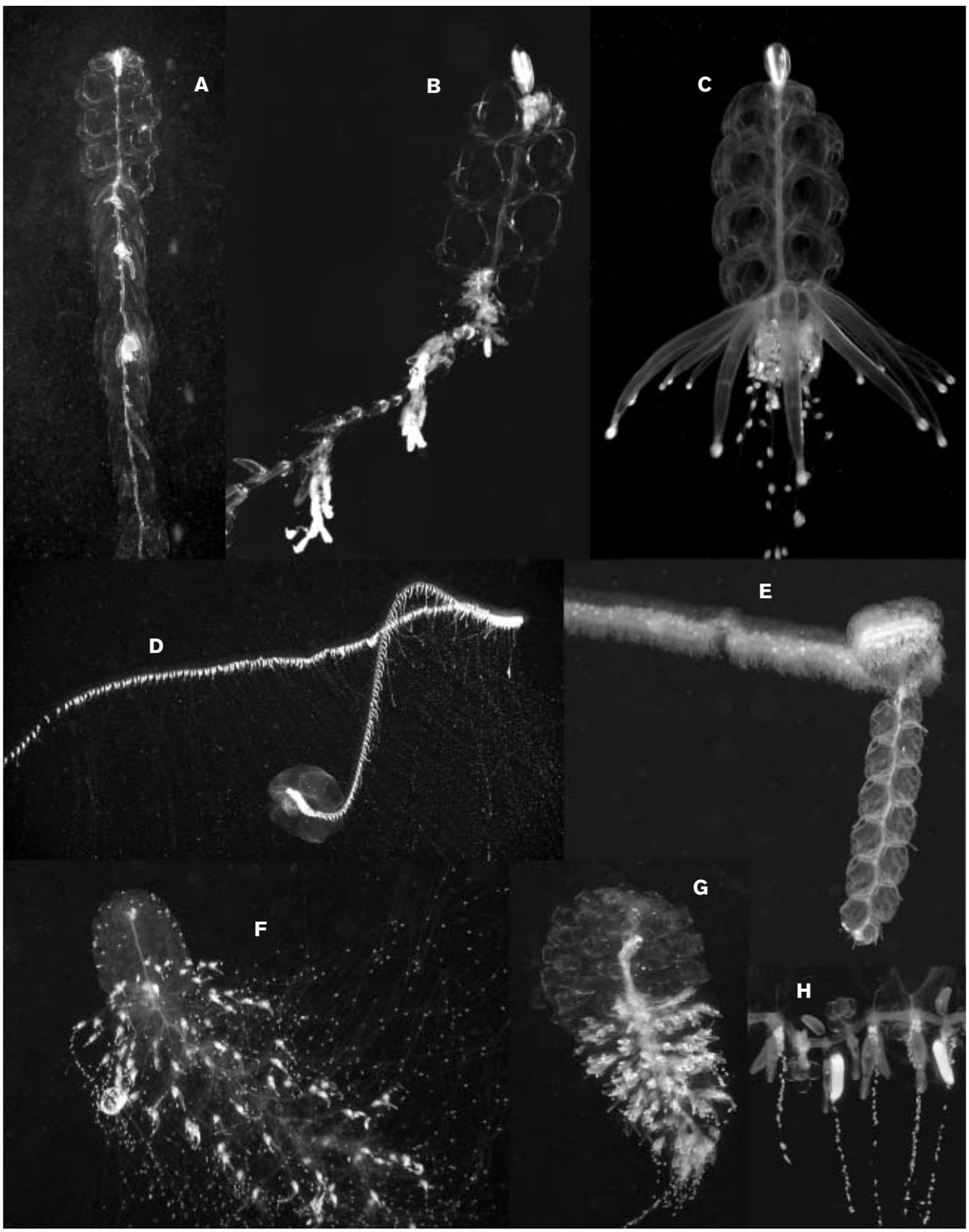

PLATE 58 Whole siphonophores, live. A, *Agalma elegans*; B, *Nanomia bijuga*; C, *Physophora hydrostatica*; D, *Praya dubia*; E, *Apolemia* sp.; F, *Forskalia* sp. 1; G, *Forskalia* sp. 2; H, *Praya dubia*, close-up of portion of the stem (A, F, G, photographs by Casey W. Dunn; B, H, photographs by Claudia E. Mills; C, photograph by Steven H. D. Haddock; D–E, in situ photograph from Monterey Bay Aquarium Research Institute [MBARI]).

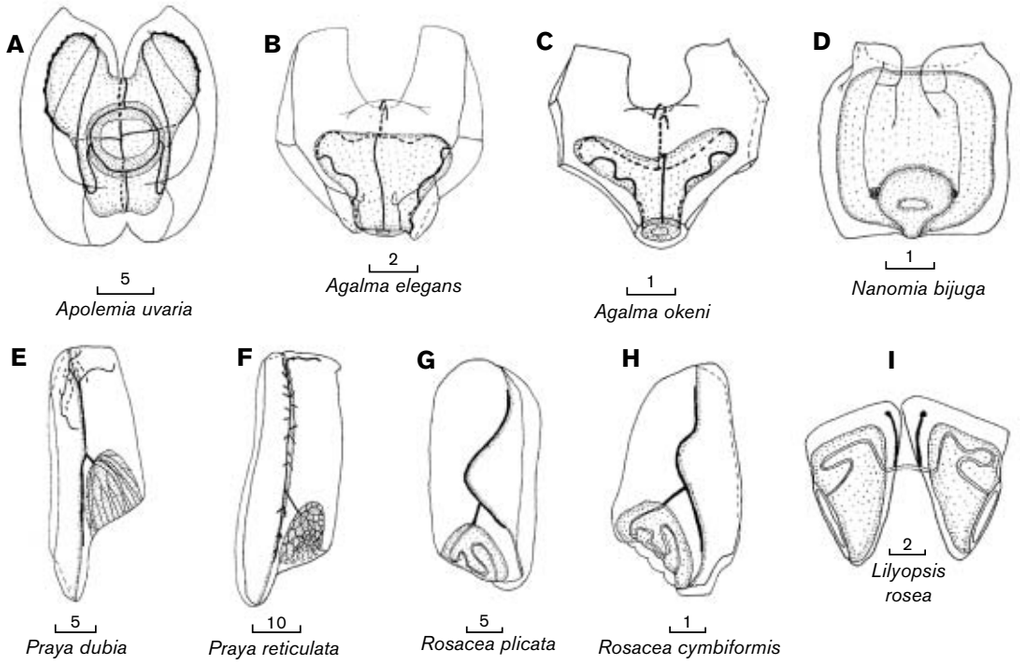

PLATE 59 Nectophores.Views from above (looking down the stem from the float–B, C) and distal views (stem running down the plane of the page–A, D) of nectophores of physonect siphonophores (A–D) and lateral views of nectophores of calycophoran siphonophores (E–I); scale bars in mm. For additional drawings of posterior nectophores, bracts, and gonophores, see Pugh (1999). A, *Apolemia uvaria*; B, *Agalma elegans*; C, *Agalma okeni*; D, *Nanomia bijuga*; E, *Praya dubia*; F, *Praya reticulata*; G, *Rosacea plicata sensu* Bigelow, 1911; H, *Rosacea cymbiformis*; I, *Lilyopsis rosea* (all from Pugh 1999).

EUDENDRIIDAE

Eudendrium californicum Torrey, 1902. Hydroid. Once a common intertidal and subtidal species in areas of open rocky coast, but apparently less frequent in recent decades. British Columbia to southern California, 4–115 m (Fraser 1937, 1946; Haderlie et al. 1980—see color photograph 3.7, plate 15).

Eudendrium spp. Hydroid. Species of this genus are characterized by typically styloid gonophores, trumpet-shaped hypostomes, and absence of desmonemes in the cnidome. Identification based on gross morphology alone is questionable and should include examination of cnidocysts. Various species of *Eudendrium* have been reported from the region, but the absence of information on cnidocyst complement makes these identifications uncertain (see Marques et al. 2000a, Zool. Meded., Leiden 74: 75–118; Marques et al. 2000b, J. Zoology, London 252: 197–213).

HYDRACTINIIDAE

Clava multicornis (Forsskål, 1775) (=*C. leptostyla L.* Agassiz, 1862). Hydroid. Additional synonyms in Edwards and Harvey 1975, J. Mar. Biol. Assoc. U.K. 55: 879–886. This species is included in the family Hydractiniidae here following Schuchert (2001a); molecular studies show that *Clava* and hydractiniids should be assigned to the same family. A cold-water species largely inhabiting the intertidal zone of bays and estuaries, sometimes forming large colonies due to stolonal growth. Hydranths and male gonophores pink, those of the female purple. Whether this well-known Atlantic hydroid still occurs in San Francisco Bay (its only known West Coast location) is uncertain. First reported in 1895 from San Francisco Bay (to which it was introduced in ship fouling), it is unclear when it was last seen in the Bay. Light et al. (1954) noted that it was "abundant on Fruitvale and Bay Farm Island bridges, Oakland, in spring," but we find no further actual records in the past 50 years. We did not find it in surveys of San Francisco Bay between 1993 and 2004.

Hydractinia armata Fraser, 1940. Hydroid. Female gonophores bearing only a single egg. Found in association with *H. milleri* (Fraser 1946), on coralline algae in tide pools at Moss Beach, a rocky intertidal site on the open coast just south of San Francisco Bay first visited by S. F. Light and his students in the 1920s and 1930s, and in later decades the most popular tide pool site for hundreds of thousands of school children from central California schools. It would be interesting to determine if these millions of little feet have obliterated this hydroid from Moss Beach.

Hydractinia laevispina Fraser, 1922. Hydroid. Female gonophores bearing only a single egg. British Columbia to central California in the low subtidal to at least 20 m deep; on kelp off Coast Guard breakwater in Monterey Harbor (Light et al. 1954).

Hydractinia milleri Torrey, 1902. Hydroid. Female gonophores bearing only a single egg. Colonies often growing in patches, sometimes covering several square centimeters on rocks exposed to breakers of the open sea (Torrey 1902). British Columbia to central California in the lower intertidal (Fraser 1937, 1946; Haderlie et al. 1980).

**Hydractinia* spp. Hydroid. Additional species of *Hydractinia* occur in the region (R. Grosberg pers. comm.).

* = Not in key.

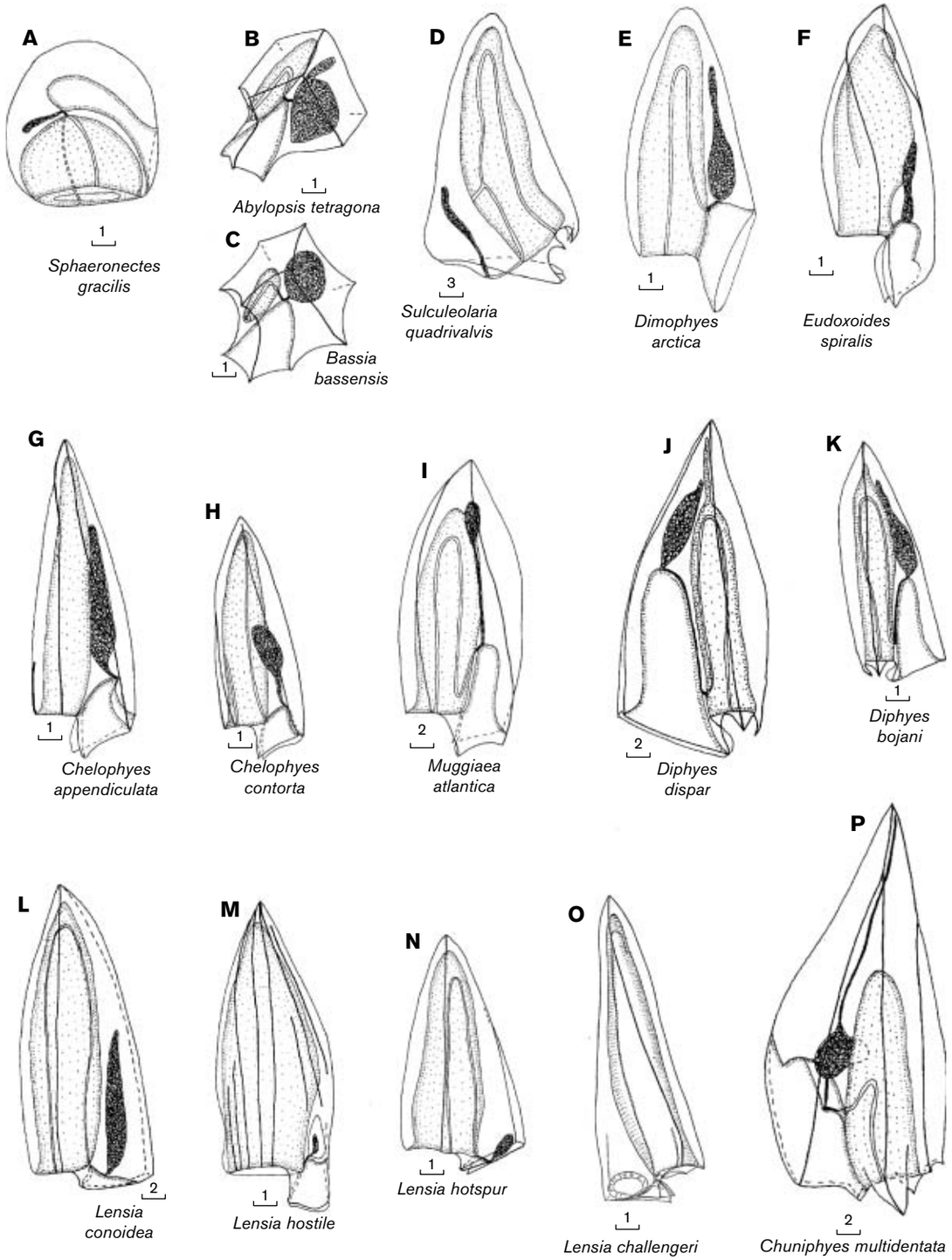

PLATE 60 Lateral views of anterior nectophores of calycophoran siphonophores; scale bars in mm. For additional drawings of posterior nectophores, bracts, and gonophores, see Pugh (1999). A, *Sphaeronectes gracilis*; B, *Abylopsis tetragona*; C, *Bassia bassensis*; D, *Sulculeolaria quadrivalvis*; E, *Dimophyes arctica*; F, *Eudoxoides spiralis*; G, *Chelophyes appendiculata*; H, *Chelophyes contorta*; I, *Muggiaea atlantica*; J, *Diphyes dispar*; K, *Diphyes bojani*; L, *Lensia conoidea*; M, *Lensia hostile*; N, *Lensia hotspur*; O, *Lensia challengeri*; P, *Chuniphyes multidentata* (all from Pugh 1999, except O, from Totton 1954, with permission, Discovery Rep. 27, 1–162, text figures 24B, 43C, 54A, 54D, 65A, 66B).

raising the medusae. Medusae to about 7 mm. Known only from Bodega Harbor. Named after Nando Boero's favorite musician, Frank Zappa, which afforded an entrée to a friendship between the two men (http://homepage.ntlworld.com/andymurkin/Resources/MusicRes/ZapRes/jellyfish.html).

PLUMULARIIDAE

Plumularia goodei Nutting, 1900. Hydroid. Small hydroids (25 mm), on shore and near-shore rocks; British Columbia to southern California (Fraser 1946).

Plumularia lagenifera Allman, 1885. Hydroid. Synonyms in Millard (1975, p. 392). Colonies to 5–10 cm high. Widely distributed in San Francisco Bay (Fraser 1937); found at Pier 39, San Francisco in 2004, and occurs all along the West Coast from the intertidal to offshore waters (Alaska to the tropics, 0–146 m) (Fraser 1937, 1946).

Plumularia setacea (Linnaeus, 1758). Hydroid. Synonyms in Cornelius (1995, p. 158). Life cycle information in Hughes 1986, Proc. R. Soc. (B) 228 (1251): 113–125. An abundant species in our region, substrate generalist; colony to 5 cm high locally; form varied, especially in epizoic colonies (Millard 1975). Recorded from boreal to tropical waters in the Eastern Pacific (Fraser 1937, 1946), the name *setacea* is applied worldwide and probably involves a multispecies complex.

SERTULARIIDAE

Abietinaria filicula (Ellis and Solander, 1786). Hydroid. Synonyms in Vervoort (1993, p. 99) and Cornelius (1995b, p. 27). Species believed to have retreated northwards in Europe over the past 150 years (Cornelius 1995). Different forms have been described (Naumov, 1969). Colonies usually less than 10 cm high. Known south to San Francisco Bay, on intertidal rocks to 66 m (Torrey, 1902; Fraser, 1937, 1946); genetic comparisons to Atlantic populations would be of interest to determine if this is indeed the same species.

Abietinaria greenei (Murray, 1860). Hydroid. Synonyms in Vervoort (1993, p. 99). Colonies in clusters, to 3 cm high. A northern species occurring south to Monterey Bay, intertidal to 37 m (Fraser 1937, 1946).

Abietinaria inconstans (Clark, 1876). Hydroid. Synonyms in Vervoort (1993, p. 99). Synonyms in Fraser (1937) include *A. amphora* Nutting, 1904 and *A. costata* Nutting, 1901. Colonies to 4 cm high, with thick stem. Alaska to Mexico, including San Francisco Bay, intertidal to 313 m (Fraser 1937, 1946, as *A. amphora*).

Abietinaria traski (Torrey, 1902). Hydroid. Synonyms in Vervoort (1993, p. 99) and Hirohito (1995, p. 156). Abundant in parts of its range and conspicuous because of the symmetry and whiteness of its colonies (Fraser 1946). Colonies pinnate, to 6 cm high. Alaska to Baja California, 10–400 m (Fraser 1937, 1946; Hochberg and Ljubenkov 1998).

Amphisbetia furcata (Trask, 1857) (=*Sertularia furcata*). Hydroid. Synonyms in Fraser (1937, p. 162). Colonies small (8 mm), common on algae, surfgrass, and shore rocks, in large patches (Fraser 1946). British Columbia to southern California and southward to the tropics, intertidal to 82 m (Fraser 1937, 1946). See color photograph in Haderlie et al., 3.11, plate 17 as *Sertularia furcata*.

Dynamena disticha (Bosc, 1802) (=*Dynamena cornicina* auct., =*Sertularia cornicina* auct.). Hydroid. Synonyms in Vervoort (1993, p. 108) and Hirohito (1995, pp. 167, 170). Colonies small (15 mm), unbranched; a warm-water species occurring north to San Francisco Bay in shallow waters (Fraser 1937, 1946, as *Sertularia cornicina*). This is another "global" species name, with numerous populations around the world requiring molecular genetic analysis.

Fraseroscyphus sinuosus (Fraser, 1948). Hydroid. New genus described by Boero and Bouillon 1993, Can J. Zool. 71: 1061-1064. Colonies small (to 20 mm), abundant on coralline algae in the shallow subtidal (6 m) on the exposed outer coast at Horseshoe Cove, Bodega Bay, in front of the Bodega Marine Laboratory.

Hydrallmania franciscana (Trask, 1857). Hydroid. Synonyms in Vervoort (1993, p. 187). According to Fraser (1946), *H. franciscana* and *H. distans* Nutting, 1899 (reported from British Columbia to San Francisco Bay) are virtually indistinguishable. Colonies 15–20 cm high. Known only from San Francisco Bay and not recorded since its original description (Vervoort 1993).

**Salacia desmoides* (Torrey, 1902) (=*Sertularia desmoides*). Hydroid (see hydroid plate 47F, 47G). Additional synonyms in Millard (1975, p. 274). Creeping stolon with stems to 4–24 mm high, San Francisco Bay to southern California, 2–150 m (Fraaser 1937). Also reported in South Africa and southern Indian Ocean (Millard 1975).

Sertularella fusiformis Hincks, 1861. Hydroid. Synonyms in Vervoort (1993, p. 190). Colonies small (20 mm), with few or no branches. Oregon and San Francisco Bay to the Galápagos, 11–366 m (Fraser 1937, 1946).

**Sertularella* spp. Hydroid. Additional species of this genus including *S. tenella* (Alder, 1856) (see hydroid plate 46K, 46L) occur in our region, as noted by Fraser (1937, 1946, 1948).

Sertularia argentea Linnaeus, 1758. Hydroid. Synonyms in Cornelius (1995b, p. 84). Similar to *Sertularia cupressina* Linnaeus, 1758. Colonies large (2–30 cm or more), growing in clusters on shore rocks. A cold-water species occurring south to San Francisco Bay, 9–119 m (Torrey 1902; Fraser 1937, 1946). As with many other Linnean (and other older Atlantic-based) taxa in our list, these species could represent either valid amphiboreal distributions or undescribed Pacific species with misapplied Atlantic names.

**Sertularia* spp. Hydroid. Other species of this genus, such as *Sertularia similis* Clark, 1876 (see hydroid plate 57D, 57E) occur in the region.

**Symplectoscyphus erectus* (Fraser, 1938) (=*Sertularella erecta* Fraser, 1938, sometimes placed in the genus *Amphisbetia*). Hydroid. Additional synonyms in Vervoort (1993, p. 239). Although still considered valid, this species (see hydroid plate 47K) is not included in the key because the description by Fraser is inconclusive. Colonies small (10 mm), erect, unbranched; southern California to the tropics, intertidal to 13 m (Fraser 1946).

Symplectoscyphus tricuspidatus (Alder, 1856) (=*Sertularella tricuspidata*). Hydroid. Additional synonyms in Vervoort (1993, p. 241), Cornelius (1995b, p. 94), and Hirohito (1995, p. 225). An epibiont on other hydroids and on mussels (Cornelius 1995b). Colonies small (to 4 cm), irregular in shape. Alaska to Baja California, 1–500 m (Fraser 1937, 1946; Hochberg and Ljubenkov 1998).

Symplectoscyphus turgidus (Trask, 1857) (=*Sertularia turgida*, *Sertularella turgida*). Hydroid. Additional synonyms in Vervoort (1993, p. 241) and Hirohito (1995, p. 225). A common species, growing on rocky bottoms and serving as a substrate for various epibionts (Hochberg and Ljubenkov 1998). Colonies small (3 cm), stiff, little branched. Alaska to Baja California, intertidal to 200 m (Fraser 1937, 1946; Haderlie et al. 1980;

* = Not in key.

Hochberg and Ljubenkov 1998). See color photograph in Haderlie et al. 1980, 3.12, plate 17 as *Sertularella turgida*.

TIAROPSIDAE

Tiaropsidium kelseyi Torrey, 1909. Medusa (hydroid unknown). Occasionally collected in San Diego, Monterey Bay, Friday Harbor, British Columbia (Arai and Brinckmann-Voss 1980; Wrobel and Mills 1998 and 2003). Color photograph in Wrobel and Mills 1998 and 2003, p. 35.

ORDER PROBOSCOIDA

CAMPANULARIIDAE

Campanularia volubilis (Linnaeus, 1758). Hydroid. Synonyms in Cornelius (1995, p. 232). Dispersive stage a planula brooded inside the female gonotheca (Cornelius 1995). Colonies stolonal. Reported from the Bering Sea to the tropics (Fraser 1937, 1946), but likely actually limited to Arctic and boreal waters.

**Clytia attenuata* (Calkins, 1899). Hydroid and medusa. A little-known species of the shallow subtidal; the hydroid is known from Vancouver Island to southern California and is also reported from the Panama Canal and Brazil (Fraser 1946, 1948; West and Renshaw [see below]). Laboratory life cycle including both hydroid and medusa from material collected at Santa Catalina Island in West and Renshaw 1970, Mar. Biol. 7: 332–339. The synonymy between *"Phialidium" lomae* (see below, as *Clytia lomae*) and *Clytia attenuata* remains open to question according to Arai and Brinckmann-Voss (1980, p. 108). They found that medusae raised by West and Renshaw from the hydroid of *C. attenuata* were smaller in size, had gonads of a different shape, and fewer tentacles than the medusa *C. lomae*, and concluded "until *Clytia attenuata* can be reared from typical *Phialidium lomae* medusae the synonymy must be considered tentative."

Clytia gregaria (A. Agassiz, 1862) (=*Phialidium gregarium*, former name of medusa). Hydroid and medusa. *Phialidium* Leuckart, 1856, long used as a generic name in medusa literature, has been shown through life cycle studies to be a junior synonym of *Clytia* Lamouroux, 1812, a name originally applied to hydroids. The medusa, which swims in bursts followed by slow, upside-down sinking (Mills 1981), is often present in large numbers, thus the species name; for feeding behavior and diet, see also Costello and Colin (2002). Color photograph in Wrobel and Mills 1998 and 2003, p. 36. Hydroid described from the laboratory, raised from gametes from medusae (Strong 1925, Publ. Puget Sound Biol. Station 3: 383–399; Roosen-Runge 1970, Biol. Bull. 139: 203–221) and not corresponding well to any known species of *Clytia* from the field (Fraser 1937, 1946; Arai and Brinckmann-Voss 1980). Alaska to central Oregon (Wrobel and Mills 1998).

Clytia hemisphaerica (Linnaeus, 1767) (=*Phialidium hemisphaericum,* =*Clytia johnstoni*). Hydroid (medusa unknown on the West Coast of North America). Synonyms in Calder (1991, pp. 57–58) and Cornelius (1995, p. 252). More than one species may exist under this name, which seems not to be applicable to any of the "*Phialidium*" medusae on the West Coast, so not included in the key to hydromedusae. Hydroid colonies at least partly stolonal. On many substrates, and apparently tolerating lower salinities (Cornelius 1995; Fraser 1937 as *C. johnstoni* (Alder), central California to Alaska).

* = Not in key.

Clytia lomae (Torrey, 1909) (=*Phialidium lomae*). Medusa (hydroid unknown). Medusa described from San Diego and perhaps present along the entire West Coast. Arai and Brinckmann-Voss (1980) suspect that there are two species of "*Phialidium*" medusae along our coast, and assign the name *C. lomae* to the slightly smaller species with fewer tentacles, acknowledging that extensive life cycle studies could show only one, variable species to be here (see note under *Clytia attenuata*, above).

Gonothyraea loveni (Allman, 1859) (=*Gonothyraea clarki* [Marktanner-Turnerestcher, 1895]). Hydroid. The synonymy of *G. loveni* and *G. clarki* is generally accepted but needs confirmation; additional synonymy in Cornelius (1982, p. 92). This is the only species of *Gonothyraea* on the West Coast. The two other species assigned to that genus by Fraser are now referred to other genera (*G. gracilis* to *Clytia; G. inornata* to *Laomedea)*; both occur north of our area. Predominantly estuarine, in colder waters. Colonies small (to 2.5 cm). Widespread in San Francisco Bay shallow waters in 2004, and occurring from there north to Alaska; intertidal to 124 m (Fraser 1937, 1946, as *G. clarki*). An abundant fouling organism.

Hartlaubella gelatinosa (Pallas, 1766) (=*Campanularia gelatinosa*). Hydroid. A boreal species found in both Atlantic and Pacific Oceans; Queen Charlotte Islands to central California, from lower intertidal to 150 m (Fraser 1937), often in harbors or estuaries. Recorded from 1859 to 1912 in San Francisco Bay including records of Agassiz 1865 and Torrey 1902, with no subsequent records (Cohen and Carlton 1995, Appendix 2, p. 1).

Laomedea calceolifera (Hincks, 1871) (=*Campanularia calceolifera*). Hydroid. Synonymy in Cornelius (1982, p. 102). A fouling species, frequent in harbors and estuaries. Colonies small (to 2.5 cm high), with sexually dimorphic gonothecae. Introduced from the Atlantic; on floating docks at Richmond Marina and Coyote Point Marina, San Francisco Bay, 2004.

Obelia bidentata Clark, 1875 (=*Obelia bicuspidata* Clark, 1875). Hydroid and medusa. While the names *O. bidentata* and *O. bicuspidata* were introduced in the same paper, the former was assigned priority under the First Reviser Principle in nomenclature by Jäderholm [1903].) Additional synonymy in Calder (1991, pp. 70–71). Medusae infrequently observed anywhere in the world. On floating dock at Pier 39, San Francisco, 2004. Hydroid throughout San Francisco Bay, 13–22 m (Fraser 1937, as *O. bicuspidata*).

Obelia dichotoma (Linnaeus, 1758) (=*Obelia commisssuralis* McCrady, 1859). Hydroid and medusa. Additional synonyms in Calder (1991, pp. 72–73), Cornelius (1995, p. 296), and Hirohito (1995, pp. 74–75). Species highly varied in form, occurring on many different substrates including swimming animals (ranging from sharks to copepods). Alaska to the tropics, frequent in our region (Fraser 1937, 1946). Standing (1976, pp. 155–164 in *Coelenterate Ecology and Behavior* [G. O. Mackie, ed.], Plenum) reports on the role of *O. dichotoma* in fouling community structure in Bodega Harbor.

Obelia geniculata (Linnaeus, 1758). Hydroid and medusa. Synonyms in Cornelius (1995, p. 301) and Hirohito (1995, p. 76). Colonies small (25 mm), immediately distinguished by asymmetrically thickened internodes and hydrothecae (Cornelius 1995), although occasional specimens occur with unthickened perisarc. On various substrates, especially algae; frequent in brackish water. British Columbia to the tropics, including our region (Fraser 1937, 1946).

Obelia longissima (Pallas, 1766). Hydroid and medusa. A large (up to 60 cm) fouling hydroid, common in harbors. Easy to confuse with *O. dichotoma*. Alaska to southern California, low

tide to 128 m (Fraser 1937, 1946). Our harbor-dwelling *Obelia* hydroids are probable ship fouling introductions. They are commonly fed upon by several nudibranch species.

Orthopyxis compressa (Clark, 1877) (=*Eucopella compressa*). Hydroid and ephemeral medusa. Discussion of synonomies and taxonomic confusion in Arai and Brinckmann-Voss (1980: 101–104). Colonies stolonal, with perisarc of varied thickness, sometimes thin but often very thick; pedicels smooth. Alaska to San Diego, 5–37 m (Fraser 1937). Common on larger hydroids or on red algae. Medusae are shed sequentially at dusk, with females released about 15–20 minutes before males from nearby colonies; the medusae live free for less than one hour, only long enough to shed gametes (see Miller 1978. J. Exp. Zool. 205: 385–392, misidentified as *O. caliculata*).

Orthopyxis everta (Clark, 1876) (=*Eucopella everta*). Hydroid. Retains gametes. Colonies stolonal, with perisarc of varied thickness, pedicels wavy or annulated. British Columbia to San Diego, 2–77 m (Fraser 1937). Sometimes abundant on kelp.

Orthopyxis integra (Macgillivray, 1842). (=*Eucopella caliculata, =Agastra mira*). Hydroid and ephemeral medusa. Synonyms in Cornelius (1982, p. 61; 1995, p. 235). Colonies largely stolonal. Alaska to southern California, low tide to 439 m (Fraser, 1937, 1946); cosmopolitan species.

SUBCLASS LIMNOMEDUSAE

OLINDIIDAE (formerly as OLINDIASIDAE)

Aglauropsis aeora Mills, Rees and Hand, 1976. Hydroid and medusa. Medusae collected primarily washed up on open beaches from Bodega Bay to Monterey Bay; minute polyp without tentacles known only from the laboratory. See Mills et al. 1976, Wasmann J. Biol. 34: 23–42. Color photograph in Wrobel and Mills 1998 and 2003, p. 36.

Craspedacusta sowerbii Lankester, 1880 (=*C. sowerbyi,* a misspelling). Hydroid and medusa. Introduced; now worldwide in fresh water, including in the upper Sacramento River near Redding, and in quarry lakes and reservoirs in many other areas in California. See Russell (1953) for detailed discussion. The simple, well-known hydroid, without tentacles, looks very much like that raised in the laboratory only through the primary polyp stage of both *Aglauropsis aeora* and *Maeotias marginata*.

Eperetmus typus Bigelow, 1915. Medusa (hydroid unknown). Distinguished from *Aglauropsis aeora* by the smaller number of thicker tentacles and presence of centripetal canals. From Alaska to Washington, where it becomes uncommon; rare sightings in Coos and Yaquina Bays. Usually pale pink. Color photograph in Wrobel and Mills 1998 and 2003, p. 37. Records from Japan are an undescribed *Aglauropsis*; see Mills et al. 1976, Wasmann J. Biol. 34: 23–42.

Gonionemus vertens A. Agassiz, 1862. Hydroid and medusa. In the shallow subtidal, usually seen clinging to algae or eelgrass, but may also be free-swimming near the surface in protected bays. Indigenous from Alaska to Washington, but known from a variety of locations worldwide and might be expected south of Washington. See plate 49Q for tiny, cryptic solitary polyp; color photograph of medusa in Wrobel and Mills 1998 and 2003, p. 37. A virulent-stinging variety or separate species occurs in the Russian Far East. See Edwards 1976, Adv. Mar. Biol. 14: 251–284 for a global review.

Maeotias marginata (Modeer, 1791). (=*Maeotias inexspectata* Ostroumoff, 1896 [misspelled occasionally as *inexpectata*]; see Mills and Rees 2000). Hydroid and medusa. Most medusae found in the San Francisco Bay system are males, but a few females discovered in 1998 allowed for the culture of embryos. Hydroids of *Maeotias* are known only from juvenile polyps raised under laboratory conditions (Rees and Gershwin 2000); these are miniscule and morphologically simple, with a cluster of cnidocysts around the mouth and without tentacles. A brackish to freshwater species, introduced to the San Francisco Bay area by the 1980s or 1990s, with an unconfirmed observation in 1959 (see Mills and Rees 2000). Color photograph in Wrobel and Mills 1998 and 2003, p. 29. A hydroid identified as this species by Mills and Sommer (1995) from the San Francisco area is *Moerisia* sp. instead (see Mills and Rees 2000).

Vallentinia adherens Hyman, 1947. Medusa (hydroid unknown). Occurs near shore, clinging to algae (see Hyman 1947, Trans. Am. Microsc. Soc. 66: 262–268); known only from the Pacific Grove area (where it is found on the kelp *Macrocystis* off Hopkins Marine Station [between the breakwater and Point Piños], Freya Sommer personal communication), and Santa Barbara (Wrobel and Mills 1998 and 2003); rare. Color photograph in Wrobel and Mills 1998 and 2003, p. 37.

SUBCLASS SIPHONOPHORA

ORDER PHYSONECTAE

AGALMATIDAE

Agalma elegans (*pro parte* M. Sars, 1846)—Sars' original description included more than one species, and authorship is thus noted as *pro parte*. A cosmopolitan species, which can be found anywhere from Alaska to Mexico. Easily distinguished from *A. okeni* as it has a long stem with leaflike bracts, while in *A. okeni* the stem is short so the bracts, with two (young) or four (mature) distal facets, interlock with each other. Pacific, Indian, and Atlantic Oceans and the Mediterranean.

*****Agalma okeni* Eschscholtz, 1825. This second cosmopolitan species of *Agalma* (siphonophore plate 59C) is also present on our coast, but more likely to be encountered off southern California and Baja California. Further distinguished from *A. elegans* by the distinctive ridges on the swimming bells, and Y-shape of the subumbrella when viewed from above. Pacific, Indian, and Atlantic Oceans and the Mediterranean.

Nanomia bijuga (delle Chiaje, 1841). Probably the most common physonect off the West Coast, thought to be responsible in some regions for the deep scattering layer (Barham 1963, Science 140: 826–828; Barham 1966, Science 151: 1399–1403), but occurs to the surface; Pacific, Indian, and Atlantic Oceans and the Mediterranean. Color photograph in Wrobel and Mills, 1998 and 2003, p. 46.

APOLEMIIDAE

Apolemia spp. This genus is quite diverse on our coast, with several undescribed species (the name *"Apolemia uvaria"* has been applied rather indiscriminately in past West Coast literature). The colonies are often tens of meters long and in deep water, but many-centimeter-long fragments can be encountered near shore at the surface. They have an overall "fuzzy" appearance, with red or white gastrozooids, and pack a substantial sting. The flimsy, jelly-filled bracts also contain patches of stinging cells on their upper surfaces. Species occur in the Pacific, Indian, and Atlantic Oceans and Mediterranean. Color photograph in Wrobel and Mills 1998 and 2003, p. 45.

***** = Not in key.

FORSKALIIDAE

Forskalia spp. Several species of *Forskalia,* which are difficult to distinguish, might be encountered along our coast. Divers sometimes liken the overall aspect of *Forskalia* to a Christmas tree: conical, widening at the base, with fine tentacles coming out from within the overall shape. They are active, strong swimmers, often spiraling around as they move. When disturbed they may release clouds of pigmented, bioluminescent material. Species occur in the Pacific, Indian, and Atlantic Oceans and the Mediterranean. Color photograph in Wrobel and Mills 1998 and 2003, p. 46.

PHYSOPHORIDAE

Physophora hydrostatica Forsskål, 1775. Colonies are typically several centimeters high and the compact complexity, symmetry, and pastel blue and pink colors of this worldwide species are sure to engender wonder in anyone who sees it; Pacific, Indian, and Atlantic Oceans and the Mediterranean. Color photograph in Wrobel and Mills 1998 and 2003, p. 46.

ORDER CALYCOPHORAE

ABYLIDAE

Abylopsis tetragona (Otto, 1823). This distinctive species is likely to be encountered only at the southern end of the range of this book; Pacific, Indian, and Atlantic Oceans and the Mediterranean.

**Bassia bassensis* (Quoy and Gaimard, 1833). Another polyhedral species (siphonophore plate 60C) similar to *Abylopsis tetragona,* which is also likely to be encountered only at the southern end of the range of this book; the ridges of the swimming bells have a bluish tinge; Pacific, Indian, and Atlantic Oceans and the Mediterranean.

CLAUSOPHYIDAE

Chuniphyes multidentata Lens and van Riemsdijk, 1908. An abundant midwater species that is occasionally encountered at the surface in central California; Pacific, Indian, and Atlantic Oceans.

DIPHYIDAE

Chelophyes appendiculata (Eschscholtz, 1829). One of the most common epipelagic temperate and tropical oceanic siphonophore species and likely to be seen anywhere along the Pacific West Coast including Baja California; Pacific, Indian, and Atlantic Oceans and the Mediterranean. When present in substantial numbers, this species has enough sting to be quite bothersome to divers and snorkellers.

**Chelophyes contorta* (Lens and van Riemsdijk, 1908). Perhaps a near-shore, rather than oceanic species (siphonophore plate 60H) (Totton 1965), with a somewhat more southern distribution that *C. appendiculata,* so to be expected only in the southern range of this book, continuing down into Mexico; appears to have an Indo-Pacific distribution (Bouillon et al 2004).

Dimophyes arctica (Chun, 1897). In spite of its name, this is a cosmopolitan species found in all oceans including the Arctic and Antarctic and can be encountered anywhere along the Pacific coast of North America.

Diphyes bojani (Eschscholtz, 1829). Might be encountered anywhere along the California and Baja California coasts; Pacific, Indian, and Atlantic Oceans and the Mediterranean.

Diphyes dispar Chamisso and Eysenhardt, 1821. More likely to be encountered in the southern range of this book, continuing down Baja California, but has worldwide distribution in warmer waters. Color photograph in Wrobel and Mills 1998 and 2003, p. 47.

Eudoxoides spiralis (Bigelow, 1911). Epipelagic species found usually south of about 40°N on our coast; Pacific, Indian, and Atlantic Oceans and the Mediterranean.

Lensia challengeri Totton, 1954. Can be encountered anywhere along the Californian and Baja Californian coast; found throughout the Pacific, usually south of about 40°N, usually near shore.

Lensia conoidea (Keferstein and Ehlers, 1860). Cosmopolitan species and likely to be seen anywhere along the Pacific West Coast including Baja California.

Lensia hostile Totton, 1941. A typically deep-water species found off California; Pacific, Indian, and Atlantic Oceans.

Lensia hotspur Totton, 1941. Can be encountered anywhere from Oregon to Baja California; Pacific, Indian, and Atlantic Oceans and the Mediterranean.

**Lensia* spp. Several other little *Lensia*s are found off the West Coast; only the most common species have been included in the key.

Muggiaea atlantica Cunningham, 1892. A coastal species of the temperate Pacific, Indian, and Atlantic Oceans and the Mediterranean that can be found throughout the study area. In some localities, *M. atlantica* can be replaced by *M. kochi* at different times of year, which might be related to water temperature, but the two species appear to be mutually exclusive. *M. atlantica* has been collected in Bodega Harbor. Photograph in Wrobel and Mills 1998 and 2003, p. 47.

Sulculeolaria quadrivalvis Blainville, 1834. The looping radial canals and lack of ridges are distinctive of this genus among the Diphyidae; Pacific, Indian, and Atlantic Oceans and the Mediterranean. Color photograph in Wrobel and Mills 1998 and 2003, p. 47.

PRAYIDAE

**Desmophyes annectens* Haeckel, 1888. Shaped like *Praya* and *Rosacea,* but with minute red pigment flecks around the opening of the subumbrella in the swimming bells in life, and with four straight radial canals; large, spherical, white somatocyst. Uncommon; Pacific, Indian, and Atlantic Oceans and the Mediterranean.

**Lilyopsis rosea* Chun, 1885. An uncommon prayid species (siphonophore plate 59I) with a large subumbrellar cavity, which has been seen in central California; Pacific, and Atlantic Oceans and the Mediterranean.

Praya dubia (Quoy and Gaimard, 1827). These siphonophores are often tens of meters long and in deep water, but several cm-long pieces of the colonies may be encountered near shore at the surface. The bright yellow color of the gastrozooids is striking; they have a substantial sting. Pacific, Indian, and Atlantic Oceans.

Praya reticulata (H. B. Bigelow, 1911). Similar to above species, but with reticulate pattern of canals on the subumbrella. The branching pattern of the somatocyst also distinguishes it. Pacific, Indian, and Atlantic Oceans.

* = Not in key.

Rosacea spp. Several species of *Rosacea* occur off the West Coast of North America and are difficult to identify and often confused with *Praya* spp. Typically, the bracts are hemispherical while those of *Praya* spp. are flattened. A near-shore observer is most likely to run into fragments of one of these colonies, which can reach many meters in length when undamaged and will sting.

SPHAERONECTIDAE

Sphaeronectes gracilis (Claus, 1873, 1874). Sometimes occurs near shore from Monterey Bay south, but can be very difficult to see; Pacific, Indian, and Atlantic Oceans and the Mediterranean.

SUBCLASS NARCOMEDUSAE

AEGINIDAE

Aegina citrea Eschscholtz, 1829. Medusa only. A variable worldwide, oceanic species (that may turn out with molecular study to be a species complex) that may occasionally be seen near shore; sometimes infused with yellow pigment. Color photograph in Wrobel and Mills 1998 and 2003, p. 38. Undescribed aeginids are also present in deep water.

CUNINIDAE

Cunina spp. Medusa only. Worldwide, oceanic species that occasionally come near shore. These are typically 10–60 mm in bell diameter and may be transparent and colorless or have some color. See Kramp (1961, 1968) for specific characters. Color photograph in Wrobel and Mills 1998 and 2003, p. 39.

Solmissus incisa (Fewkes, 1886). Medusa only. A worldwide, oceanic species, this is the larger (to 100 mm bell diameter) and less common *Solmissus*; it can be colorless or sometimes infused with transparent purple color (see Kramp 1961, 1968).

Solmissus marshalli A. Agassiz and Mayer, 1902. Medusa only. A worldwide, oceanic species, this is the smaller and more common of the two *Solmissus* that might be encountered near shore. It is usually colorless and <60 mm in bell diameter (see Kramp 1961, 1968). Color photograph in Wrobel and Mills 1998 and 2003, p. 39.

SOLMARISIDAE

Pegantha spp. Medusa only. Worldwide, oceanic species that occasionally come near shore. These are typically 25–50 mm in bell diameter and may be transparent and colorless or have some color. See Kramp (1961, 1968) for specific characters. Color photograph in Wrobel and Mills 1998 and 2003, p. 38.

Solmaris spp. Medusa only. Worldwide, oceanic and coastal species that are sometimes encountered near shore, sometimes in great numbers. These are small transparent medusae with a rapid pulsation rate. See Kramp (1961, 1968) for specific characters. Color photograph in Wrobel and Mills 1998 and 2003, p. 39.

TETRAPLATIDAE

**Tetraplatia volitans* Busch, 1851. Highly reduced narcomedusa up to about 1 cm long that looks more like a flying worm or pteropod than a jellyfish, with a ringlike constriction fairly near the midpoint dividing the oral and aboral ends, which are connected by four flying buttress–like structures. Oceanic in the upper 900 m, but occasionally found near shore; feeds on zooplankton (see Hand 1955, Pac. Sci. 9: 332–348; color photograph in Wrobel and Mills 1998 and 2003, p. 52, and at http://jellieszone.com/tetraplatia.htm). The two species of *Tetraplatia* have been proposed as both coronate scyphomedusae and as narcomedusae, but a genetic study by Collins et al. (2006) has placed these unusual medusae in the hydrozoan Narcomedusae.

SUBCLASS ACTINULIDAE (=HALAMMOHYDROIDA)

HALAMMOHYDRIDAE

**Halammohydra* sp. Medusa only. Minute (0.5–2 mm), highly reduced medusa (without a polyp phase, although it looks like a polyp), living interstitially in sand; solitary not colonial form. Found on a beach near Moss Landing (as reported by Robert Higgins and James Nybbaken). The entirely ciliated animal consists mostly of a manubrium with two whorls of long, contractile tentacles; there is a statocyst between each pair of tentacles and an aboral adhesive organ. A number of species have been described.

SUBCLASS TRACHYMEDUSAE

GERYONIDAE

Geryonia proboscidalis (Forsskål, 1775). Medusa only. Oceanic warm waters in the Pacific, Atlantic, and Mediterranean; occasionally seen near shore in the southern range of this book; six-part symmetry distinguishes this less-common species from *Liriope tetraphylla*. Color photograph in Wrobel and Mills 1998 and 2003, p. 40.

Liriope tetraphylla (Chamisso and Eysenhardt, 1821). Medusa only. Oceanic, Pacific, Atlantic, and the Mediterranean; occasionally seen near shore throughout the range of this book, sometimes in great numbers in warm water masses; four-part symmetry distinguishes this species from the less-common *Geryonia proboscidalis*. Color photograph in Wrobel and Mills 1998 and 2003, p. 40.

RHOPALONEMATIDAE

Aglantha digitale (O. F. Müller, 1776). Medusa only. A common species in the North Pacific, North Atlantic, and Arctic, typical of the upper 200 m and sometimes found nearshore. This species has two modes of swimming: a general slow swim and a strong escape swim separately mediated by giant axons. Usually colorless, but may have red, pink or orange color on the tentacles. For feeding behavior and diet see Costello and Colin (2002). Color photograph in Wrobel and Mills 1998 and 2003, p. 42.

Aglaura hemistoma Péron and Lesueur, 1809. Medusa only. Oceanic, Pacific, Atlantic, and the Mediterranean; occasionally nearshore, between about 40°N and 40°S, replacing *Aglantha* as the most abundant epipelagic species in warmer waters. It is smaller and more fragile than *Aglantha* and has two modes of swimming (slow feeding mode and fast escape swim). Color photograph in Wrobel and Mills 1998 and 2003, p. 42.

* = Not in key.

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Scyphozoa: Scyphomedusae, Stauromedusae, and Cubomedusae

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(Plates 61–63)

The relatedness of the 200 worldwide species of scyphozoan jellyfish (Mianzan and Cornelius 1999) known as semaeostome medusae, rhizostome medusae, coronate medusae, stauromedusae, and cubomedusae remains unclear (Dawson 2004b, Marques and Collins 2004). Here we use the names for the three jellyfish groups that we treat in this section without making phylogenetic judgments.

The jellyfish we cover are those that are likely to be found in the intertidal, shallow subtidal, or in bays and harbors along the coast. The semaeostome scyphomedusae are usually large and often colorful, pelagic medusae that are not encountered in the intertidal zone as adults except when cast ashore, but may often be seen in harbors. Nearshore species of semaeostome scyphomedusae are considered here. The stauromedusae, in contrast, are small, inconspicuous, stalked medusae that are found either in protected bays or in high-current or wave-swept areas in the lower intertidal and subtidal,

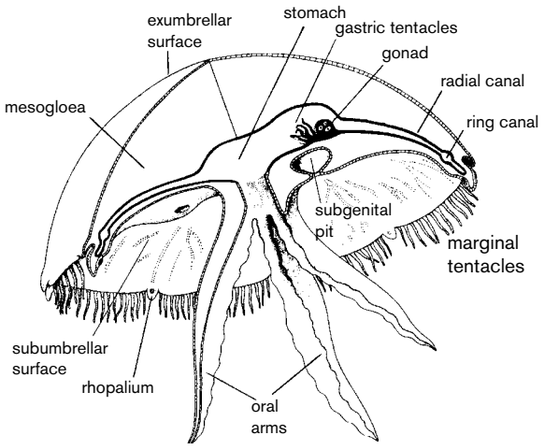

PLATE 61 Scyphozoa. Scyphomedusan structure, diagrammatic (modified after Naumov from Bayer and Owre, *The Free-Living Lower Invertebrates*, 1968; used with permission of The MacMillan Company).

attached by an aboral stalk to eelgrass, seaweed, or rock. One cubomedusa, *Carybdea* sp., may be found from Santa Barbara south in the shallow subtidal along the open coast. Two species of rhizostome scyphomedusae, *Phyllorhiza punctata* and *Stomolophus meleagris*, may also occasionally be found in Southern California.

Scyphomedusae (sometimes rather objectionably called the "true" jellyfish) can be distinguished from hydromedusae by their usually larger size, frilly mouth lobes, scalloped margins bearing lappets, absence of a velum, presence of marginal rhopalia, and often-complex pattern of radial canals (plates 61 and 62). In contrast, hydromedusae (see plate 39) usually are small, often glassy-clear, and possess a velum; most have four simple radial canals. For an account of the more fundamental morphological differences, the student is referred to Hyman (1940a), Russell (1970), or any detailed invertebrate zoology textbook.

Semaeostome scyphomedusae that live near our coast have an attached polypoid part of their life cycle: the soft, white "scyphistoma" stage, which can be encountered in great numbers under shaded parts of floats in harbors or marinas or on boat hulls. Most (probably all) of these scyphistomae (plate 62A, 62B) encountered in harbors on the West Coast of America belong to *Aurelia*. The polyp phases of other West Coast scyphomedusae have not been located in the field, although most have now been cultured in the laboratory by curators at the Monterey Bay Aquarium (some are described in Gershwin and Collins 2002).

Semaeostome scyphomedusae, when they are plentiful, play a significant role in coastal food webs by consuming a variety of zooplankton prey, ranging from small copepods to ctenophores and other large medusae. A number of other species depend on them for food or protection. Jellyfish are eaten by sunfish (*Mola mola*) and leatherback turtles. Gotshall et al. (1965) note that in California the blue rockfish *Sebastes mystinus* "stalks" *Chrysaora,* biting off pieces of the oral arms while avoiding contact with the marginal tentacles, and show a photograph of about a dozen fish feeding on a single *C. fuscescens*. Other jellyfish found in guts of the blue rockfish included *Aurelia* and *"Pelagia"* (= *C. colorata*?). A variety of species "hitchhikes" on the larger medusae, especially crustaceans such as amphipods and crab larvae.