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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DALE R. CALDER, AND CADET HAND

(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

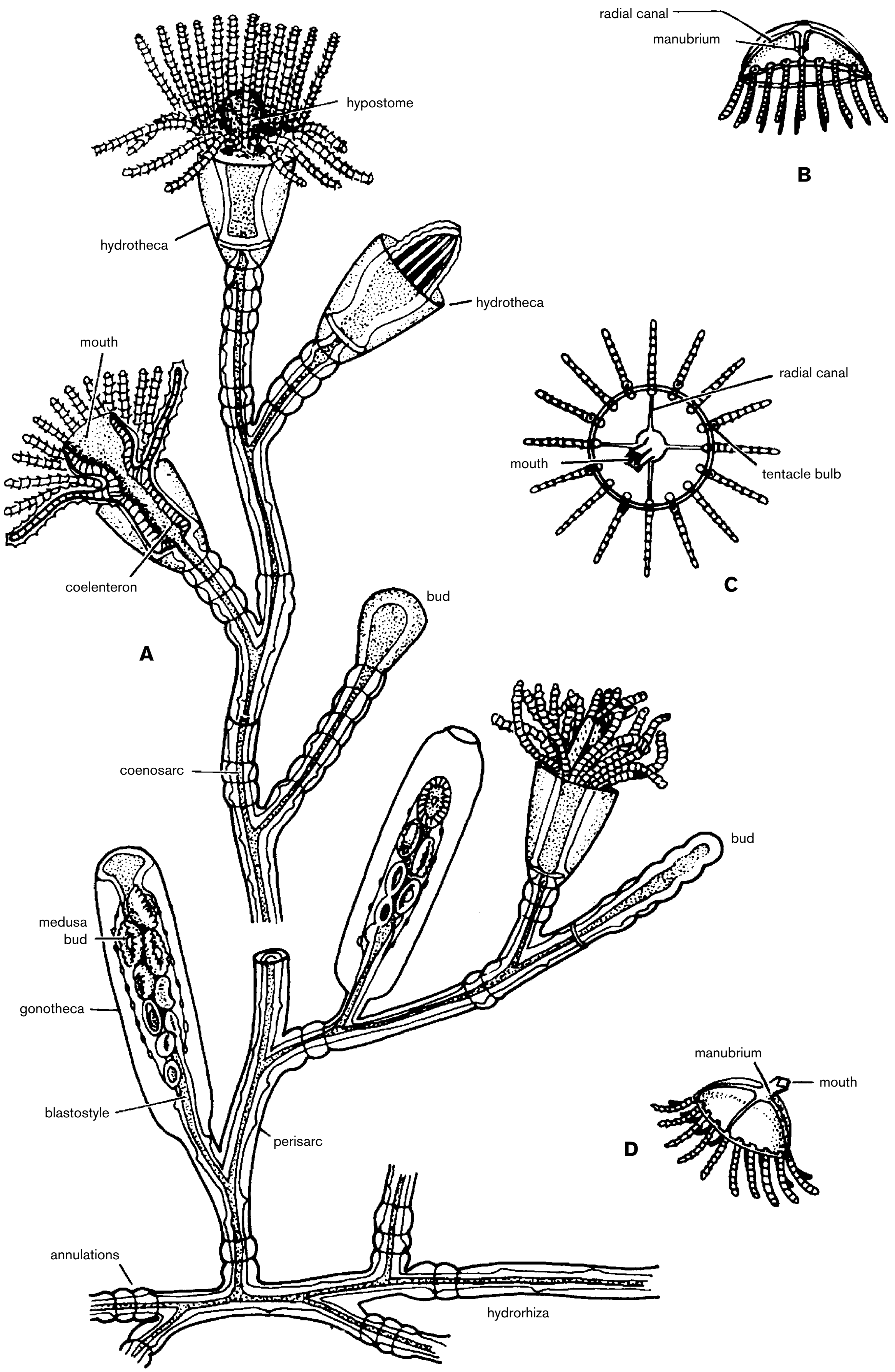


PLATE 38 Hydrozoan polymorphism (*Obelia*). A, the polypoid colony; B and C, immature medusae; D, medusa swimming inside out; note that *Obelia* lacks the typical hydromedusan velum (modified from Hand in Marshall and Williams 1972; used with permission of The Macmillan Company).

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).

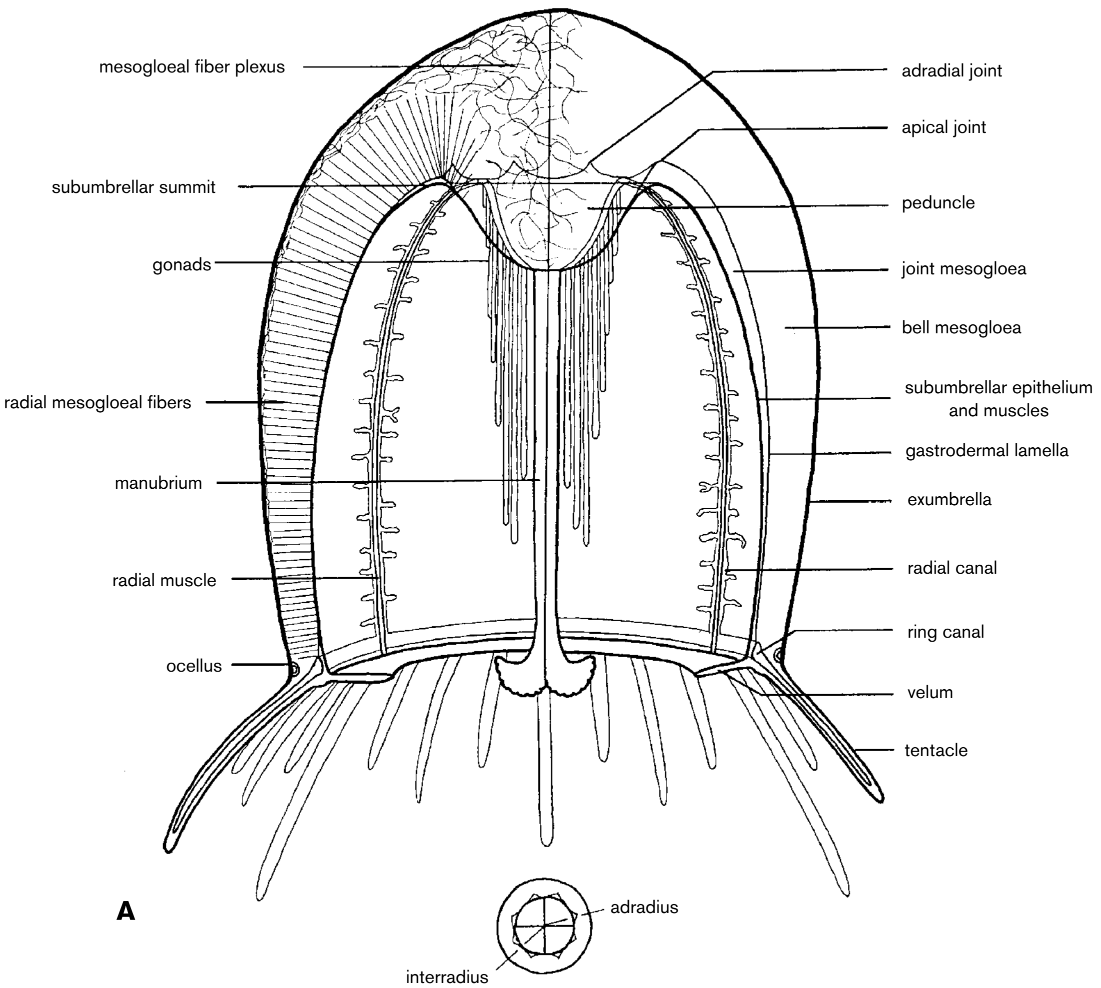
The bell margin is usually simple and unscalloped. Tentacles usually arise from the bell margin and may be simple, few, or many in number, occurring singly or in groups, or they may be branched (e.g., *Cladonema,* plate 54F–54I) or rudimentary. The margin may also be provided with specialized sense organs. 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,



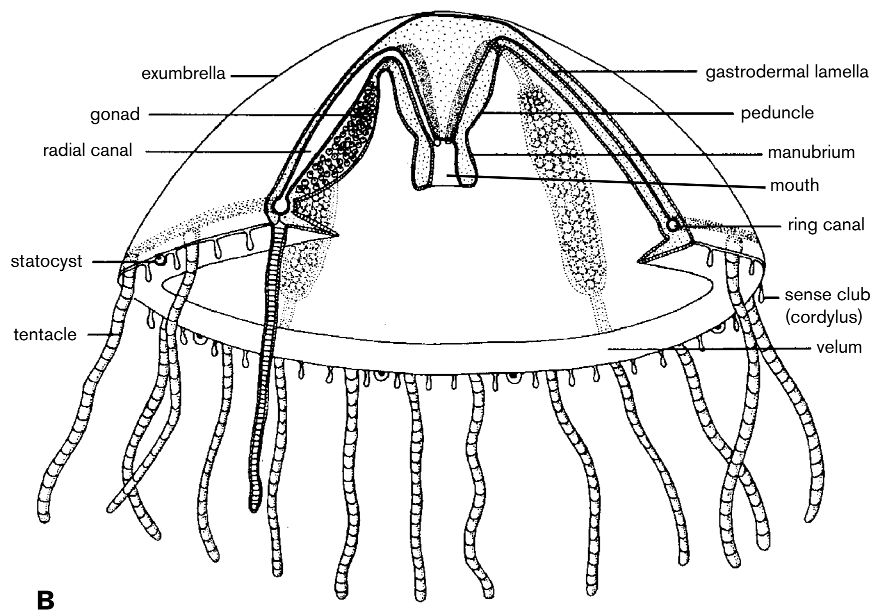


PLATE 39 Hydromedusa structure diagrammatic, with sections of bells removed. A, Anthomedusa *Polyorchis penicillatus* (from Gladfelter 1975, Helgoländer wiss. Meeresunters. 23: 41, fig. 1); B, generalized Leptomedusa.

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).

ACKNOWLEDGMENTS

For information and assistance, we thank Charles M. D. Santos, Jeff Goddard, Stephen Cairns, Cathy McFadden, David Wrobel, John Moore, and Garry McCarthy. ACM received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo. DRC received financial support from the Natural Sciences and Engineering Research Council of Canada and the National Science Foundation Partnerships for Enhancing Expertise in Taxonomy.

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

ANTONIO C. MARQUES, ALVARO E. MIGOTTO, DALE R. CALDER, AND CLAUDIA E. MILLS

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*

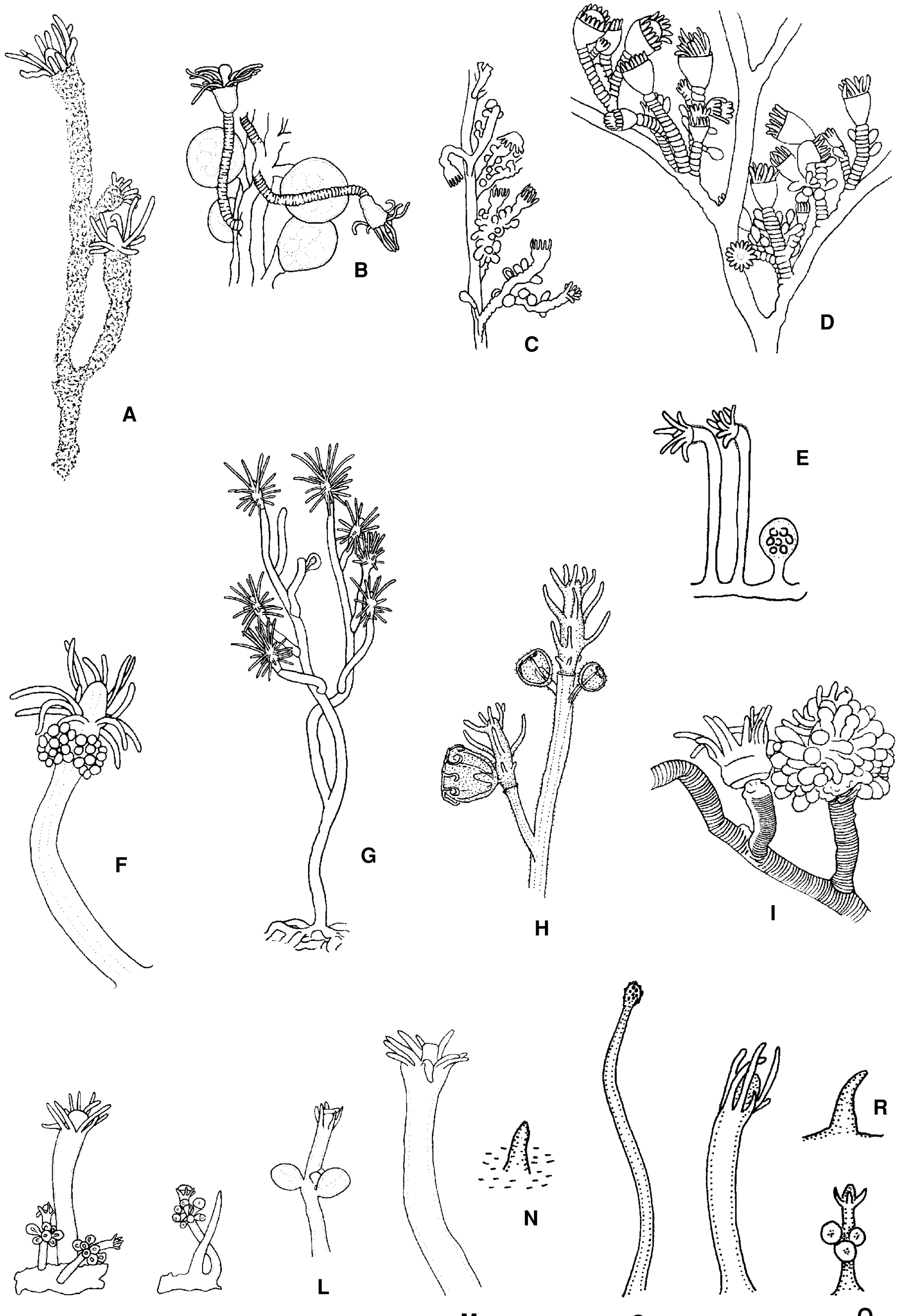


PLATE 40 Athecata. A, *Bougainvillia muscus*; B, *Garveia annulata*; C–D, *Garveia franciscana*; E, *Rhizorhagium formosum*; F, *Clava multicornis*; G, *Cordylophora caspia*; H, *Turritopsis* sp. I, *Eudendrium californicum*; J, K, *Hydractinia armata*; L–M, N (spine), *Hydractinia milleri*; O–Q, R (spine), *Hydractinia laevispina* (A, after Calder 1988; D, after Torrey 1902; G, after Schuchert 1996; H, after Mayer 1910; I, after Marques et al. 2000; J–K, after Fraser 1940; rest, after Fraser 1937).

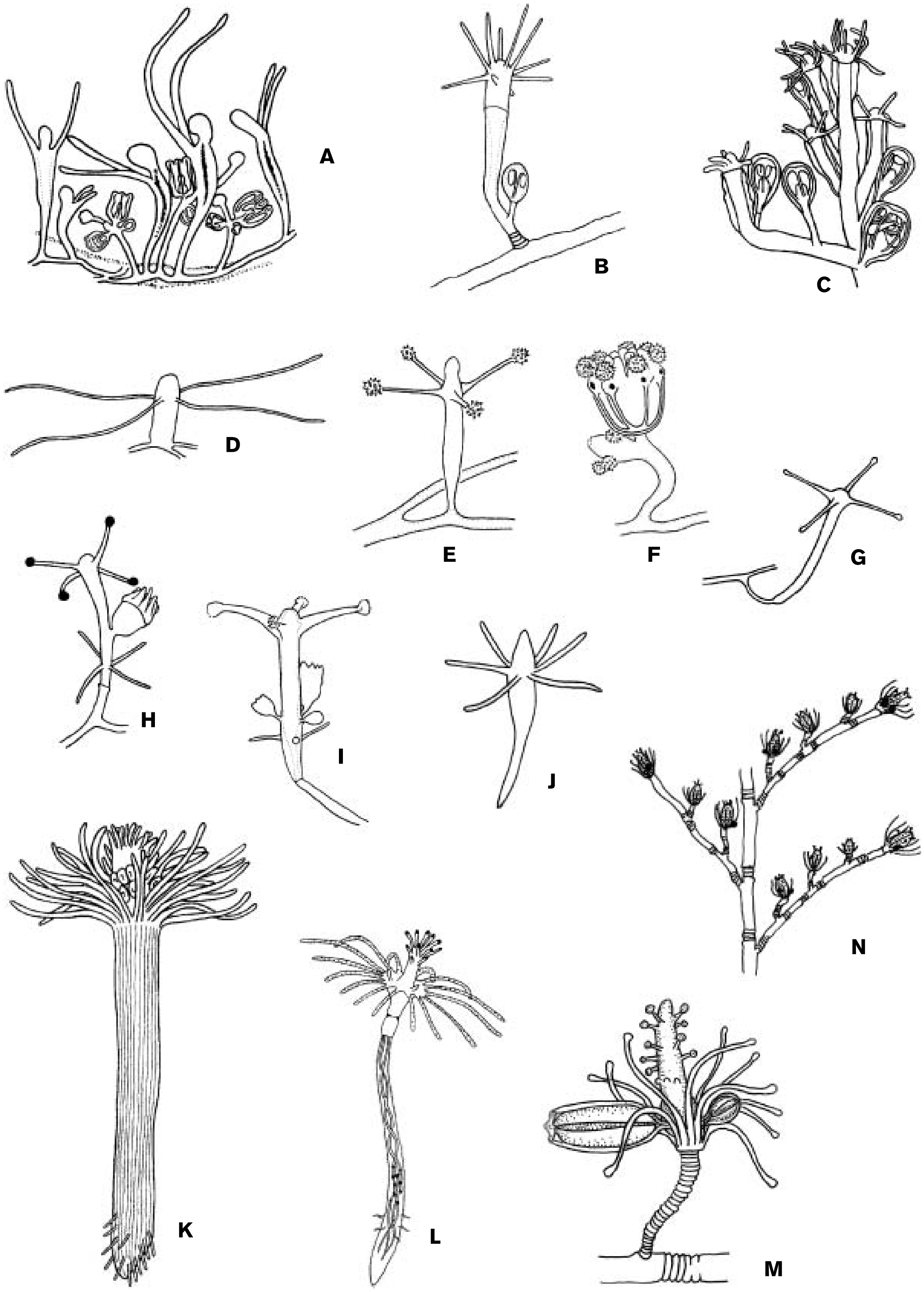


PLATE 41 Athecata (continued). A, *Proboscidactyla flavicirrata*; B, *Amphinema* sp.; C, *Leuckartiara octona*; D, *Rathkea octopunctata*; E, F, *Cladonema myersi*; G, *Cladonema pacificum*; H, *Cladonema radiatum*; I, *Cladonema californicum*; J, unidentified corymorphid from Lake Merritt, Oakland, in San Francisco Bay; K, *Corymorpha palma*; L, *Euphysora bigelowi*; M, N, *Pennaria disticha* (A, after Naumov 1969; B, from unpublished photographs by J. T. Rees; C, H, after Migotto 1996; D, after Schuchert 1996; E, F, after Rees 1949; G, after Hirohito 1988; I, after Rees 1979; J, from 1967 drawing by Jim Carlton and Dustin Chivers; K, after Fraser 1937; L, after Sassaman and Rees 1978; M, after Mayer 1910; N, after Millard 1975).

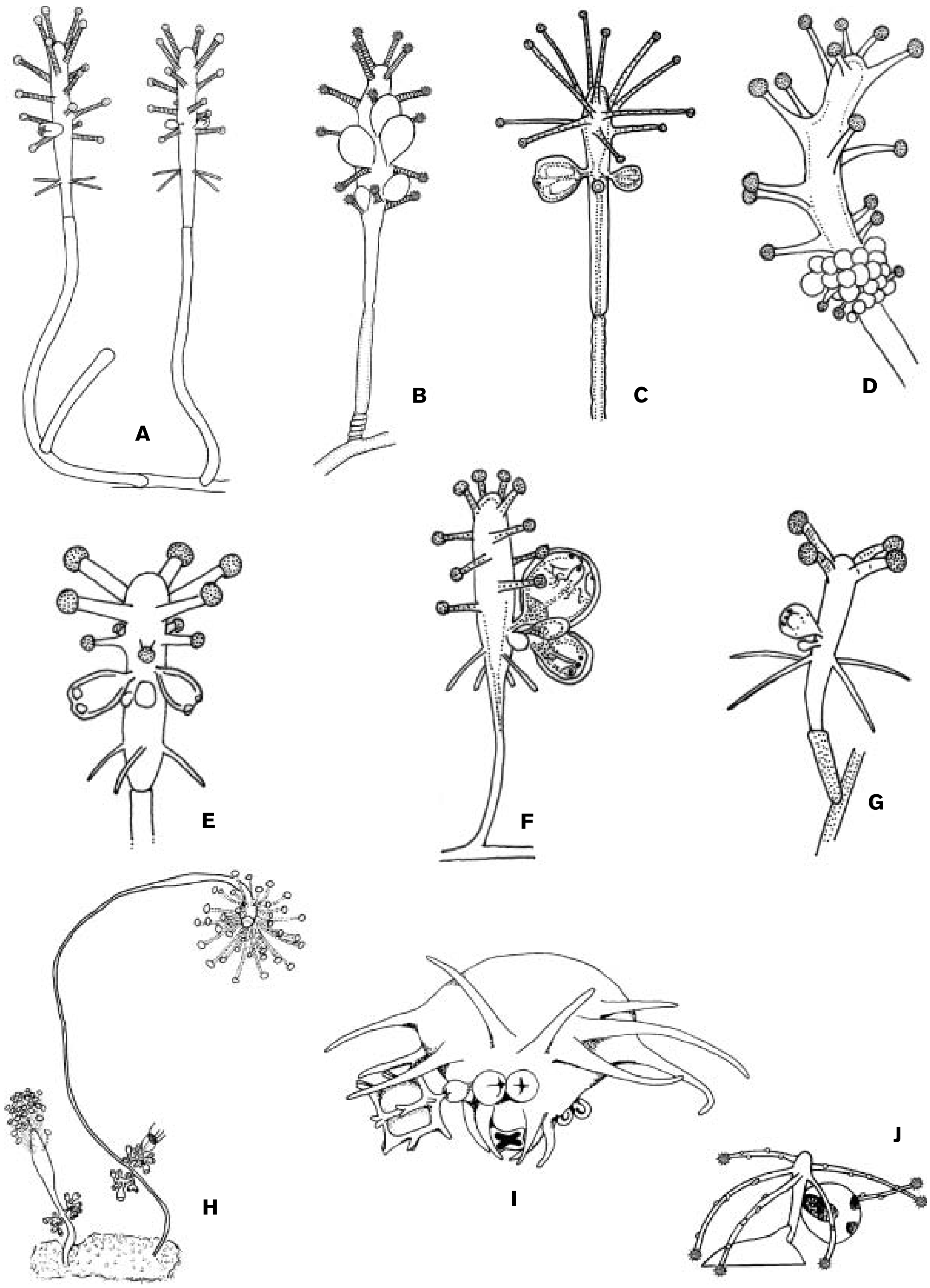


PLATE 42 Athecata (continued). A, *Coryne japonica*; B, *Coryne eximia*; C, *Sarsia tubulosa*; D, *Coryne* sp.; E, *Dipurena bicircella*; F, *Dipurena ophiogaster*; G, *Dipurena reesi*; H, *Hydrocoryne bodegensis*; I, *Climacocodon ikarii*; J, *Halimedusa typus* (A, after Schuchert 1996; B, after Brinckmann-Voss 1989; C, E–G, after Schuchert 2001; D, from unpublished photographs by J. T. Rees; H, after Rees et al. 1976; I, after Uchida 1924; J, after Mills 2000).

— Hydranths small (generally <5 mm long); tentacles 15–40 or less, scattered along hydranth body or in whorls 18
18. Tentacles up to 40; colony branched or unbranched, not growing on a bryozoan host 19
— Tentacles up to about 15, colony stolonal with hydrorhiza growing under the skeleton of a bryozoan host (plate 43K–43N) . . . . *Zanclea bomala*
19. Colonies much branched; perisarc irregularly annulated (plate 42B) . . . . *Coryne eximia*
— Colonies unbranched or slightly branched; perisarc not annulated. 20
20. Hydranths 0.8–2.6 mm tall with 12–20 capitate tentacles scattered or arranged in lose whorls and confined to distal one-half of the hydranth; with one to eight medusa buds in an irregular whorl mid-hydranth, below the tentacles (plate 42C) . . . . *Sarsia tubulosa*
— Hydranths 2.0–4.5 mm tall with four or five loosely arranged whorls of five capitate tentacles; with up to 80 medusa buds on a single hydranth (plate 42D) . . . . *Coryne* sp. (undescribed)
21. Hydranths with scattered tentacles 22
— Hydranths with tentacles in defined whorls 25
22. Hydranths usually solitary; when colonial, limited to a few budding polyps arising from hydrorhiza; tentacles moniliform (estuarine) (plate 43B) . . . . *Moerisia* sp.
— Hydranths colonial; tentacles filiform 23
23. Colony stolonal; hydranths naked; perisarc limited to hydrorhiza and forming a shallow collar at base of hydranth (plate 40F) . . . . *Clava multicornis*
— Colony erect, branched; stems, branches and pedicels covered by perisarc 24
24. Branches adnate to stem for some distance; gonophores forming free medusae; marine (plate 40H). . . . . . . *Turritopsis* sp.
— Branches free from stem except at base; gonophores fixed; brackish or fresh water (plate 40G) . . . . *Cordylophora caspia*
25. Hydranths with tentacles in two whorls, one oral and one aboral; gonophores borne between tentacle whorls 26
— Hydranths with tentacles concentrated at oral end; gonophores borne below tentacles. 31
26. Perisarc of stem well-developed, usually stiff, reaching to base of hydranth body; anchoring filaments absent 27
— Perisarc restricted to base of stem, weakly developed; anchoring filaments present 30
27. Hydranths solitary; gonophores fixed or releasing free medusae. 28
— Hydranths colonial; gonophores fixed. 29
28. Stem with distinct, deeply annulated expansion just below the hydranth; gonophores attached directly to the hydranth, without pedicels, asymmetrical and developing into free medusae (plate 43G) . . . . *Hybocodon prolifer*
— Stem with a few deep annulations, but not as a series of several rings just below the hydranth; gonophores fixed, each with three to four tentaclelike projections, borne in long, densely crowded pedicellate bunches, like grapes (plate 43C, 43D). . . . . *Tubularia harrimani*
29. Female gonophores with short distal crests; colony branched, forming a large tangled tuft to 15 cm high (plate 43H) . . . . *Pinauay crocea*
— Female gonophores with fingerlike, long processes distally; colony unbranched, polyps solitary or in small groups, to 5 cm long (plate 43E, 43F) . . . . *Pinauay marina*
30. Aboral tentacles 50–70; gonophores fixed (plate 41K) . . . . *Corymorpha palma*
— Aboral tentacles 15–20; gonophores free medusae (plate 41L). . . . . *Euphysora bigelowi*
31. Hydranths with trumpet- or urn-shaped hypostome; body vasiform 32
— Hydranths with conical, dome-, or nipple-shaped hypostome; body elongated to cylindrical (vasiform only when hypostome nipple-shaped) 33
32. Stems and branches heavily annulated throughout; hydranth somewhat squarish (plate 40I) . . . . *Eudendrium californicum*
— Stems and branches generally annulated at origins but not throughout entire length; hydranth not squarish . . . . *Eudendrium* spp.
33. Hydranth body covered to some extent by a variously developed pseudohydrotheca, usually encrusted with detritus. 34
— Hydranth without a pseudohydrotheca. 38
34. Hypostomes nipple-shaped; colonies with unbranched stems having a single terminal hydranth (rarely another lateral one) (plate 40E) . . . . *Rhizorhagium formosum*
— Hypostomes dome-shaped or conical; colonies erect, with branched stems 35
35. Colonies stolonal; on shells (plate 41C). . . . . *Leuckartiara octona*
— Colonies erect, branched; on many kinds of substrates 36
36. Stems polysiphonic; gonophores free medusae (plate 40A) . . . . *Bougainvillia muscus*
— Stems monosiphonic or polysiphonic, gonophores fixed 37
37. Stems strongly polysiphonic, annulated throughout; marine (bright yellow or orange in color) (plate 40B) . . . . *Garveia annulata*
— Stems monosiphonic, slightly or not at all annulated; estuarine (plate 40C, 40D) . . . . *Garveia franciscana*
38. Hydranths partially covered by perisarc; bright orange-red (plate 41B) . . . . *Amphinema* sp.
— Hydranths naked. 39
39. Hydranths polymorphic, with gonophores borne on gonozooids. 40
— Hydranths not polymorphic, with highly extensible threadlike tentacles; medusa-buds borne on hydrorhiza (plate 41D) . . . . *Rathkea octopunctata*
40. Gastrozooids up to 5 mm; tentacles usually 12–20; four or fewer gonophores borne about midway between tentacles and base of hydranth, in a single whorl (plate 40L–40N) . . . . *Hydractinia milleri*
— Gastrozooids up to 2.5 mm; tentacles usually 12 or fewer; four or more gonophores borne about midway between tentacles and base of hydranth, in a double or single whorl 41
41. Gastrozooids with nine to 12 tentacles; gonophores usually several, in a double whorl; gonozooids with a distinctive dark cap of closely packed cnidocysts that forms the distal half of the proboscis; spines numerous, smooth and long (about 1.2 mm), often with broken tips (plate 40J, 40K) . . . . *Hydractinia armata*
— Gastrozooids usually with eight tentacles; gonophores usually four, in a single whorl; gonozooids without distinctive dark cap of cnidocysts; spines few, smooth, short (about 0.5 mm) and blunt, slightly curved (plate 40O–40R). . . . . *Hydractinia laevispina*

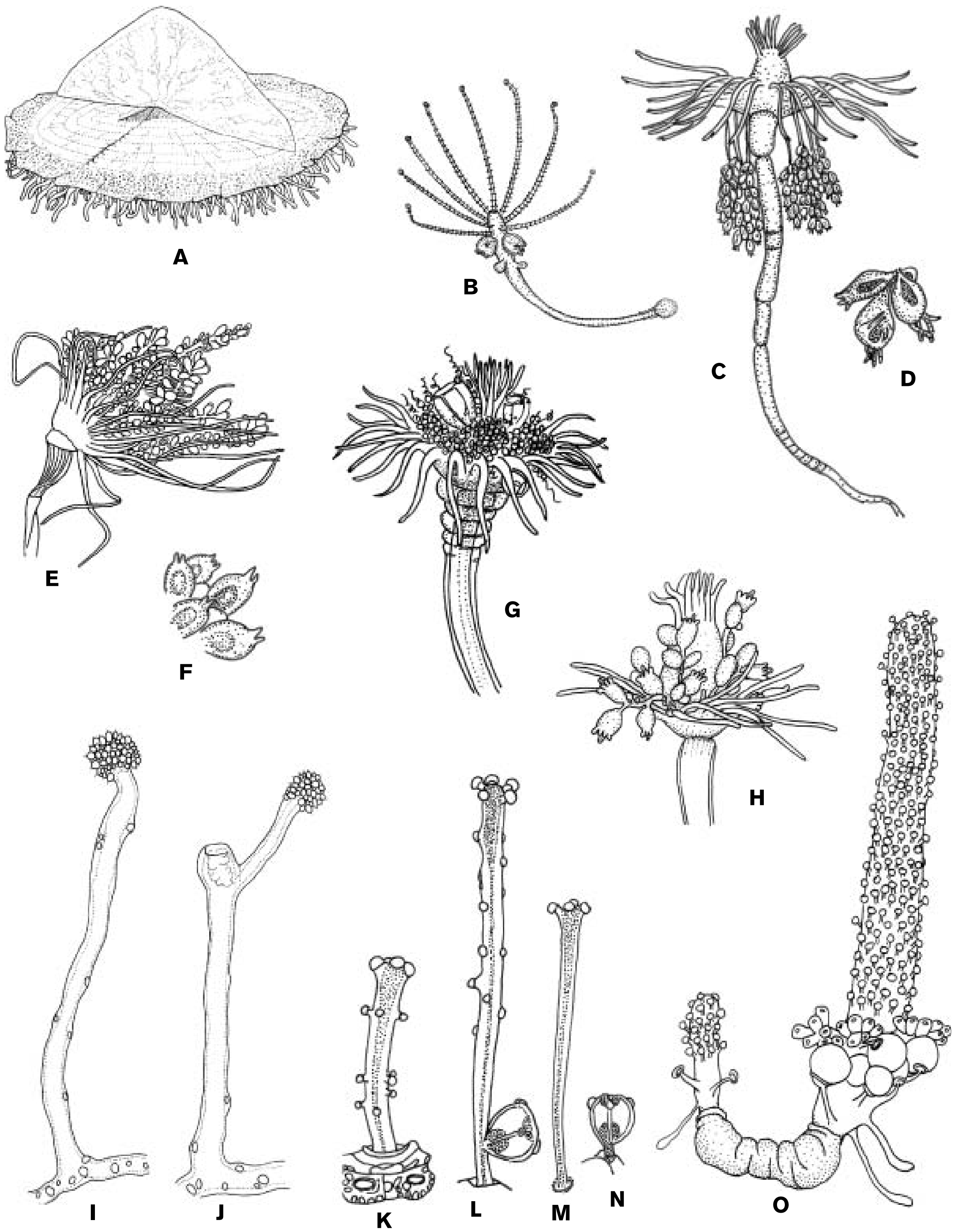


PLATE 43 Athecata (continued). A, *Velella velella*; B, *Moerisia* sp.; C, D, *Tubularia harrimani*; E, F, *Pinauay marina*; G, *Hybocodon prolifer*; H, *Pinauay crocea*; I, J, *Zanclella bryozoophila*; K–N, *Zanclea bomala*; O, *Candelabrum fritchmanii* (A, after Schuchert 1996; B, from unpublished photographs by J. T. Rees; C, D, F, G, after Fraser 1937 [G after Agassiz]; E, after Petersen 1990; H, after Brinckmann-Voss 1970; I, J, after Boero and Hewitt 1992; K–N, after Boero et al. 2002; O, after Hewitt and Goddard 2001, and unpublished photographs by Jeff Goddard).

42. Hydrothecae saucer- to basin-shaped, usually wider than deep, too small to contain contracted hydranth, margin entire (plate 45A, 45B) . . . . *Halecium* spp.
— Hydrothecae as deep or deeper than wide, able to contain contracted hydranth 43
43. Stem with segments becoming progressively longer distally, in the form of sausage-shaped links; hydroids epizoic on mollusk shells on sandy beaches (plate 48A–48C) . . . . *Eucheilota bakeri*
— Stem smooth or annulated, segments not sausage-shaped; hydroids not living on sandy beaches 44
44. Hydrothecae with an operculum 45

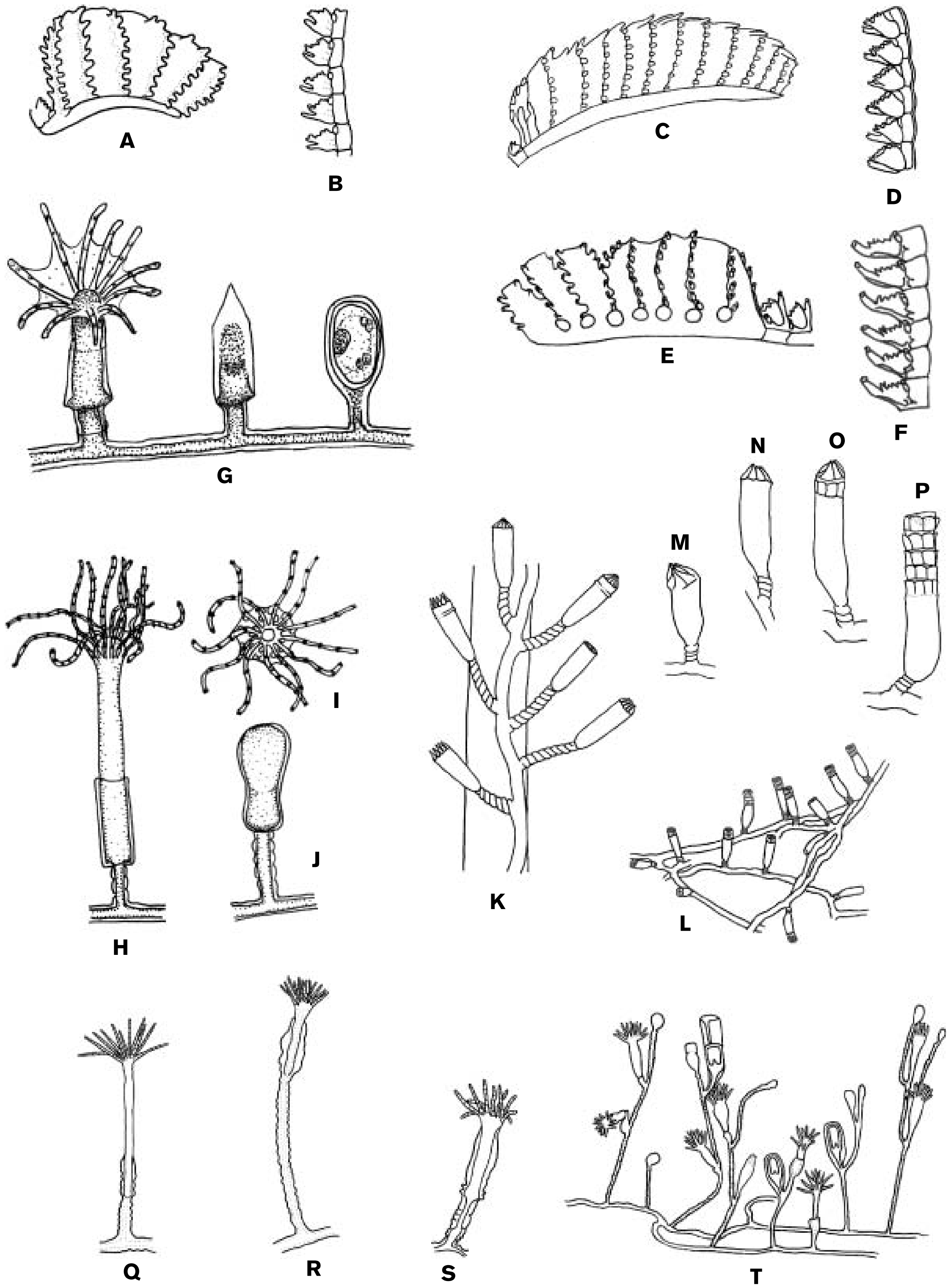


PLATE 44 Thecata. A, B, *Aglaophenia inconspicua*; C, D, *Aglaophenia struthionides*; E, F, *Aglaophenia latirostris*; G, *Blackfordia virginica*; H–J, *Aequorea victoria*; K–P, *Calycella syringa*; Q–T, *Eutonina indicans* (A–F, after Fraser 1937; G, after Mills and Rees 2000, and C. E. Mills unpublished observations; H–J, after Strong 1925; K, T, after Cornelius 1995; L–P, after Hirohito 1995; Q–S, after Naumov 1969).

— Hydrothecae without an operculum 63

45. Hydrothecae radially symmetrical, never with true marginal cusps 46

— Hydrothecae bilaterally symmetrical, usually with marginal cusps 52

46. Colonies with fixed gonophores; hydrothecal pedicels spirally grooved; crease lines present at bases of opercular plates (opercular valves clearly demarcated from margin of hydrotheca) (plate 44K–44P) . . . . *Calycella syringa*

— Colonies liberating free medusae; hydrothecal pedicels ringed and not spirally grooved (may be ringed with smooth regions); no crease lines at bases of opercular plates (opercular valves merely extensions of margin of hydrotheca). 47

47. Walls of hydrothecae usually irregular or wrinkled (plate 44Q–44T) . . . . *Eutonina indicans*

— Walls of hydrothecae usually straight 48

48. Colonies stolonal. 49

— Colonies erect (some brackish water colonies stolonal) 51

49. Hydrothecae sessile, without a pedicel (plate 45J, 45K) . . . . *Mitrocoma cellularia*

— Hydrothecae pedicellate 50

50. Hydrothecae with longitudinal striations; intertentacular web present, studded with cnidocysts (plate 44H–44J) . . . . *Aequorea victoria*

— Hydrothecae with smooth walls; intertentacular web absent (see key to hydromedusae, couplet 76) (plate 45H) . . . . *Phialella zappai*

51. Hydrothecae with longitudinal striations; intertentacular web present (estuarine) (plate 44G) . . . . *Blackfordia virginica*

— Hydrothecae with smooth walls; intertentacular web absent (note that some colonies are largely stolonal; see key to hydromedusae, couplet 76) (plate 45I) . . . . *Phialella fragilis*

52. Hydrothecae with pyramid-shaped operculum, consisting of three to four valves; hydrothecal rim with three to four cusps of equal size 53

— Hydrothecae with operculum not pyramid-shaped, consisting of one to two valves; hydrothecal rim with no cusps or with two cusps 56

53. Hydrothecae with four marginal cusps and operculum of four valves; mouth quadrangular (plate 46I, 46J). . . . . *Sertularella fusiformis*

— Hydrothecae with three marginal cusps and operculum of three valves; mouth triangular 54

54. Gonothecae arise from hydrothecae; distal, but not terminal, clinging organ resembling rayed horizontal plate sometimes present (plate 46P, 46Q) . . . . *Fraseroscyphus sinuosus*

— Gonothecae arise from stem; without distal clinging organs 55

55. Gonothecae with transverse rings (plate 47N–47P). . . . . *Symplectoscyphus tricuspidatus*

— Gonothecae with spines (plate 47L, 47M) . . . . *Symplectoscyphus turgidus*

56. Operculum of one valve 57

— Operculum of two valves (one valve sometimes divided) 60

57. Stem stout (ca. two times width of hydrotheca) (plate 46E, 46F) . . . . *Abietinaria inconstans*

— Stem slender (ca. same width as hydrotheca) 58

58. Gonothecae with transverse annulations (plate 46C, 46D) . . . . *Abietinaria greenei*

— Gonothecae smooth 59

59. Hydrothecae short (length: width ratio ca. 1) and thick (plate 46G, 46H) . . . . *Abietinaria traski*

— Hydrothecae longer and more slender (length: width ratio ca. 2), with distinct neck (plate 46A, 46B). . . . . *Abietinaria filicula*

60. Bases of hydrothecae forming one longitudinal row, their distal ends bending alternately to right and left; adcauline valve of operculum larger than abcauline (plate 47H) . . . . *Hydrallmania franciscana*

— Bases of hydrothecae forming two longitudinal rows more or less along either side of stem; abcauline valve of operculum larger than adcauline. 61

61. Hydranths without an abcauline caecum; gonothecae with transverse annulations (plate 46M–46O) . . . . *Dynamena disticha*

— Hydranths with an abcauline caecum; gonothecae without annulations 62

62. Colonies large (ca. 40 mm or more); hydrothecae sub-opposite; gonothecae typically with one to two pairs of distolateral spines (plate 47A–47C) . . . . *Sertularia argentea*

— Colonies small (ca. 8 mm); hydrothecae strictly opposite (except two or three pairs near base); gonothecae smooth (plate 47I, 47J) . . . . *Amphisbetia furcata*

63. Hydrothecae campanulate and pedicellate, on two or more sides of stem or branches; nematophores absent; hypostome trumpet-shaped 71

— Hydrothecae neither campanulate nor pedicellate, always restricted to one side of stem or branches; nematophores present and with regular arrangement; hypostome conical 64

64. Lateral nematothecae fused to hydrotheca; corbulae present 65

— Lateral nematothecae not fused to hydrotheca; corbulae absent. 66

65. Hydrothecal margins with nine cusps; corbulae with four to six pairs of leaves (plate 44A, 44B). . . . . *Aglaophenia inconspicua*

— Hydrothecal margins with 11 cusps; corbulae with 13 pairs of leaves (plate 44C, 44D) . . . . *Aglaophenia struthionides*

66. Hydrocladia arising directly from hydrorhiza or from erect stem; stem or branches if present with hydrothecae 67

— Hydrocladia arising from erect stem; stem and larger branches lacking hydrothecae. 68

67. Hydrocladia unbranched, arising directly from hydrorhiza (plate 45C, 45D) . . . . *Antennella avalonia*

— Hydrocladia branched from posterior surface; main axis of colony formed by the bases of successive hydrocladia (plate 45E, 45F). *Monostaechas quadridens*

68. Hydrocladia with alternating hydrothecate and nonhydrothecate internodes 69

— Hydrocladia with all internodes bearing hydrothecae 70

69. Hydrocladial internodes with strong internal annular ridges of perisarc (plate 45O–45R) . . . . *Plumularia lagenifera*

— Hydrocladial internodes with indistinct internal annular ridges (plate 45S–45U) . . . . *Plumularia setacea*

70. Lateral nematothecae present (plate 45L–45N). . . . . *Plumularia goodei*

— Lateral nematothecae absent (plate 45G). . . . . *Kirchenpaueria plumularioides*

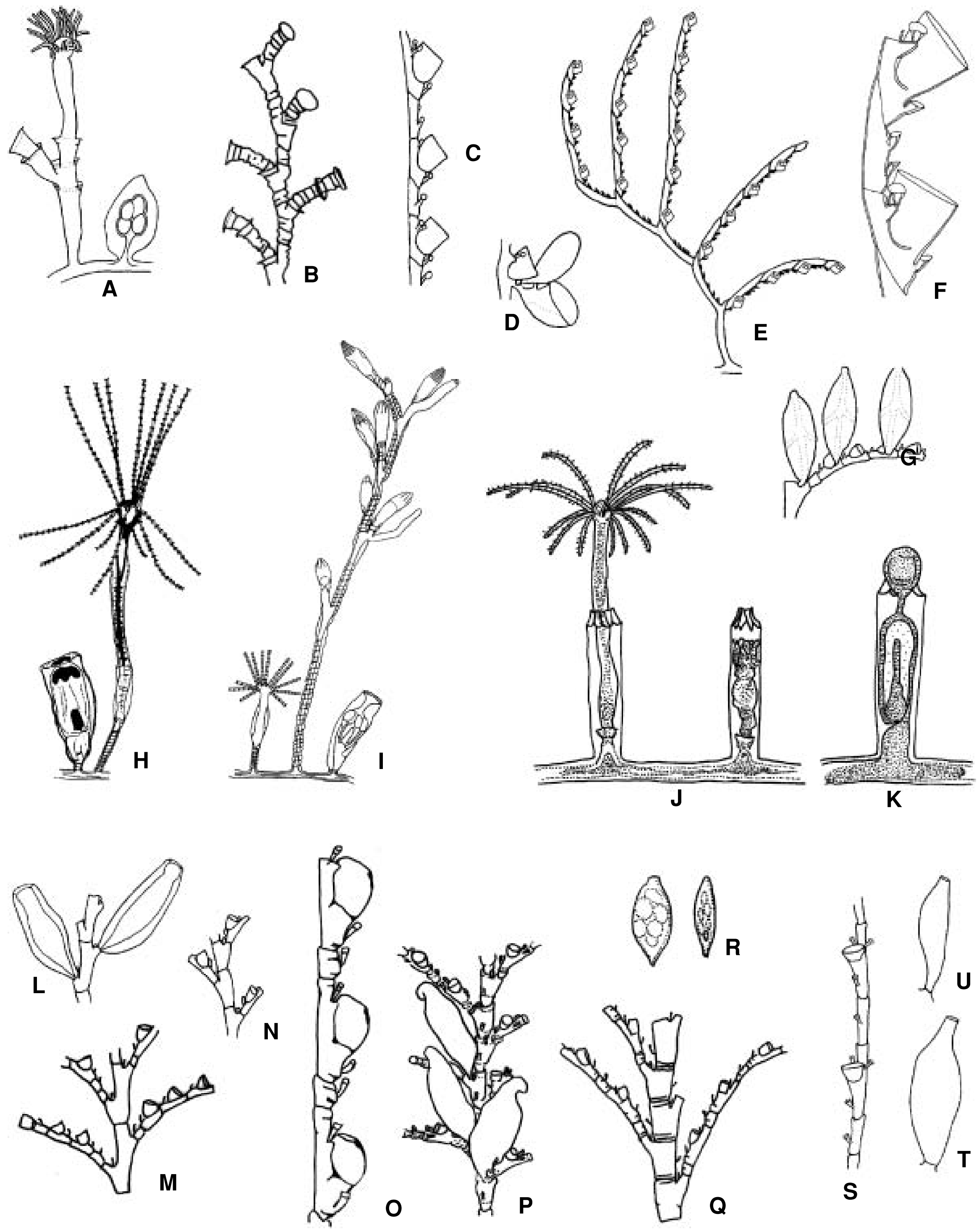


PLATE 45 Thecata (continued). A, *Halecium tenellum*; B, *Halecium annulatum*; C, D, *Antennella avalonia*; E, F, *Monostaechas quadridens*; G, *Kirchenpaueria plumularioides*; H, *Phialella zappai*; I, *Phialella fragilis*; J, K, *Mitrocoma cellularia*; L–N, *Plumularia goodei*; O–R, *Plumularia lagenifera*; S–U, *Plumularia setacea* (A, after Migotto 1996; B, after Torrey 1902; E, F, after Schuchert 1997; H, I, after Boero 1987; J, K, after Widmer 2004; L, M, after Millard 1975; S–U, after Cornelius 1995b; rest, after Fraser 1937).

71. Colonies with erect stems, each supporting several to many hydrothecae 72
— Colonies stolonal, each pedicel (stalk) supporting a single hydrotheca (occasionally with a few branched upright stems) 79
72. Hydrothecal rims even, sinuous, or crenulate, sometimes abrading to smooth (note: search for an undamaged specimen) 73
— Hydrothecal rims cusped (note: stain with chlorazol black, if necessary) 77
73. Hydrothecae bell-shaped and distinctly concave beneath rim; female gonothecae folded over distally (plate 48S–48U)

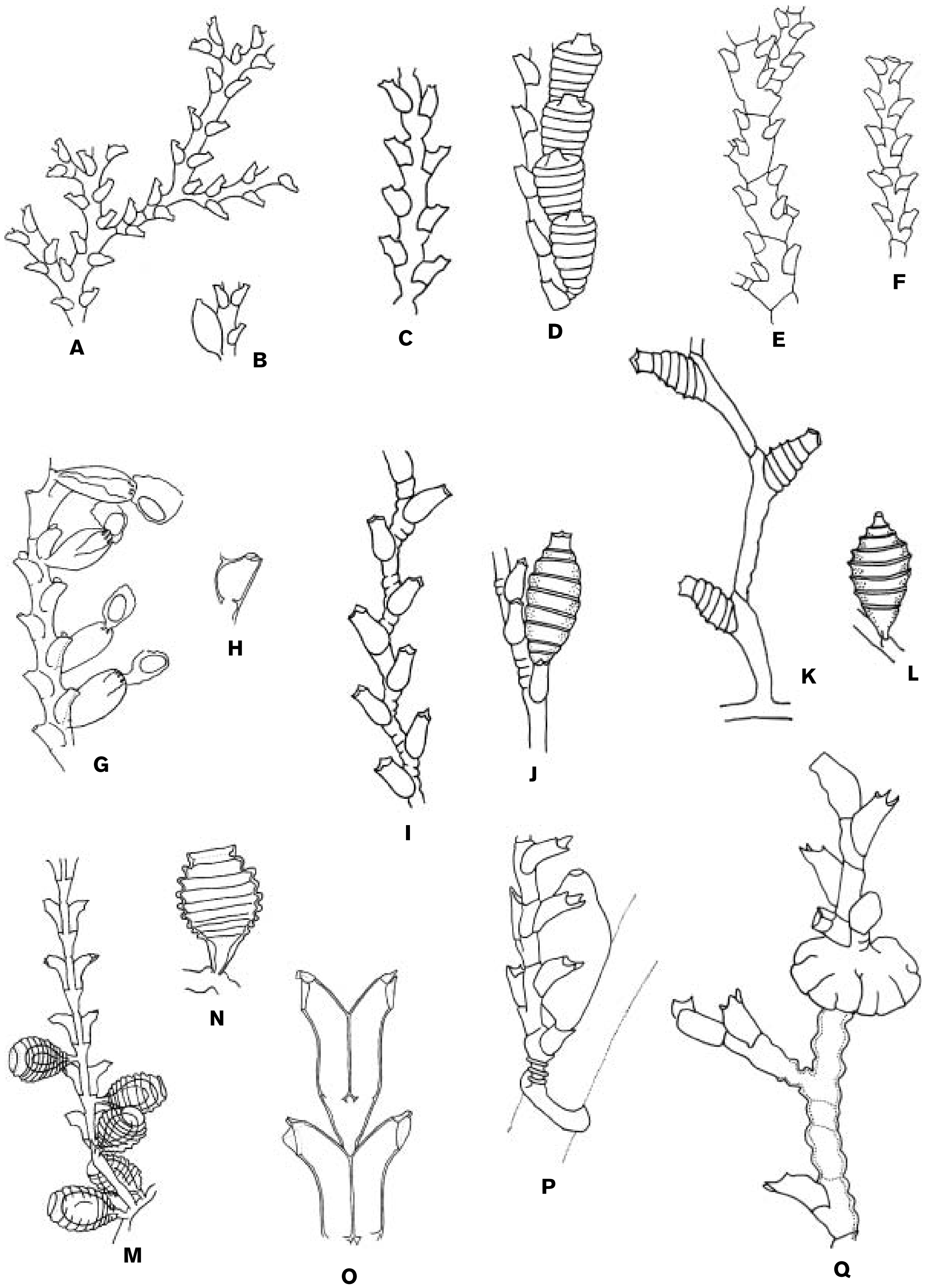


PLATE 46 Thecata (continued). A, B, *Abietinaria filicula*; C, D, *Abietinaria greenei*; E, F, *Abietinaria inconstans*; G, H, *Abietinaria traski*; I, J, *Sertularella fusiformis*; K, L, *Sertularella tenella*; M–O, *Dynamena disticha*; P, Q, *Fraseroscyphus sinuosus* (G, H, M–O, after Hirohito 1995; P, Q, after Boero and Bouillon 1993; rest, after Fraser 1937).

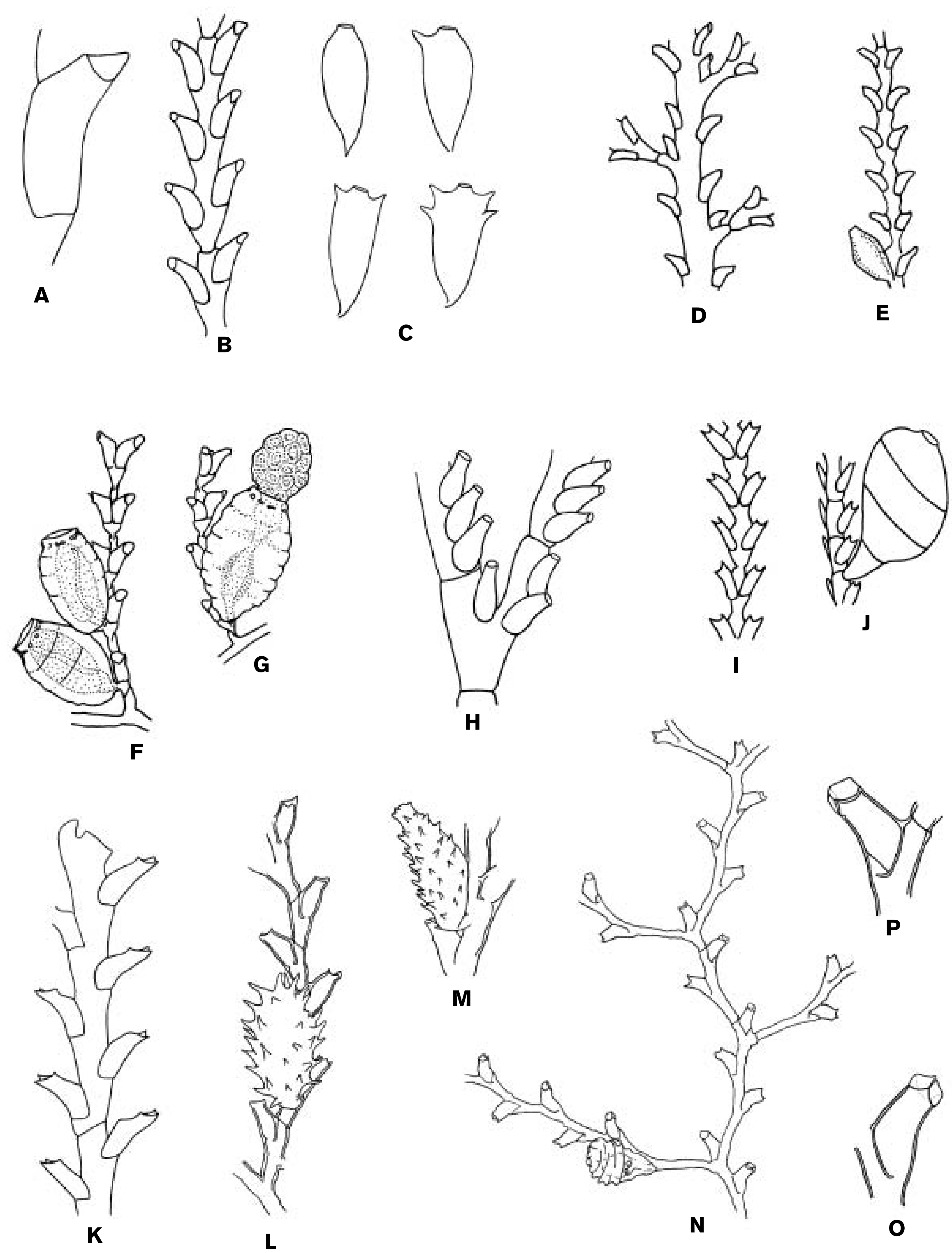


PLATE 47 Thecata (continued). A–C, *Sertularia argentea*; D, E, *Sertularia similis*; F, G, *Salacia desmoides*; H, *Hydrallmania franciscana*; I, J, *Amphisbetia furcata*; K, *Symplectoscyphus erectus*; L, M, *Symplectoscyphus turgidus*; N–P, *Symplectoscyphus tricuspidatus* (A–C, after Cornelius 1995b; F, G, after Millard 1975; L–P, after Hirohito 1995; rest, after Fraser 1937).

. . . . *Laomedea calceolifera*

— Hydrothecae cup- or tumbler-shaped, not distinctly concave below rim; gonothecae with terminal collar 74

74. Internodes of stem distinctly curved 75

— Internodes of stem quite straight, or only slightly curving 76

75. Hydrothecae usually thickened; internodes usually thickened asymmetrically (plate 48H, 48I) . . . . *Obelia geniculata*

— Hydrothecae and internodes not conspicuously thickened (plate 48J, 48K) . . . . *Obelia dichotoma*

76. Colonies very long, flexible; stem monosiphonic exceptsometimes towards base, brown to black; side branches in

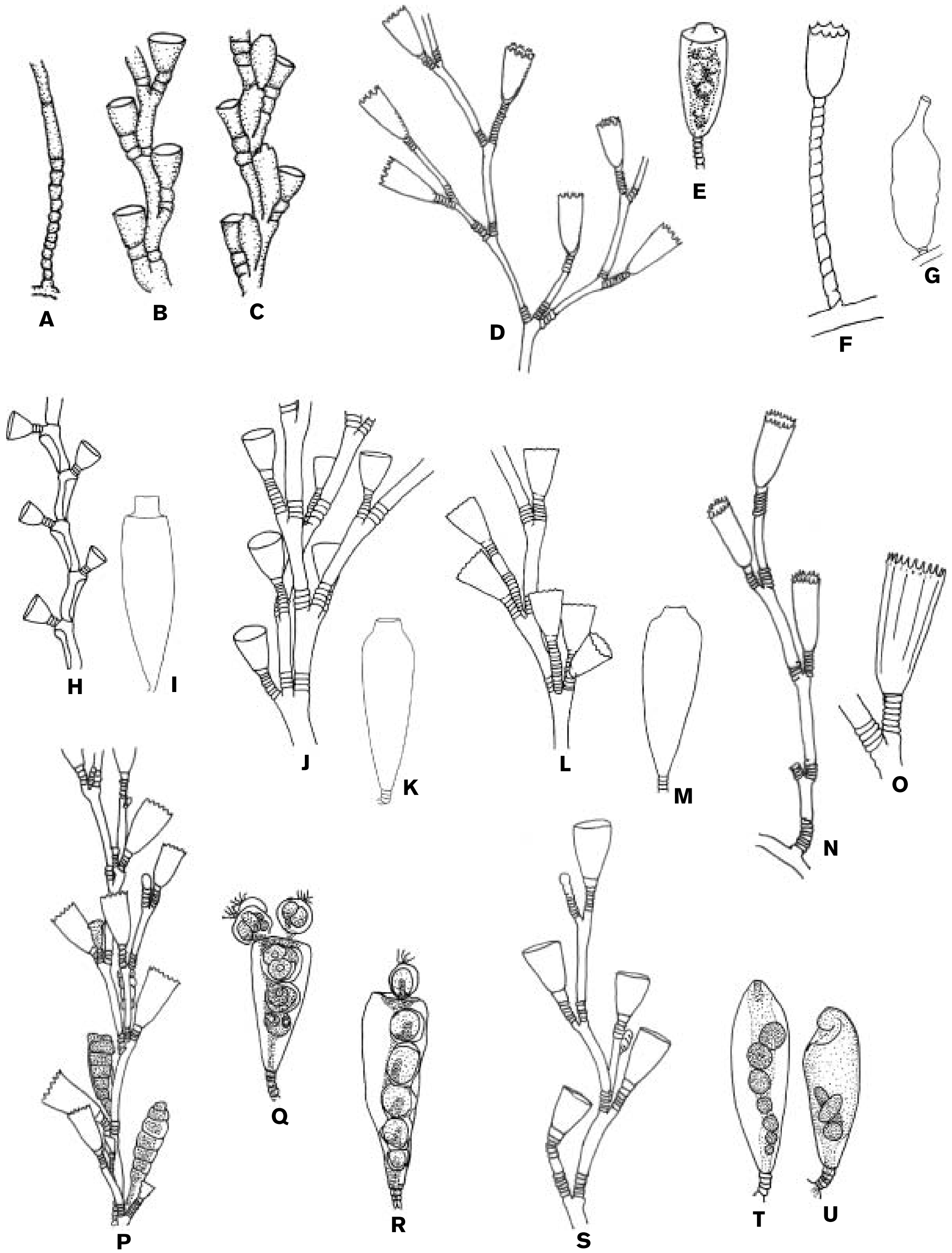


PLATE 48 Thecata (continued). A–C, *Eucheilota bakeri*; D, E, *Hartlaubella gelatinosa*; F, G, *Campanularia volubilis*; H, I, *Obelia geniculata*; J, K, *Obelia dichotoma*; L, M, *Obelia longissima*; N, O, *Obelia bidentata*; P–R, *Gonothyraea loveni*; S–U, *Laomedea calceolifera* (A–E, after Fraser 1937; F–M, after Cornelius 1995b; N, O, after Calder 1991; P–U, after Millard 1975).

older colonies ceasing growth at roughly uniform length, but gradually shorter towards growing tip (plate 48L, 48M) . . . . *Obelia longissima*

— Colonies loosely fan-shaped; stem monosiphonic or polysiphonic basally, pale to medium brown, never black; side branches typically irregular in length (plate 48J, 48K) . . . . *Obelia dichotoma*

77. Cusps on hydrothecal rim flattened to slightly notched distally; stem monosiphonic (plate 48P–48R). . . . . *Gonothyraea loveni*

— Cusps on hydrothecal rim distinctly bimucronate; stem monosiphonic or polysiphonic 78

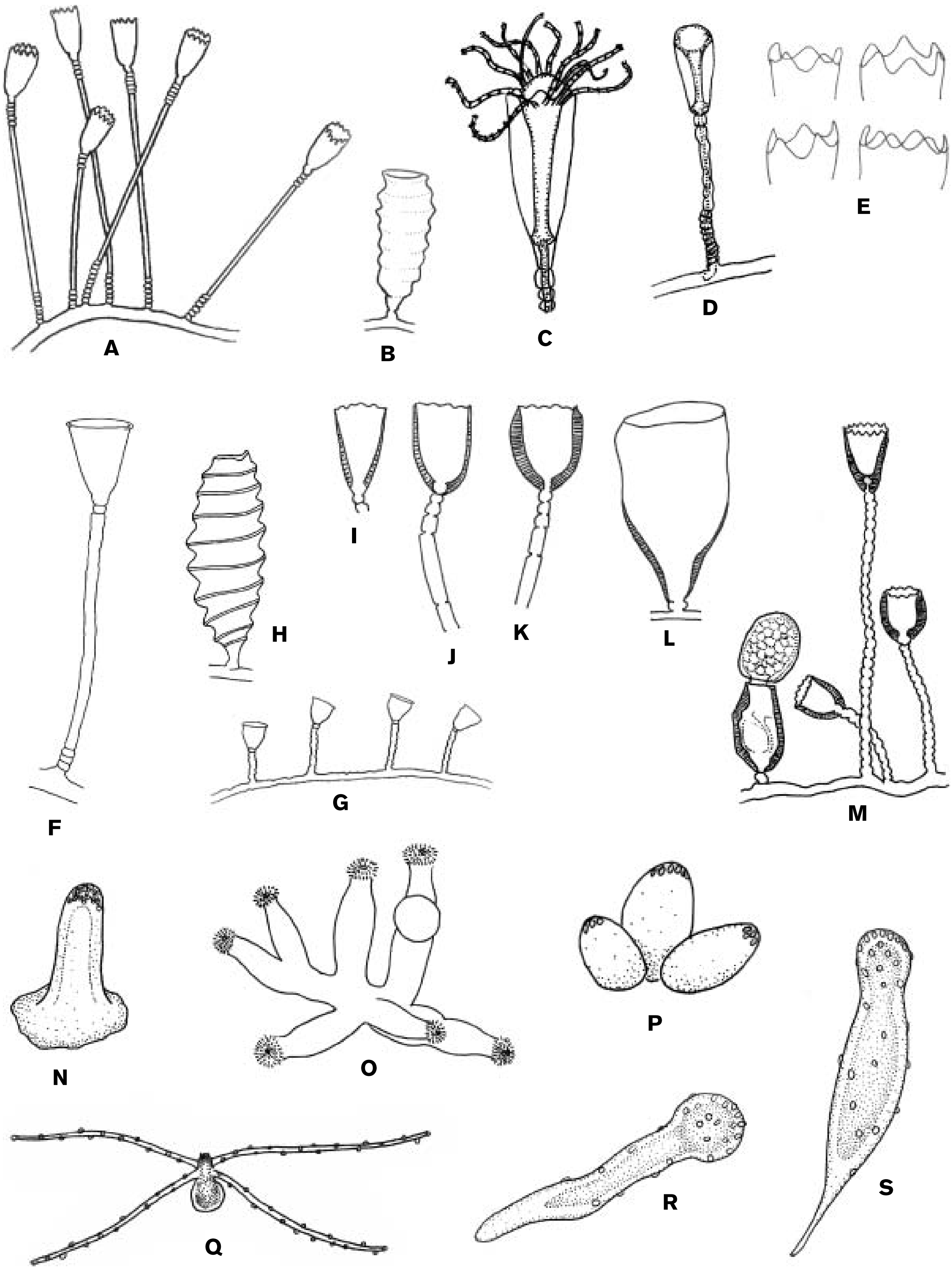


PLATE 49 Thecata (continued), polyps of Limnomedusae, and *Protohydra*. A, B, *Clytia hemisphaerica*; C–E, *Clytia gregaria*; F–H, *Orthopyxis integra*; I–L, *Orthopyxis compressa*; M, *Orthopyxis everta*; N, *Aglauropsis aeora*; O, *Craspedacusta sowerbii*; P, *Maeotias marginata*; Q, *Gonionemus vertens*; R, S, *Protohydra leuckarti* (A, B, F–H, after Cornelius 1995b; C–E, after Strong 1925; I–K, after Torrey 1902 and Naumov 1969; L, M, after Naumov 1969; N, after Mills et al. 1976; O, after Russell 1953; P, after Rees and Gershwin 2000; Q–S, original drawings by Claudia E. Mills).

78. Two points of each bimucronate cusp separated by a U-shaped notch; stem monosiphonic or polysiphonic; gonophores if present release free medusae (plate 48N, 48O) . . . . *Obelia bidentata*
— Two points of each bimucronate cusp separated by a V-shaped notch; stem strongly polysiphonic; gonophores if present fixed sporosacs (plate 48D, 48E) . . . . *Hartlaubella gelatinosa*
79. Hydrothecal rims with long, triangular cusps; gonothecae ovate with strong transverse annulations, produce swimming medusae (plate 49A, 49B) . . . . *Clytia hemisphaerica*
— Hydrothecal rims even or undulating; gonothecae may or may not produce swimming medusae 80
80. Hydrothecal rims undulating or with low cusps 81
— Hydrothecal rims even 82
81. Hydrothecae fairly cylindrical, with about 10 or more very low, rounded cusps or undulations; gonothecae flask-shaped with narrow neck, smooth, do not produce swimming medusae (plate 48F, 48G) . . . . *Campanularia volubilis*
— Hydrothecae bell-shaped, rim variable with as few as five to six low cusps, or up to 12 more-triangular (but fragile and easily broken) cusps; gonothecae ovate and smooth (without transverse annulations), produce swimming medusae (plate 49C–49E) . . . . *Clytia gregaria*
82. Pedicels of hydrothecae wavy or annulated (plate 49M) . . . . *Orthopyxis everta*
— Pedicels of hydrothecae smooth 83
83. Gonothecae decidedly flattened laterally (plate 49I–49L) . . . . *Orthopyxis compressa*
— Gonothecae round to oval in cross section (plate 49F–49H) . . . . *Orthopyxis integra*

Key to the Hydromedusae

CLAUDIA E. MILLS AND JOHN T. REES

Plates refer to hydromedusa plates 50–57.

1. With one or more tentacles and a manubrium (unless the specimen is damaged); size variable, but mature specimens generally >2 mm high 3
— Without tentacles and with or without a manubrium; bell <2 mm high 2
2. With fully developed gonads along each of the four radial canals; without a manubrium (plate 52N–52P) . . . . *Orthopyxis* spp.
— With fully developed gonads covering the lower two-thirds of the manubrium (plate 52I). . . . . *Zanclella bryozoophila*
3. All or most tentacles originating at the margin of the bell (although they may then run through grooves in the jelly in a few cases) 4
— All or most tentacles originating decidedly above the margin of the bell 84
4. With four or fewer tentacles, with or without additional marginal tentacula or rudimentary tentacles. 5
— With more than four tentacles, which may be of two types 27
5. With two tentacles, or two pairs of tentacles, situated on opposite sides of the bell (there may also be rudimentary tentacles, cirri, or tentacula elsewhere on the bell margin, but not at the bases of these tentacles) 6
— Arrangement of tentacles not as above 11
6. Bell rounded, <2 mm in diameter 7
— Bell usually pointed, may be conical or sharply pointed (occasionally rounded) and usually >2 mm in diameter 8
7. Bell with numerous zooxanthellae and a row of nematocysts running up the exumbrella above each tentacle bulb; with two opposite pairs of tentacles in mature specimens, or with only 2 tentacles in immature specimens; tentacles each with prominent terminal cnidocyst cluster (rare in the field) (plate 52E, 52F). . . . . *Velella velella*
— Bell without zooxanthellae; with two opposite tentacles; tentacles with many stalked cnidocyst clusters, each attached to the main tentacle by a fine contractile filament (plate 52K) . . . . young medusa of *Zanclea bomala*
8. With a large manubrium on a broad gelatinous peduncle that hangs well below the bell margin; with two long tentacles and numerous (about 80) rudimentary tentacles around the bell margin (plate 52D). . . . . *Stomotoca atra*
— With manubrium hanging directly from the roof of the subumbrella (not on a gelatinous peduncle); with two long tentacles and numerous tentacula or marginal swellings around the bell margin (rare) 9
9. With rudimentary marginal tentacle bulbs at the bases of short tentacula 10
— With rudimentary marginal tentacle bulbs that do not produce tentacles or tentacula; without ocelli (this is the same species as in couplet 38 of the key to polypoid stages) (plate 52G) . . . . *Amphinema* sp.
10. Gonads highly folded, extending from sides of manubrium out along most of the radial canals; with conical tentacle bulbs on the two large tentacles, and with about 14 small pendent solid tentacula, each with a red ocellus (plate 52C) . . . . *Amphinema turrida*
— Gonads covering manubrium smooth or lumpy, but not folded; with broad marginal bulbs on the two large tentacles and 26 small pendent solid tentacula, without ocelli (plate 52H). *Amphinema platyhedos*
11. With three or four tentacles, each originating from separate tentacle bulbs, one opposite pair may be very reduced, the other opposite pair may each have a pair of associated cirri. 12
— With one to four tentacles originating from a single tentacle bulb (medusae are also produced asexually from this bulb); with three other rudimentary tentacle bulbs and five exumbrellar cnidocyst tracks running from the tentacle bulbs toward the apex (plate 52A, 52B) . . . . *Hybocodon prolifer*
12. With three tentacles when mature (but medusae <2 mm high may have only one tentacle and a rounded bell profile; young *E. flammea* medusae have one to three tentacles, but later develop four) (plate 53K) . . . . *Euphysa tentaculata*
— With four tentacles (many small medusae with four tentacles are young Anthomedusae or Leptomedusae that will develop more tentacles as they mature; immature stages are usually difficult to identify and most will not be dealt with in this key) 13
13. With marginal vesicles (four or eight) 14
— Without marginal vesicles, but there may be ocelli on the tentacle bulbs 15
14. With four marginal vesicles, without ocelli; with two well-developed opposite tentacles, each with a pair of cirri at the base, with two opposite very small reduced tentacles without cirri, and with a total of only two opposite gonads on the four radial canals (plate 52M). . . . .

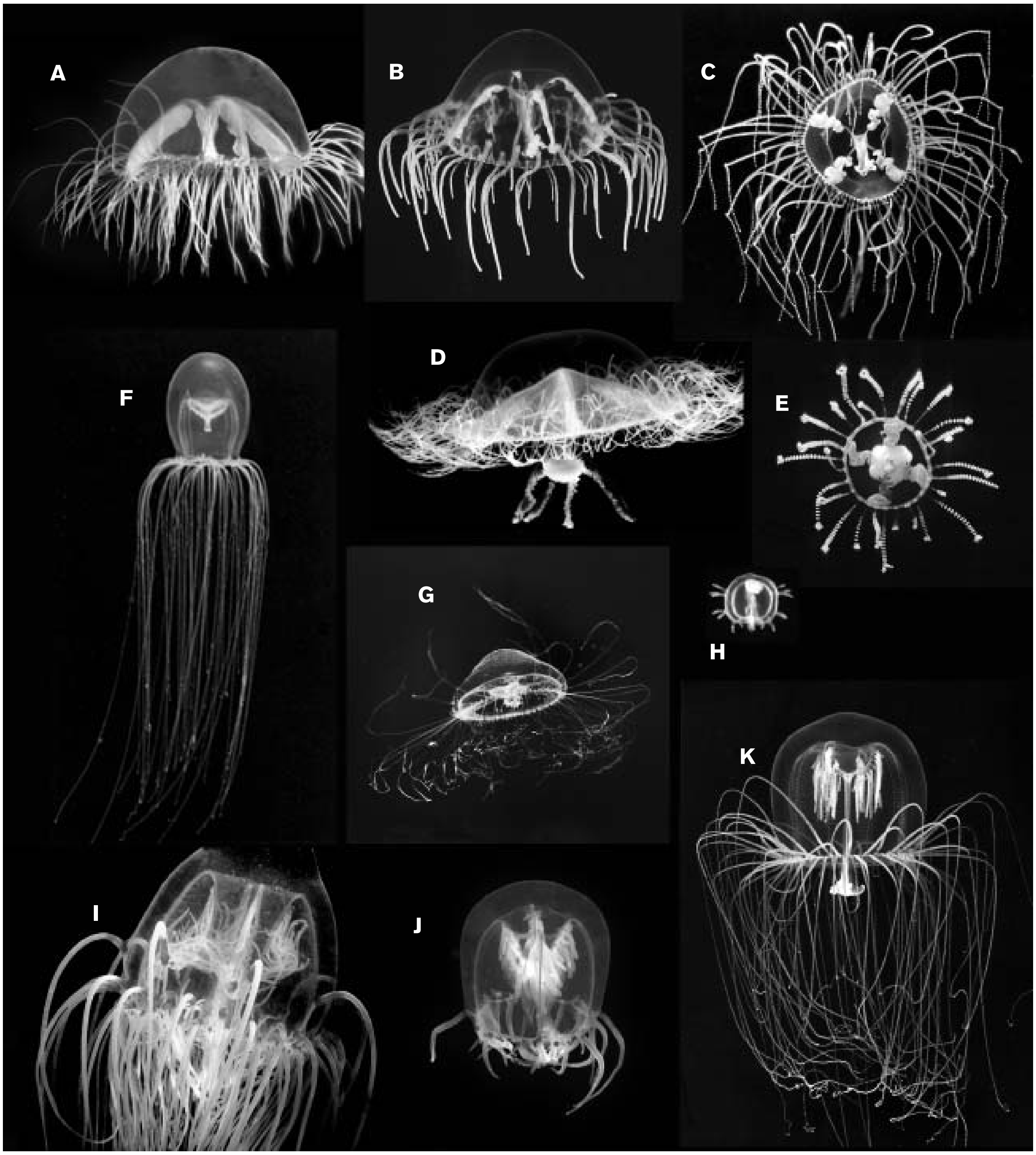


PLATE 50 Limnomedusae and Anthomedusae. A, *Aglauropsis aeora*; B, *Eperetmus typus*; C, *Gonionemus vertens*; D, *Maeotias marginata*; E, *Vallentinia adherens*; F, *Halimedusa typus*; G, *Proboscidactyla flavicirrata*; H, *Climacocodon ikarii*; I, *Scrippsia pacifica*; J, *Polyorchis haplus*; K, *Polyorchis penicillatus* (E, David Wrobel; H, Richard Emlet; I, Garry McCarthy; J, Paul Foretic; all with permission; rest, Claudia E. Mills).

.... young medusa of *Eucheilota bakeri*
— With eight marginal vesicles, each with a black ocellus, spaced evenly around the bell margin .... young medusa of *Tiaropsidium kelseyi*
15. Tentacles with many stalked cnidocyst clusters, each attached to the main tentacle by a fine contractile filament; bell with four prominent gelatinous bumps bearing cnidocysts just above the four tentacle bulbs (plate 52L) .... *Zanclea bomala*
— Tentacles without stalked cnidocyst clusters and bell without gelatinous cnidocyst-bearing bumps just above tentacle bulbs 16
16. With four tentacles, all alike; bell apex rounded 17
— With one long tentacle armed with round cnidocyst clusters on the subumbrellar side and with three short tentacles; bell with pointed apical projection (plate 53I) .... *Euphysora bigelowi*
17. Broad, vase-shaped manubrium covered by four gonads; with uniformly scattered cnidocysts covering the exumbrella even on mature specimens 18

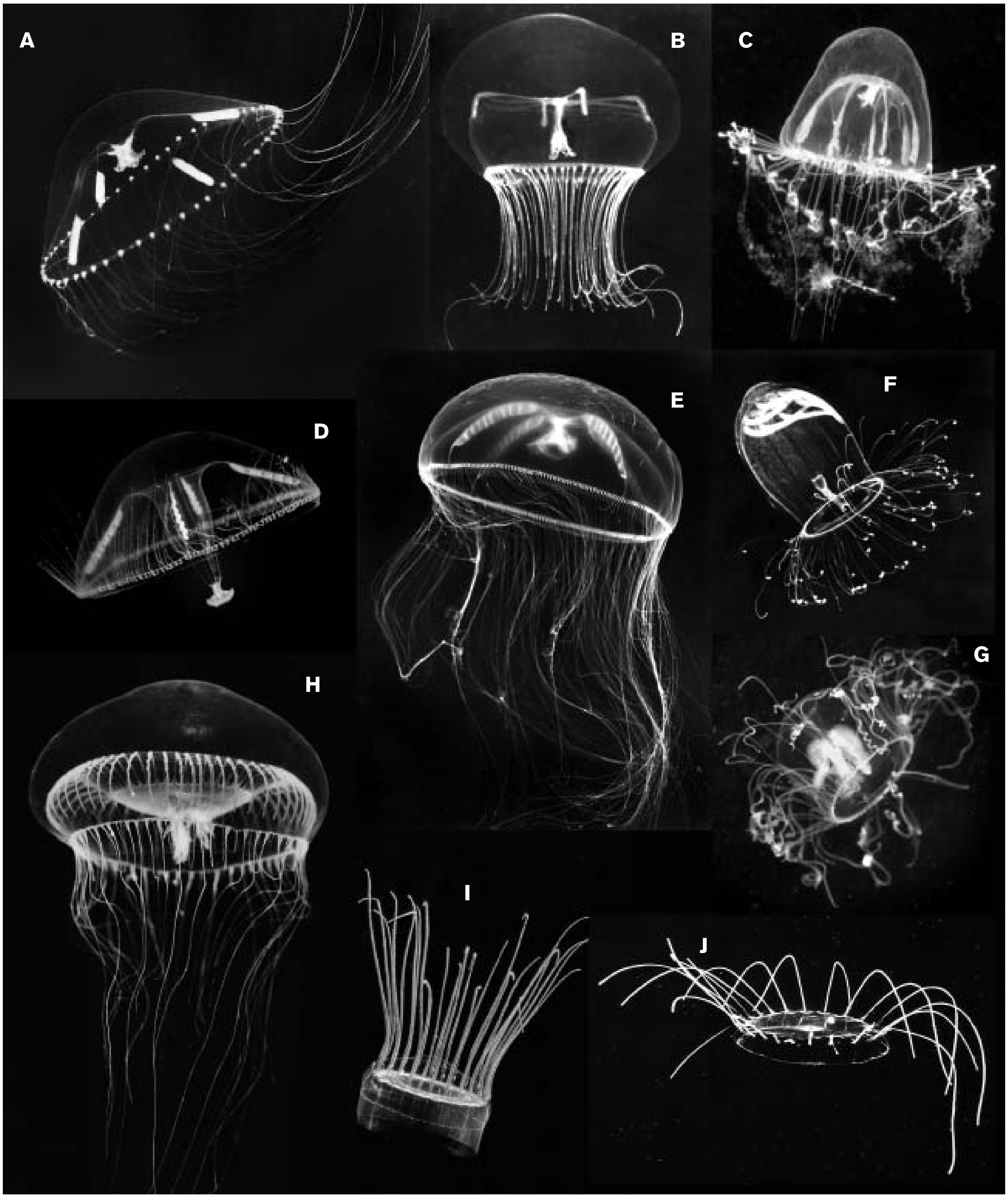


PLATE 51 Leptomedusae, Trachymedusae and Narcomedusae. A, *Clytia gregaria*; B, *Blackfordia virginica*; C, *Melicertum octocostatum*; D, *Eutonina indicans*; E, *Mitrocoma cellularia*; F, *Aglantha digitale*; G, *Aglaura hemistoma*; H, *Aequorea victoria*; I, *Solmaris* sp.; J, *Solmissus marshalli* (D, I, David Wrobel; G, Kevin Raskoff, MBARI; all with permission; rest, Claudia E. Mills).

— Tubular manubrium covered by cylindrical gonad or gonads in mature individuals (or without gonad on young medusae); exumbrella with or without scattered or clusters of cnidocysts on young medusae, but most cnidocysts not remaining on the exumbrellas of mature specimens 19

18. Manubrium attached directly to the subumbrella without a gelatinous peduncle; tentacles with a prominent, elongate, terminal swelling in which cnidocysts are concentrated (scattered cnidocysts may also occur in the tentacles, but they are not in swollen clusters); basal tentacle bulbs small to nonexistent and without ocelli, although they have more diffuse reddish-brown pigment; bell to about 5 mm tall (rare) (plate 54D) . . . . *Bythotiara stilbosa*

— Manubium attached to a broad, rounded gelatinous peduncle; tentacles with a round terminal knob of cnidocysts and distinct swollen clusters of cnidocysts along the entire

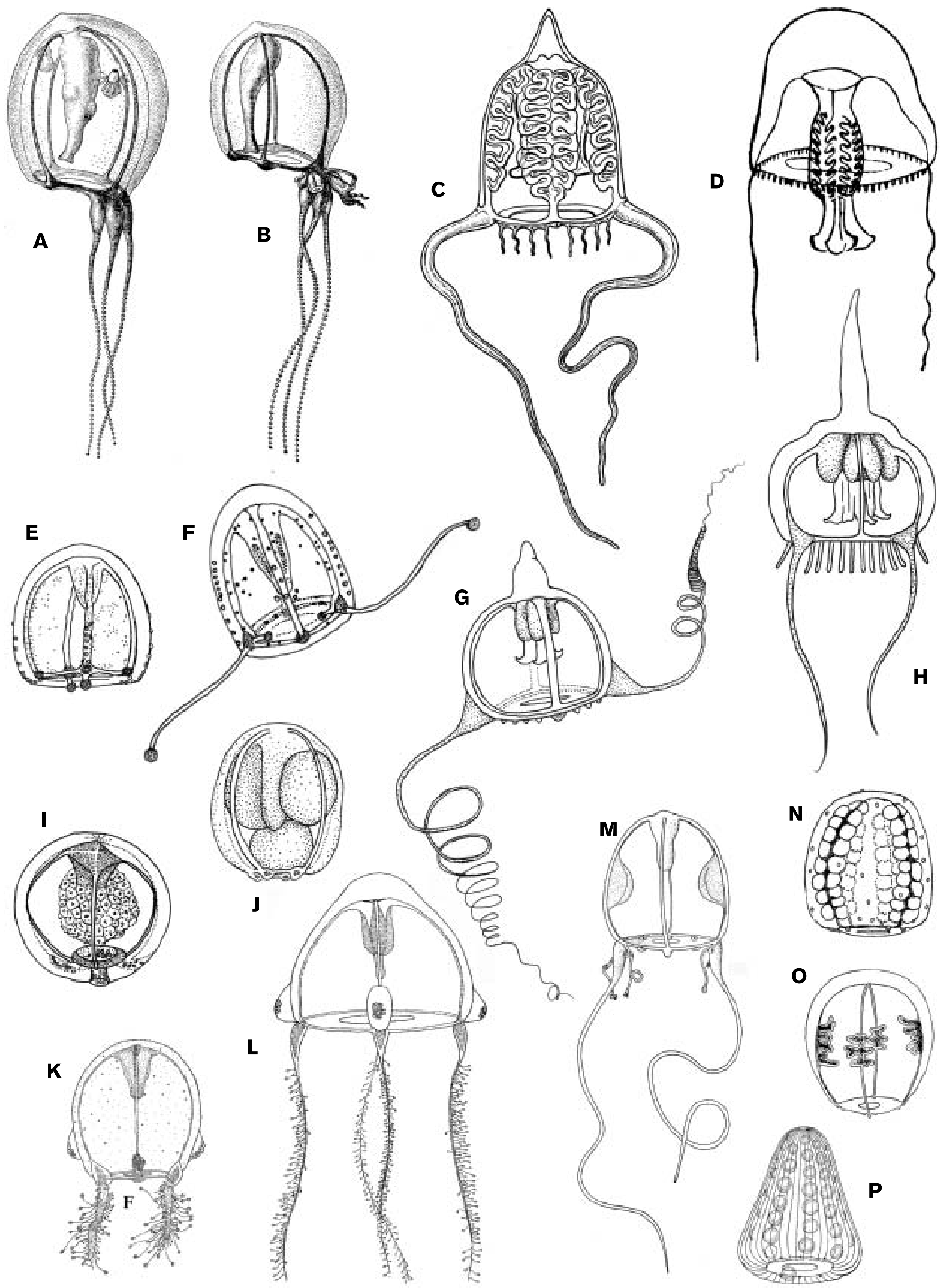


PLATE 52 Anthomedusae with four or fewer tentacles. A, B, *Hybocodon prolifer*; C, *Amphinema turrida*; D, *Stomotoca atra*; E, F, *Velella velella*; G, *Amphinema* sp. from Bodega Harbor; H, *Amphinema platyhedos*; I, *Zanclella bryozoophila*; J, *Pennaria disticha*; K, L, *Zanclea bomala*; M, *Eucheilota bakeri*; N, *Orthopyxis compressa*; O, P, *Orthopyxis integra* (A, B, from Naumov 1960; C, from Kramp 1968, after Mayer; D, from Kramp 1968, after Hartlaub; E, F, after Brinckmann-Voss 1970; G, H, original drawings by C. E. Mills; I, after Boero and Hewitt, 1992; J, after Hirohito, 1988; K, L, from Boero et al. 2000 with permission; M, from Torrey 1909; N, after Miller 1978; O, from Mayer 1910, after Browne; P, from Mayer 1910, after von Lendenfeld).

length; tentacle bulbs with red ocelli; bell to about 2.5 mm tall (rare) (plate 54A, 54B). . . . . *Hydrocoryne bodegensis*

19. With a red or black ocellus on each tentacle bulb; manubrium of variable length 20

— Without ocelli, although tentacle bulbs may be red; manubrium not reaching the level of the margin of the bell and often with bright red pigment (plate 53K, 53L) . . . . *Euphysa* spp.

20. With 24 small, well-defined clusters of cnidocysts on the exumbrella (with six clusters per quadrant, in three rows of two, spaced approximately evenly over bell surface) (plate 53F) . . . . . . young medusa of *Polyorchis penicillatus*

— With scattered cnidocysts on the exumbrella, or other than six distinct clusters per quadrant, or without cnidocysts on the exumbrella 21

21. Manubrium not longer than the bell cavity in mature medusae. 22

— Manubrium hanging well below the base of the bell in mature medusae 24

22. Exumbrella without bubblelike vesicles 23

— Exumbrella with numerous, closely set bubblelike vesicles (about 10 μm diameter, and 20–70 μm apart); bell to 3 mm high and slightly less wide with jelly substantially thicker at the apex; manubrium with short, rounded apical chamber protruding into the mesogloea above the subumbrella; egg size 70 μm (plate 53E) . . . . . *Coryne* sp. (undescribed)

23. Bell 2–3 mm high and slightly less wide with jelly of nearly uniform thickness; manubrium without pointed apical chamber protruding into the mesogloea above the subumbrella; egg size 180–200 μm (plate 53H). . . . . *Coryne eximia*

— Bell 3–6 mm high and slightly less wide with jelly substantially thicker at the apex; manubrium with or without pointed apical chamber protruding into the mesogloea above the subumbrella; egg size 90–120 μm (plate 53A) . . . . *Coryne japonica*

24. Gonad a single continuous cylinder, covering nearly all of the manubrium 25

— Gonad divided into two or more separate cylinders around the manubrium 26

25. Bell 6–10 mm high, rounded, higher than wide, with jelly of nearly uniform thickness and with four interradial exumbrellar furrows beginning at the bell margin; apex of subumbrella rounded, not pointed; manubrium usually with short, rounded apical chamber protruding into the mesogloea above the subumbrella; manubrium long, two to three times the bell height, with a short gonad-free portion at the apex and the stomach also free of gonad; stomach swollen and spindle-shaped and covered at upper end with warts with cnidocysts (plate 53D) . . . . *Sarsia tubulosa*

— Not as above (includes plate 53B, 53C) . . . . *Sarsia* spp. or *Coryne* spp.

26. Bell 1.6–2.1 mm high and wide; manubrium about twice as long as bell height with two gonad rings and a bullet-shaped apical chamber protruding into the mesogloea above the subumbrella; tentacles short, only about as long as the bell is tall (plate 53G) . . . . *Dipurena bicircella*

— Bell 2–6 mm high and wide; manubrium about twice as long as bell height with two to four gonad rings and a bullet-shaped apical chamber protruding into the mesogloea above the subumbrella; tentacles much longer than the bell height (plate 53J) . . . . *Dipurena reesi* and *Dipurena ophiogaster*

27. Tentacles branched (medusae small, <4 mm high). 28

— Tentacles not branched 31

28. Tentacles (usually nine) branched once or twice, one branch ending in a sucker, the other one or two branches having swollen clusters of cnidocysts at the tip and along the length; medusa with nine unbranched radial canals (polyps with two whorls of four tentacles each, the upper ones capitate and the lower ones filiform, but may be difficult to see) (plate 54H, 54I). . . . . *Cladonema californicum*

— Tentacles (five to eleven) branched several times, the lower one to four branches ending in a sucker, the upper four to seven branches bearing swollen clusters of cnidocysts at the tip and along the length (polyps with either two whorls of tentacles or with only a single whorl of capitate tentacles) 29

29. With usually seven (rarely, five or six) unbranched radial canals and the same number of branched tentacles (polyps with only a single whorl of [usually four] capitate tentacles and without filiform tentacles) (plate 54G) . . . . *Cladonema myersi*

— With at least some dichotomously branched radial canals, resulting in five to 11 radial canals reaching the bell margin and the same number of branched tentacles 30

30. With usually five (sometimes four to seven) radial canals emanating from the manubrium, most of which branch dichotomously so that five to 11 reach the bell margin; usually with 10 branched tentacles, corresponding to the number of radial canals (polyps with two whorls of [usually four] tentacles each, the upper ones capitate and the lower ones filiform [but may be difficult to see]) (plate 54F) . . . . *Cladonema radiatum*

— With usually six radial canals emanating from the manubrium, with every other one branching dichotomously so that nine radial canals reach the bell margin, and with nine branched tentacles (polyps with only a single whorl of [usually four] capitate tentacles and without filiform tentacles). . . . . *Cladonema pacificum*

31. Manubrium suspended far below the bell margin from a long, slender, gelatinous peduncle 32

— Manubrium not suspended far below the bell margin, from a long, slender, gelatinous peduncle 33

32. With four broad radial canals and four gonads on the radial canals; with four long tentacles with cnidocyst rings, each at the end of a radial canal and four small solid tentacles between these; with eight marginal marginal vesicles (plate 57N). . . . . *Liriope tetraphylla*

— With six broad radial canals and six gonads on the radial canals; with six long tentacles with cnidocyst rings, each at the end of a radial canal and six small solid tentacles between these; with 12 marginal marginal vesicles (plate 57O). . . . . *Geryonia proboscidalis*

33. Radial canals branching, with all branches reaching the bell margin 34

— Radial canals not branching (they may, however, have numerous lateral diverticula) 38

34. Bell to 10 mm tall and as wide or a bit wider, with jelly thickest at apex, bell diameter usually broadening toward the margin; manubrium with four paired gonads, with or without irregular folds; with four radial canals that give rise to lateral branches at several levels so that about 20–70 canals reach the ring canal; with about 20–70 tentacles with swollen marginal basal bulbs, but without large terminal knob of cnidocysts; exumbrella with small clusters

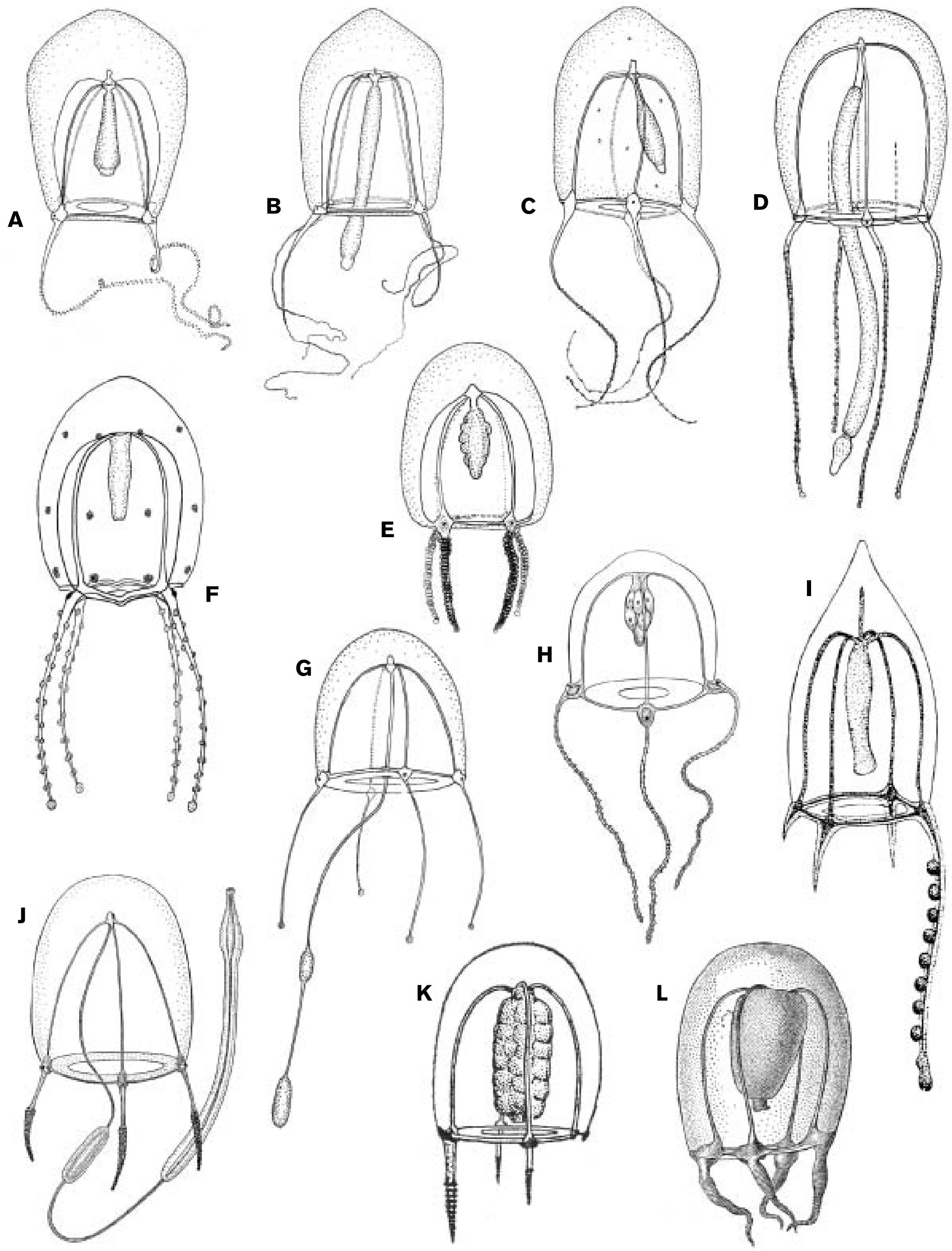


PLATE 53 Anthomedusae with three or four tentacles. A, *Coryne japonica*; B, *Sarsia* or *Coryne* sp. A from Bodega Harbor; C, *Coryne* sp. B from Bodega Harbor; D, *Sarsia tubulosa*; E, *Coryne* sp. (undescribed) from San Francisco Bay; F, *Polyorchis penicillatus*, young juvenile; G, *Dipurena bicircella*; H, *Coryne eximia*; I, *Euphysora bigelowi*; J, *Dipurena ophiogaster*; K, *Euphysa tentaculata*; L, *Euphysa flammea* (indistinguishable from mature *E. japonica* medusa) (A–C, after Rees 1975; D, after Schuchert 2001; E, F, original drawings by Claudia E. Mills; G, after Rees 1977; H, J, from Mayer 1910; I, from Sassaman and Rees 1978, Biol. Bull. fig 1c, p. 488, reprinted with permission from the Marine Biological Laboratory, Woods Hole, MA; K, from Naumov 1960, after Kramp; L, from Naumov, 1960).

of cnidocysts called cnidothalacies between the tentacles, on tracks, varying distances above the bell margin 35

— Bell to 30–40 mm tall and a little less wide, broadly rounded with jelly of fairly uniform thickness; manubrium with eight laterally folded gonads; with four radial canals that give rise to lateral branches at several levels so that about 40 canals reach the ring canal; with about 20–50 tentacles without marginal basal bulbs, but each terminating distally in a large knob of cnidocysts; exumbrella without clusters of cnidocysts above the bell margin. 37

35. Manubrium with barely folded, recurved lips; gonads comprise four swollen, but not folded, paired masses covering the manubrium; bell to 2.5 mm high and a little wider, apical jelly to about one-fourth bell height; with up to 32 tentacles when mature (central California) (plate 55B) . . . . *Proboscidactyla circumsabella*

— Manubrium with highly folded lips; gonads comprise four irregularly folded paired masses covering the manubrium; bell to 10 mm high and about as wide, but may be much less, with apical jelly accounting for about one-half bell height; with 40–72 tentacles when mature. 36

36. Bell to 10 mm high and a little wider, usually considerably wider at the base than at the apex, but sometimes nearly hemispherical; with 50–70 radial canals reaching the margin and about the same number or more of tentacles in fully grown medusae (Japan to central Oregon) (plates 50G, 55A) . . . . *Proboscidactyla flavicirrata*

— Bell to 3.5 mm high and wide, often tending to appear taller than a hemisphere and uniformly rounded; with up to 40 radial canals reaching the margin and about the same number of tentacles (southern California) (plate 55C) . . . . *Proboscidactyla occidentalis*

37. With 20–40 tentacles all of one type; manubrium with lightly folded lips that are not edged with cnidocyst clusters (rare) (plate 55J) . . . . *Sibogita geometrica*

— With four or more large tentacles and up to 45 small tentacles; manubrium with much-folded lips edged with a row of prominent cnidocyst clusters (rare) (plate 55M) . . . . *Calycopsis nematophora*

38. With four or eight radial canals (may have additional centripetal canals originating from the ring canal, see couplet 56) 40

— With numerous radial canals 39

39. Bell to about 10 cm wide, with up to 100 (or more) symmetrical radial canals (in mature specimens, all radial canals reach the bell margin, and gonads extend along nearly the entire length of the radial canals); with approximately as many tentacles as radial canals (plate 51H) . . . . *Aequorea victoria*

— Bell to 25 cm wide, with up to 100 (or more) symmetrical radial canals (in mature specimens, all radial canals reach the bell margin, and gonads extend along nearly the entire length of the radial canals); with three to six times as many tentacles as radial canals (uncommon) . . . . *Aequorea ?coerulescens*

40. With four radial canals (may have additional centripetal canals originating from the ring canal, see couplet 55) 43

— With 8 radial canals 41

41. Tubular or globular gonads attached to the radial canals only at the apex of the subumbrella or on the peduncle 42

— Sinuous gonads attached to most of the length of the radial canals beginning some distance below the apex of the subumbrella; with up to 90 large tentacles alternating with as many small ones; without any marginal sense organs; bell transparent, gonads orangish (plate 51C) . . . . *Melicertum octocostatum*

42. Bell to about 10–40 mm tall and about half as wide; manubrium suspended on a long peduncle; tubular gonads attached to the eight radial canals at the apex of the subumbrella near the base of the peduncle (plate 51F) . . . . *Aglantha digitale*

— Bell to about 6 mm tall and about half as wide; manubrium suspended on a long peduncle; sausage-shaped gonads attached to the eight radial canals near the midpoint of the peduncle (plate 51G). . . . . *Aglaura hemistoma*

43. Tentacles evenly distributed around the bell margin, although some may exit the jelly some distance above the base of the bell 47

— Most tentacles arranged in clusters, although some single tentacles may also be present 44

44. With a cluster of several tentacles in line with each radial canal and with or without additional clusters of tentacles between these; manubrium with four oral tentacles, which are either simple or much branched; gonad without dark horizonal line 45

— With a single marginal tentacle in line with each radial canal, and with an interradial cluster of tentacles (these arising from separate bulbs) in each quadrant; manubrium with simple lips and without oral tentacles of any kind; tentacle bulbs with red or black ocelli; gonad with distinctive dark horizontal line near the midpoint (plates 50F, 54C) . . . . *Halimedusa typus*

45. With eight clusters of tentacles on the bell margin originating from eight tentacle bulbs (clusters with three and five tentacles, or one and three tentacles, usually alternate); with four short oral tentacles (these may be branched) at the corners of the mouth; may be budding small medusae from the manubrium walls (plate 55F) . . . . *Rathkea octopunctata*

— With four clusters of tentacles on the bell margin originating from four broad tentacle bulbs; with a simple tubular mouth and four dichotomously branched oral tentacles inserted above the mouth opening; never budding medusae from the manubrium walls 46

46. Oral tentacles short, branching one or two times; with up to nine marginal tentacles originating from each of four bulbs; black ocelli on the tentacle bulbs; <4 mm high at maturity (plate 55D, 55G) . . . . *Bougainvillia muscus*

— Not as above, but with several times branched oral tentacles, with numerous marginal tentacles originating from each of four bulbs; with ocelli on the tentacle bulbs or on the bases of tentacles (includes plate 55E). . . . . *Bougainvillia* spp.

47. Gonads either covering the manubrium, or as four clusters of numerous pendant tubes associated with the four radial canals, but not running along the lengths of the radial canals 48

— Gonads linear or globular, attached to and running along the four radial canals (and may *also* cover the manubrium) 62

48. Gonads as four clusters of numerous pendant tubes associated with the radial canals. 49

— Gonads covering the manubrium 51

49. Manubrium suspended from a short, rounded, or conical gelatinous peduncle extending less than one-fourth the length of the subumbrella; numerous tubular, fingerlike

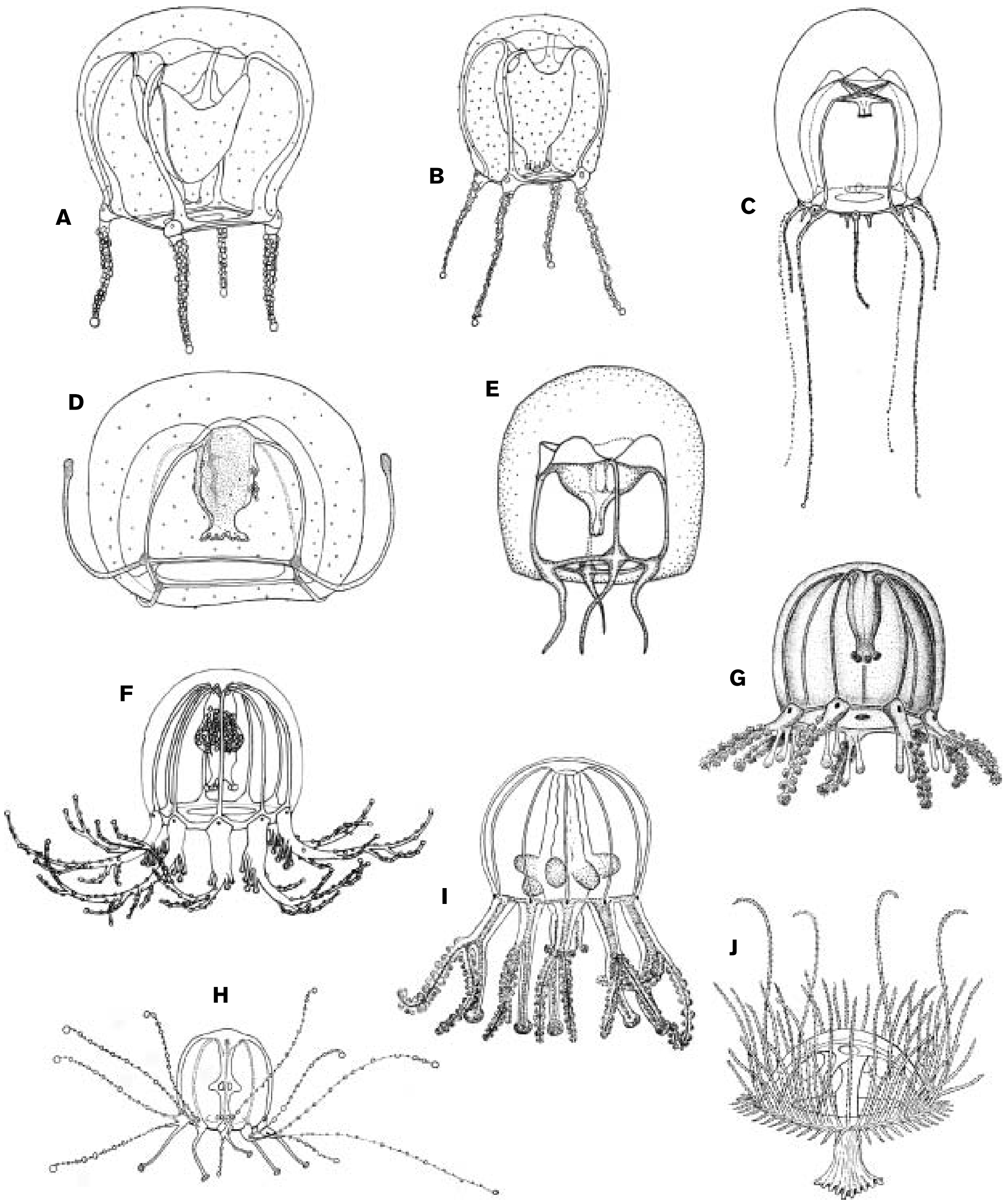


PLATE 54 Anthomedusae with four or more tentacles and one Limnomedusa. A, B (juvenile), *Hydrocoryne bodegensis*; C, *Halimedusa typus*, juvenile; D, *Bythotiara stilbosa*; E, *Protiara* sp.; F, *Cladonema radiatum*; G, *Cladonema myersi*; H, I, *Cladonema californicum*; J, *Craspedacusta sowerbii* (A, B, from Rees, Hand, and Mills 1976; C, from Mills 2000; D, from Mills and Rees 1979; E, modified from unpublished drawing by Ronald Larson, with permission; F, after Hirohito 1985; G, from Rees 1949 with permission; H, from Rees 1979; I, from Hyman 1947 with permission; J, from Mayer 1910, after Allman; A–E, drawings all by Claudia E. Mills; H; drawing by John T. Rees).

gonads in four groups, attached to the radial canals running up the peduncle to the bell apex, hanging down into the subumbrellar cavity; tentacles nearly all in a single row around the bell margin 50

— Manubrium suspended from a large, conical gelatinous peduncle extending about half the length of the subumbrella; numerous tubular, fingerlike gonads in four groups, attached to the radial canals along the surface of the gelatinous peduncle below the apex of the subumbrella; some tentacles exiting from the jelly well above the bell margin (plate 50I) . . . . *Scrippsia pacifica*

50. With up to 160 tentacles and 60 mm bell height; radial canals with 15–25 pairs of short lateral diverticula that are longer than twice the width of the radial canal (plate 50K) . . . . *Polyorchis penicillatus*

— With up to 30 tentacles and 20 mm bell height; radial

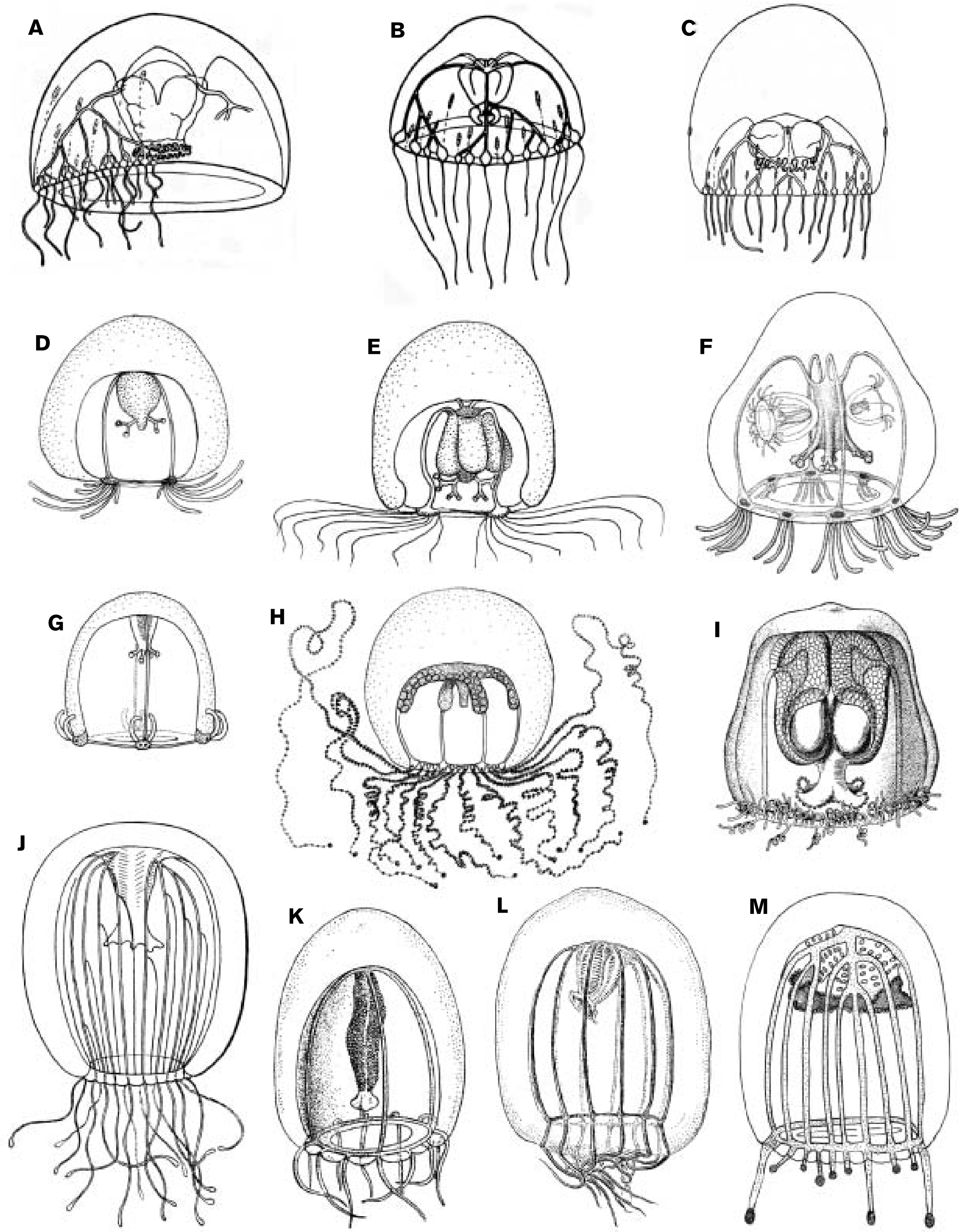


PLATE 55 Anthomedusae with more than four tentacles. A, *Proboscidactyla flavicirrata*; B, *Proboscidactyla circumsabella*; C, *Proboscidactyla occidentalis*; D, *Bougainvillia muscus*; E, *Bougainvillia* sp. from Bodega Harbor; F, *Rathkea octopunctata*; G, *Bougainvillia muscus* juvenile; H, *Moerisia* sp. from San Francisco Bay; I, *Turritopsis* sp.; J, *Sibogita geometrica*; K, *Heterotiara anonyma*; L, *Calycopsis simulans*; M, *Calycopsis nematophora* (A–C, from Hand 1954 with permission; F, from Naumov 1960; I, from Mayer 1910, after Brooks; J, from Mayer 1910; K, L, from Kramp 1968, after Bigelow; M, after Arai and Brinckmann-Voss 1980; D, E, G, H, original drawings by Claudia E. Mills).

canals largely without diverticula, although large specimens may have closely set knoblike branches on the radial canals (rare) (plate 50J). . . . . *Polyorchis haplus*

51. With more than 60 marginal tentacles, densely packed 52

— With <60 marginal tentacles 54

52. Manubrium with mass of vacuolated cells above the digestive part, the lips lined with a single row of cnidocyst knobs; gonads on manubrium, without folds or pits, red in life, without "mesentery" connections to radial canals (see

below); bell to 7 mm high and less wide; jelly uniformly thin; with about 80–120 marginal tentacles, each with an ocellus on the inner surface of the basal bulbs (plate 55I). . . . . *Turritopsis* sp.

— Manubrium without masses of vacuolated cells above the digestive part and lips not edged with cnidocyst knobs; gonads on manubrium with peripheral folds and also a central pitted region, attached to radial canals by "mesentery" tissue connection on upper third to half of the manubrium; without ocelli 53

53. Bell to 45 mm high and less wide; jelly thick at the apex; with more than 100 tentacles, on laterally compressed marginal bulbs; radial canals broad, with jagged edges; gonads, manubrium and lips orange to rosy red in life (plate 56E) . . . . *Neoturris breviconis*

— Bell to 80 mm high and 65 mm wide, jelly slightly thicker at apex, with or without a small pointed apical process; with about 80 tentacles on laterally compressed marginal bulbs; radial canals broad with about 10 broad, tablike diverticula on each edge; colorless in life (plate 56F) . . . . *Neoturris* sp. (undescribed)

54. Bell with mesogloea of nearly uniform thickness, or somewhat thicker at the apex, but the apex is not pinched off from the lower portion of the bell or distinctly pointed 55

— Bell with an apical projection of mesogloea that is noticeably pinched off from the lower portion of the bell, or conically pointed. 57

55. With up to 44, highly contractile, tapering, filamentous tentacles, these with conical marginal bulbs, each with an ocellus, but without any specialized structures at the tips; manubrium broad and extending out onto radial canals, with vertically or obliquely folded gonads; bell to 23 mm high and wide (rare) (plate 56D). . . . . *Annatiara affinis*

— With up to about 12–15 thick, not very contractile tentacles, these without marginal bulbs, but with distinctive terminal bulbs or tapering tip structures; without ocelli; with cylindrical manubrium 56

56. With four radial canals and 12 or more centripetal canals arising at the ring canal, most of which meet the manubrium, but not at the corners; with 12 or more large tentacles and a few small ones, each with a distinctive tapering tip; bell to 40 mm high and a little less wide, with deep brick red gonads on the manubrium (rare) (plate 55L) . . . . *Calycopsis simulans*

— With four radial canals and no centripetal canals; with six to 12 tentacles, each with a swollen knob of cnidocysts at the tip; bell to 22 mm high and a little less wide, with bright orange-red tentacle tips and yellowish manubrium in life (rare) (plate 55K) . . . . *Heterotiara anonyma*

57. Upper one-third or more of the manubrium attached to the four radial canals by thin tissue "mesenteries"; radial canals broad and often with jagged edges; with or without rudimentary tentacles along with the normal tentacles at the bell margin 58

— Manubrium not attached to the radial canals by mesenteries, although the top of manubrium may be somewhat elongated along the proximal portions of the radial canals; radial canals not broad, with mostly smooth edges; with four to 16 tentacles of varying sizes (these with ocelli), and with rudimentary marginal bulbs (with ocelli) between tentacles; with bulbous or conical apical projection (includes plate 56C) . . . . *Halitholus* spp.

58. Gonads (four) horseshoe-shaped with folds directed towards the radial canals 59

— Gonads (four) with folds and/or papillae and also a central pitted region, or only with pits or reticulations throughout 60

59. Bell to 20 mm high with conical or spherical apical projection, manubrium broad with gonads (red) on the whole surface; with 12–24 (usually 16) tentacles, each with a pronounced elongate spur directed upwards a short distance on the exumbrella from its tentacle bulb, and with 16 or more rudimentary marginal bulbs or tentacles; tentacle bulbs and rudiments with red ocelli; radial canals with smooth or slightly jagged edges (plate 56B). . . . . *Leuckartiara octona*

— Not as above (includes plate 56A) . . . . . . *Leuckartiara* spp.

60. With ocelli; manubrium filling less than one-half of the subumbrellar space, covered with gonads without folds, but forming a complex, reticulated pitted surface; bell to 21 mm high, tall with a conical apex and with longitudinal ribs and ridges; radial canals fairly narrow and smooth-walled, with mesenteries connected to most of the manubrium; with 12–24 tentacles with laterally compressed marginal bulbs (plate 56J) . . . . *Pandea conica*

— Without ocelli; manubrium large, nearly filling the subumbrellar space and covered by gonads with folds facing the radial canals; bell to about 20–25 mm high, but otherwise not as above 61

61. Bell barrel-shaped, with bulbous, pointed apical projection; gonads irregularly transversely folded with numerous papillae and with a central pitted area; with 30–32 tentacles, with large, laterally compressed bulbs, these without exumbrellar spurs or pores; radial canals broad, with smooth or somewhat jagged margins (plate 56I) . . . . *Neoturris pelagica*

— Bell-shaped, with small apical projection over thickened apical jelly; gonads on manubrium with many transverse folds; with 16–20 large tentacles of varying sizes with laterally compressed bulbs, each with a distinct pore and spur pointed upward on exumbrella, and with about 40 rudimentary tentacles or bulbs; radial canals broad, with glandular diverticula throughout their lengths (plate 56H) . . . . *Neoturris fontata*

62. Tentacles with prominent rings of cnidocysts along their entire length 63

— Tentacles without prominent rings of cnidocysts along their entire lengths 71

63. Medusa bell-shaped, nearly hemispherical or wider; bell of mature specimens usually >6 mm in diameter. 64

— Medusa nearly disk-shaped, not deeply convex; bell of mature specimens not more than 6 mm in diameter 71

64. Tentacles with adhesive discs, allowing the medusae to adhere to algae; medusae orange, brownish orange, or reddish 65

— Tentacles without adhesive discs; medusae pale pink, blue, greenish, tan, or colorless 66

65. With about 60–80 tentacles, each with an adhesive pad located about midway, and characteristically angled where the pad is located; bell to about 25 mm in diameter (plate 50C). . . . . *Gonionemus vertens*

— With up to about 40 tentacles, most with a terminal adhesive disk; bell to about 8 mm in diameter (plate 50E) . . . . *Vallentinia adherens*

66. With (microscopic) marginal vesicles at the bell margin, manubrium with four distinct lips. 67

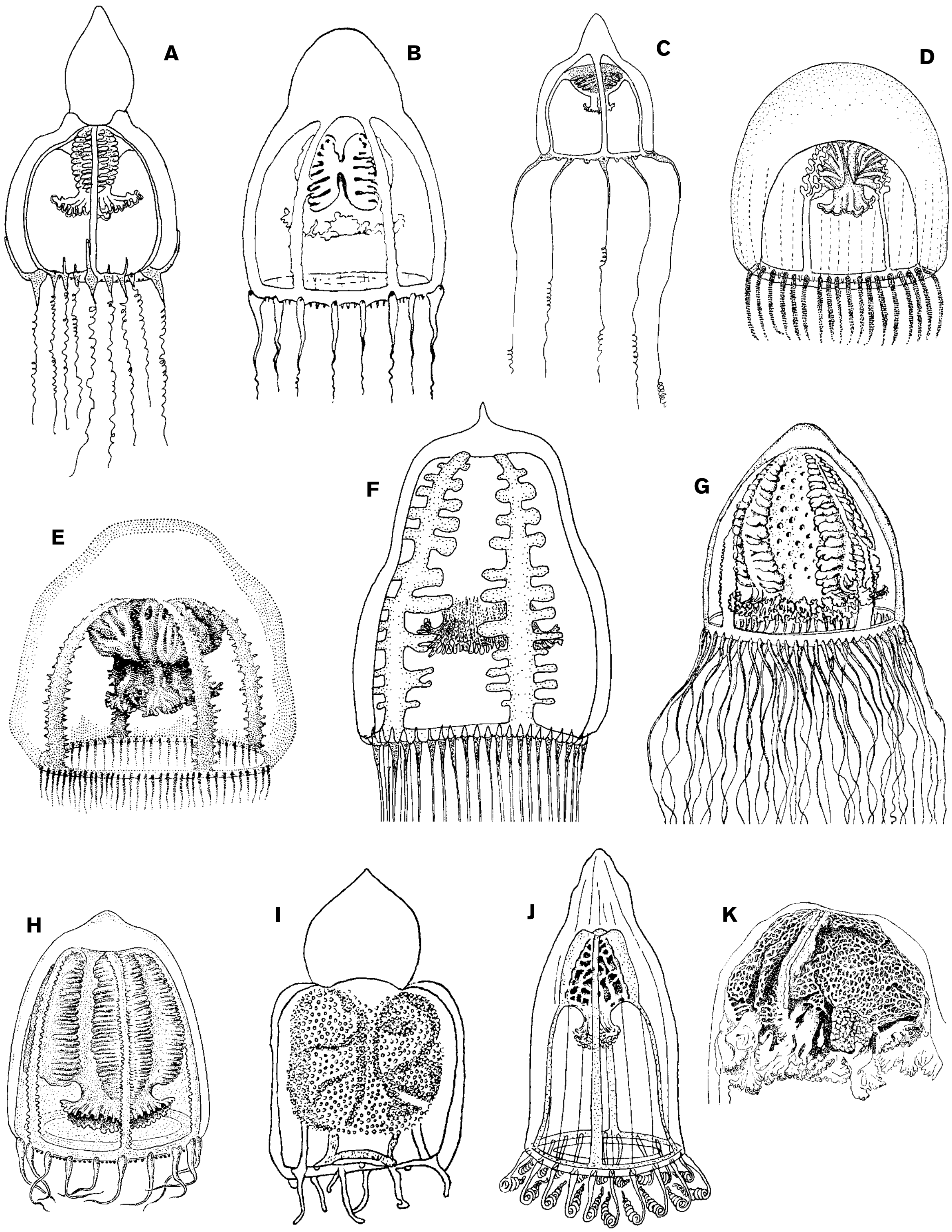


PLATE 56 Anthomedusae with many tentacles (all family Pandeidae). A, *Leuckartiara* sp. from Monterey Bay; B, *Leuckartiara octona*; C, *Halitholus sp*. from Friday Harbor; D, *Annatiara affinis*; E, *Neoturris breviconis*; F, *Neoturris* sp. (undescribed); G, *Neoturris pileata*; H, *Neoturris fontata*; I, *Neoturris pelagica*; J, *Pandea conica*; K, *Pandea rubra* manubrium (A, C, D, F, original drawings by Claudia. E. Mills; B, G, H, I, from Kramp 1968, each after Russell, Hartlaub, Bigelow, and Foerster, respectively, with permission; E, from Naumov 1960; J, from Kramp 1968 with permission; K, from Naumov 1969 after Bigelow).

— Without marginal vesicles, manubrium tubular without distinct lips; with cruciform gonad covering the manubrium and extending out about one-half the length of the radial canals, with very thick jelly, bell to about 8 mm in height; in low salinity (plate 55H) . . . . *Moerisia* sp.

67. With eight marginal vesicles; with up to 16 or 36 marginal tentacles 76

— With numerous marginal vesicles, usually one or two between every pair of tentacles; with hundreds of tentacles, some of which may emerge through grooves in the jelly some distance above the bell margin 68

68. Marine, although may be up rivers, in very low salinity 69

— In fresh water; with up to 400 tentacles in several series; mouth with four slightly folded short lips; bell to about 20 mm in diameter (plate 54J) . . . . *Craspedacusta sowerbii*

69. With up to 200 tentacles, ring canal with or without centripetal canals extending upward in each quadrant; gonads hang as a wavy curtain from, and restricted to, the four radial canals; mouth with four frilly, short lips; in full salinity on outer coasts 70

— With up to 600 tentacles, ring canal with several centripetal canals extending upward in each quadrant; gonads hang curtainlike from the four radial canals, extending onto "arms" of the manubrium out along each radial canal; mouth with four very elongate, frilly lips; bell to about 55 mm diameter; in low salinity, often up coastal rivers (plate 50D) . . . . *Maeotias marginata*

70. With up to 200 tentacles, ring canal without centripetal canals extending upward in each quadrant; bell to about 20 mm diameter (plate 50A) . . . . *Aglauropsis aeora*

— With up to 100 tentacles, ring canal with up to six broad centripetal canals extending upward in each quadrant; bell to about 45 mm diameter (rare) (plate 50B) . . . . *Eperetmus typus*

71. Gonads ovoid or nearly spherical, occupying only a short section of each radial canal; tentacles more or less of fixed length (not highly extensile); bell not >6 mm in diameter in mature specimens and very flat (plate 38) . . . . *Obelia* spp.

— Gonads elongated, associated with the radial canals for a substantial portion of their length; tentacles highly extensile; bell usually more than 6 mm in diameter in mature specimens and bell-shaped, not flat 72

72. With ocelli on the tentacle bulbs or on the marginal vesicles 73

— Without ocelli 74

73. With ocelli on some or all of the tentacle bulbs; without marginal vesicles, but with short marginal clubs; <40 mm bell diameter (rare) . . . . *Laodicea* sp.

— Without ocelli on the tentacle bulbs, but with a black ocellus on each of the eight marginal vesicles; with eight to 16 large tentacles and up to 128 additional short or rudimentary tentacles; lips of mouth slightly frilled; large—to 80 mm bell diameter (rare) (plate 57C) . . . . *Tiaropsidium kelseyi*

74. With manubrium directly attached to the subumbrella 75

— With manubrium suspended on a gelatinous peduncle 82

75. With only eight marginal vesicles around the bell margin; tentacles moniliform, ending in a distinct terminal cnidocyst cluster 76

— With 16 or more marginal vesicles or marginal clubs (cordyli) around the bell margin; tentacles filiform, without a distinct terminal cnidocyst cluster 77

76. With 16 tentacles, gonads linear, attached to lower one-third length of radial canals; mouth lips upturned and smooth, not frilly (plate 57H) . . . . *Phialella fragilis*

— With 36 tentacles, gonads short and rather hemispherical, in the middle of the radial canals; mouth lips upturned and frilly (plate 57G) . . . . *Phialella zappai*

77. With marginal vesicles (containing statoliths) at the bell margin 78

— With free-hanging marginal clubs (cordyli) at the bell margin 81

78. With up to 80 tentacles; with one to two marginal vesicles between each two tentacles, each vesicle with one to three statoliths; lips of mouth relatively short; bell diameter <30 mm 79

— With up to 350 tentacles; with a total of 16–24 marginal vesicles, each with numerous statoliths; lips of mouth long and extended; bell diameter to 90 mm (plate 51E) . . . . *Mitrocoma cellularia*

79. Tentacle bulbs without fingerlike extensions into the bell margin, marginal vesicles each with a single statolith 80

— Tentacle bulbs each with a distinctive fingerlike extension pointing inward toward the subumbrella, marginal vesicles each with two to three statoliths (estuarine) (plate 51B) . . . . *Blackfordia virginica*

80. Gonads not usually mature until diameter of bell is >1.5 cm; gonads, when sectioned transversely, with an elliptical outline; gonads usually light-colored, but may have a stripe of dark pigment running lengthwise; bell margin may have a ring of dark pigment; up to 20 tentacles per quadrant at maturity (plates 51A, 57A) . . . . *Clytia gregaria*

— Gonads mature by the time the bell reaches a diameter of 1 cm; gonads, when sectioned transversely, with a circular outline; gonads usually fairly dark in color (brown, gray, or yellowish); bell margin without a ring of dark pigment; <10 tentacles per quadrant at maturity (plate 57B) . . . . *Clytia lomae*

81. Bell to 10 mm wide and nearly as high; with about 48 tentacles and one to five cordyli between tentacles; gonads with 12–14 folds in proximal half of radial canals (rare) (plate 57I) . . . . *Ptychogena californica*

— Bell to 90 mm wide and 30 mm tall; with 300–500 tentacles and as many cordyli; gonads on 20–30 lamelliform diverticula of radial canals along their entire length (rare) (plate 57F) . . . . *Ptychogena lactea*

82. With eight marginal vesicles; with up to 200 marginal tentacles; (colorless or with white or sepia pigment in the manubrium, gonads, and tentacle bases); conical peduncle bearing manubrium may extend nearly to the bell margin (plate 51D, 57D) . . . . *Eutonina indicans*

— With many more than eight marginal vesicles; usually with <200 marginal tentacles; peduncle low, with manubrium not reaching to bell margin 83

83. With up to 180 marginal tentacles and with as many or more marginal vesicles; manubrium, gonads, and radial canals faintly yellow, tentacle bulbs brick red in life (rare) (plate 57E) . . . . *Eirene mollis*

— With up to 150 marginal tentacles and about half as many marginal vesicles; manubrium and radial canals (and sometimes gonads) purple (rare) (plate 57J) . . . . *Foersteria purpurea*

84. Bell about 1 mm tall and a little less wide, with very thin jelly; with four radial canals and with several pairs of

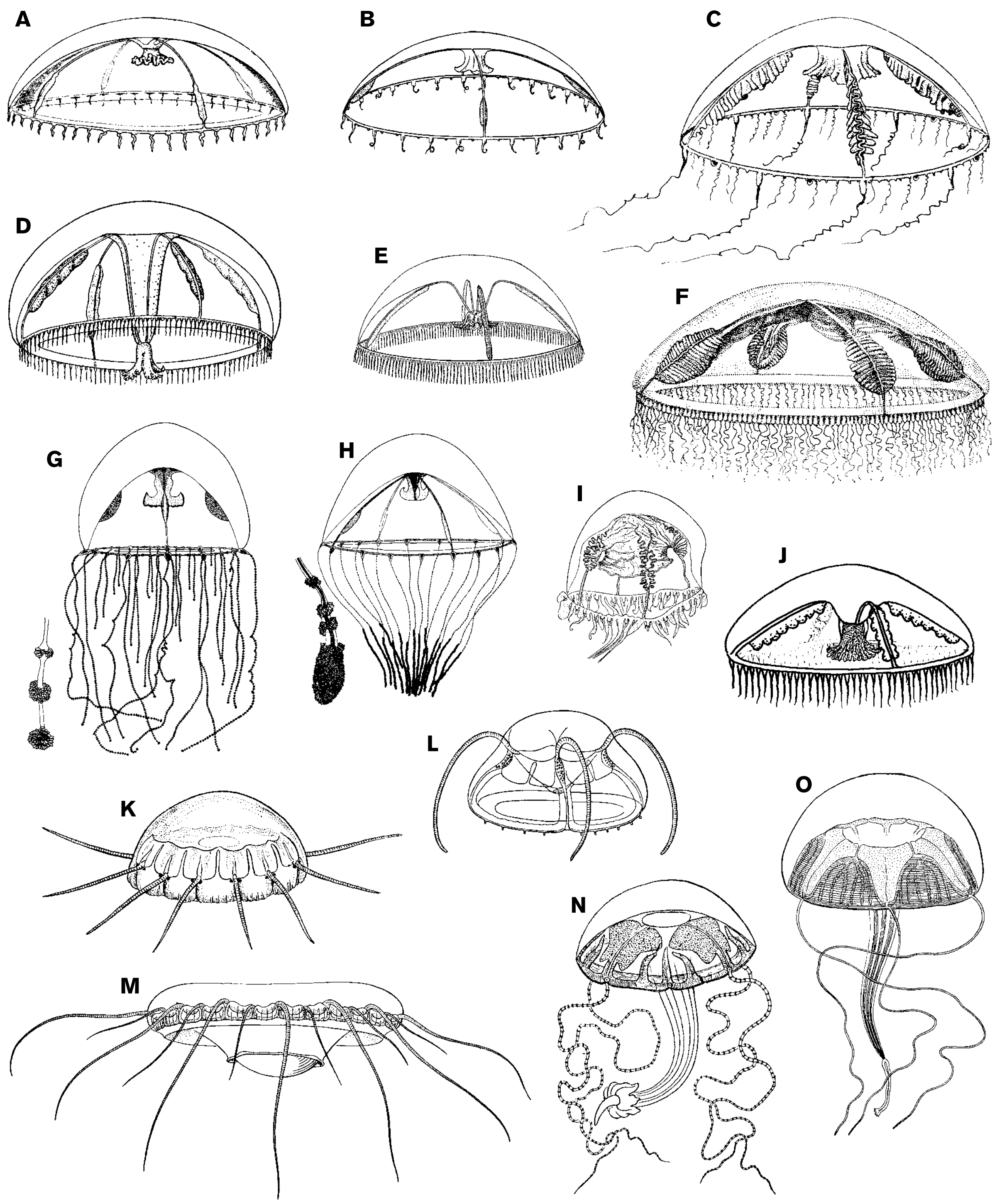


PLATE 57 Leptomedusae, Narcomedusae, and Trachymedusae. A, *Clytia gregaria*; B, *Clytia lomae*; C, *Tiaropsidium kelseyi*; D, *Eutonina indicans*; E, *Eirene mollis*; F, *Ptychogena lactea*; G, *Phialella zappai*; H, *Phialella fragilis*; I, *Ptychogena californica*; J, *Foersteria purpurea*; K, *Cunina peregrina*; L, *Aegina citrea*; M, *Pegantha clara*; N, *Liriope tetraphylla*; O, *Geryonia proboscidalis* (A, from Kramp 1968, after Murbach and Shearer; B, E, I, from Torrey 1909; D, K, from Kramp 1968; C, after Torrey 1909, and from life; F, from Naumov 1960; G, H, from Boero 1987, reprinted by permission of Taylor & Francis Ltd, http://www.tandf.co.uk/journals; J, original drawing by Claudia E. Mills; L, from Kramp 1968, after Mayer; M, O, from Mayer 1910; N, from Mayer 1910, after Haeckel).

tentacles arising at several levels on the exumbrella in line with each radial canal (plate 50H). . . . . *Climacocodon ikarii*

— Bell broad with thick jelly; without radial canals and with tentacles arising all at the same level, some distance above the bell margin 85

85. With stomach pouches 86

— Without stomach pouches 89

86. With four tentacles (rarely, five or six), and usually eight (rarely, to 12) well-defined stomach pouches containing the gonads (plate 57L). . . . . *Aegina citrea*

— With more than six tentacles, and an equal number of tentacles and stomach pouches 87

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

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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.

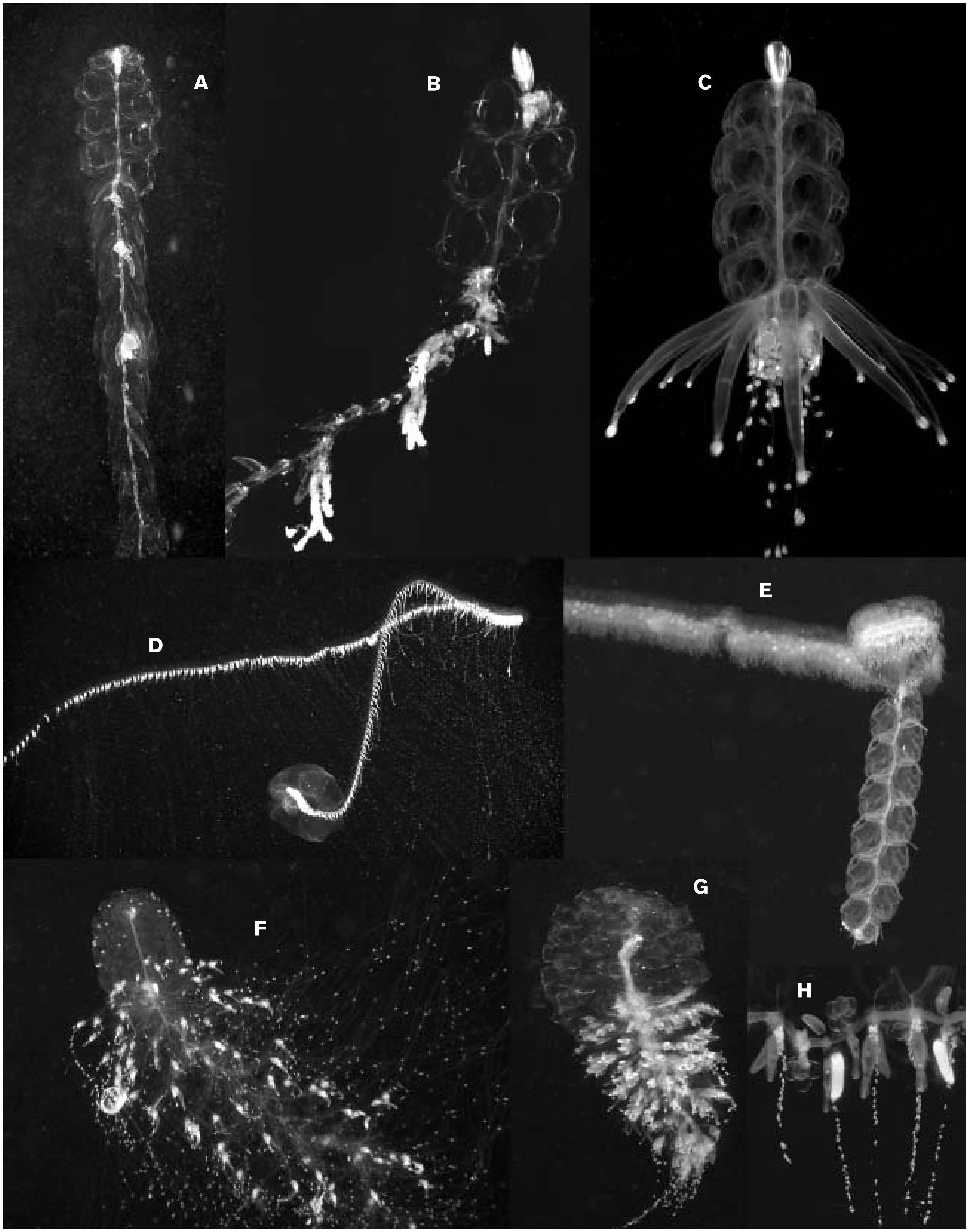

PLATE 58 Whole siphonophores, live. A, *Agalma elegans*; B, *Nanomia bijuga*; C, *Physophora hydrostatica*; D, *Praya dubia*; E, *Apolemia* sp.; F, *Forskalia* sp. 1; G, *Forskalia* sp. 2; H, *Praya dubia*, close-up of portion of the stem (A, F, G, photographs by Casey W. Dunn; B, H, photographs by Claudia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

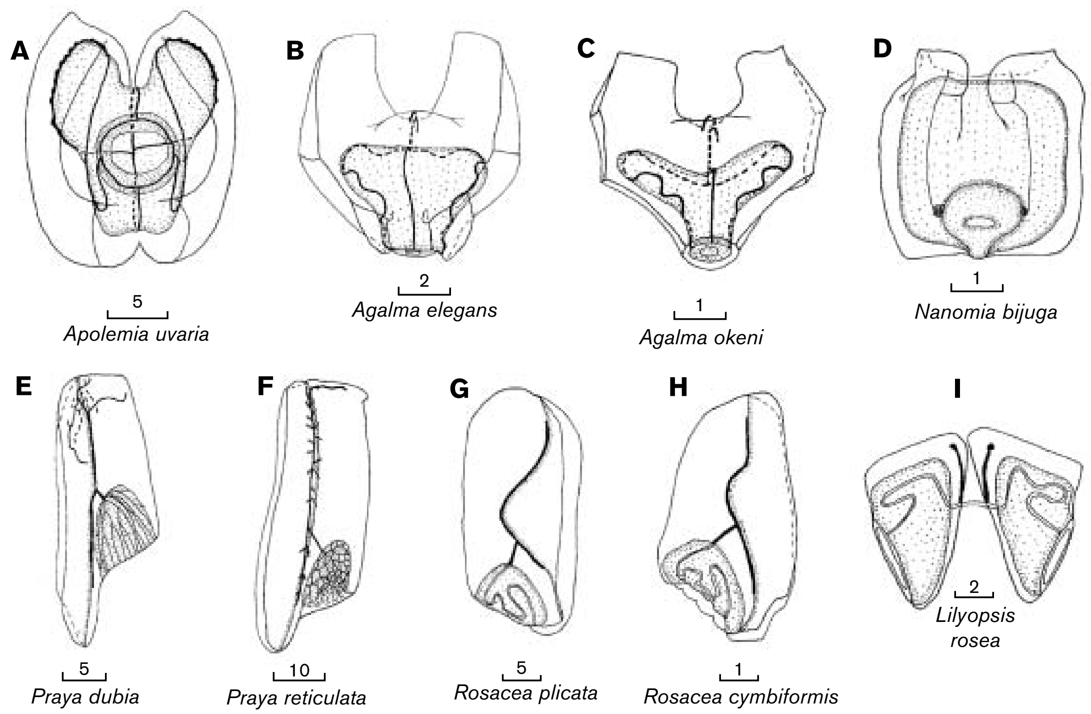

PLATE 59 Nectophores. Views from above (looking down the stem from the float–B, C) and distal views (stem running down the plane of the page–A, D) of nectophores of physonect siphonophores (A–D) and lateral views of nectophores of calycophoran siphonophores (E–I); scale bars in mm. For additional drawings 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.

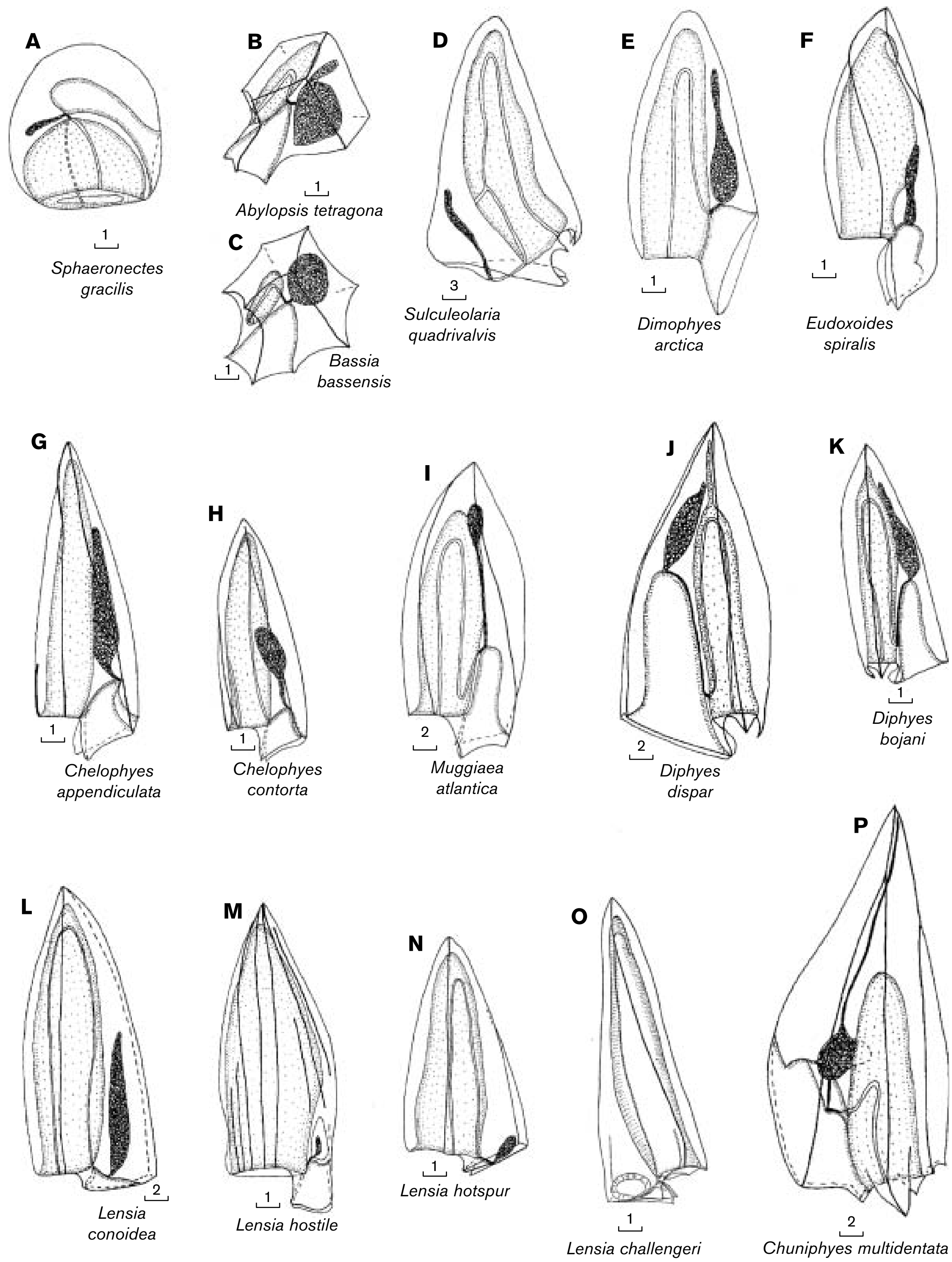

PLATE 60 Lateral views of anterior nectophores of calycophoran siphonophores; scale bars in mm. For additional drawings of posterior nectophores, bracts, and gonophores, see Pugh (1999). A, *Sphaeronectes gracilis*; B, *Abylopsis tetragona*; C, *Bassia bassensis*; D, *Sulculeolaria quadrivalvis*; E, *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).

OCEANIDAE (=CORDYLOPHORIDAE, a junior synonym)

Cordylophora caspia (Pallas, 1771) (=*C. lacustris* Allman, 1844). Hydroid. Additional synonyms in Schuchert (1996, p. 15; 2004, p. 346). Hydroids phenotypically variable, in part related to salinity (Roch 1924, Z. Morph. ökol. Tiere 2, 350–426). Eggs develop into planulae within the gonangia (see Schuchert 1996). Restricted to areas of brackish or fresh water. Colonies occurring on a wide variety of substrates including pilings, barnacles, floats, and tubes of the polychaete *Ficopomatus*; abundant in the San Francisco Bay Delta and recorded in Lake Merced on the San Francisco peninsula. Thought to be Ponto-Caspian in origin, it appears to have a remarkable temperature breadth (if only one species is involved), being introduced in ship fouling from British Columbia to Panama in the shallow subtidal.

Turritopsis sp. Hydroid and medusa. Previously identified from San Francisco Bay as *Turritopsis nutricula* McCrady, 1857; but from Schuchert's (2004) revision of the genus *Turritopsis,* it is now evident that there are several similar-looking species, so we do not attempt here a specific identification of this seemingly non-native species. *Turritopsis* medusae still found occasionally in San Francisco Bay in the late 1990s (these to 8 mm tall, with about 25 tentacles and pale red manubrium), but the hydroid has not been recorded there since 1940; San Francisco Bay, 0–9 m (Fraser 1937, 1946). What was previously seen as a widely introduced single species, usually in estuaries and bays, with affinities to warmer waters in many locations worldwide, has now been identified as at least four species, some or one of which may be quite widely introduced.

PANDEIDAE

Several species of Pandeidae have been assigned in the past to *Perigonimus,* a junior synonym of *Bougainvillia* (see Calder 1988). These are now referred to genera such as *Amphinema*, *Leuckartiara*, *Neoturris* and *Catablema* (Bouillon 1985; Calder 1988).

Amphinema platyhedos Arai and Brinckmann-Voss, 1983. Medusa (hydroid unknown). Rare; known from deep water in British Columbia and southern California. Compare with other *Amphinema* medusae (below) in the area.

Amphinema turrida (Mayer, 1900). Medusa (hydroid unknown). Rare; known from surface waters from Monterey Bay south into Mexico; Pacific and Atlantic. The two stout yellow tentacles and folded gonads that extend most of the way down the radial canals are distinctive. Color photograph in Wrobel and Mills 1998 and 2003, p. 26.

Amphinema sp. Hydroid and medusa. Hydranths bright orange-red; when disturbed, they bend over nearly 180º towards the substrate. This hydroid resembles *Amphinema rugosum* (Mayer 1900) in having medusa buds on the hydrocaulus (Schuchert 1996), but the medusae showed significant differences from *A. rugosum*. Colony occurred on non-native encrusting bryozoan *Watersipora* sp. on floating docks in Bodega Harbor. Medusa known only from rearing in the laboratory from field-collected hydroid. See Rees 2000, Sci. Mar. 64 (Suppl. 1): 165–172. Probably introduced.

Annatiara affinis (Hartlaub, 1913). Medusa (hydroid unknown). Genus name was created by reversal of *Tiaranna* in which this species was originally placed. A species that has been infrequently collected in the Pacific, Atlantic, and Indian Oceans; considered to live in deep water, but several medusae have been found near the surface in Monterey Bay. Color photograph in Wrobel and Mills 1998 and 2003, p. 26.

Halitholus spp. Medusa (hydroid unknown). Similar to and usually smaller than *Leuckartiara,* there are at least two undescribed *Halitholus* species on our coast. Color photograph in Mills and Wrobel 1998 and 2003, p. 27.

Leuckartiara octona (Fleming, 1823) (=*Perigonimus repens* [Wright, 1857]). Hydroid and medusa. Synonyms in Schuchert (1996, p. 68). Stolonal colonies on shells of gastropods including *Hima mendica* and *Callianax biplicata*. Colony form varies according to the host shell and the amount of friction to which it is subjected. The best-developed colonies, sometimes with branches and producing gonophores, are usually found on the upper surface of the shell where there is no abrasion (Torrey 1902; Millard 1975). Alaska to tropics, including San Francisco Bay (Fraser 1937, 1946, as *P. repens*). *L. octona* medusae collected in Bodega Bay and Bodega Harbor by Rees (1975). Medusae that meet this description except are two times larger (to 40 mm tall) and with up to 72 tentacular rudiments are sometimes very abundant offshore in central California near Monterey. This species, said to occur all over the world, likely represents a species complex, especially considering its specialized shallow-water habitat association with gastropods.

**Leuckartiara* spp. Hydroid and medusa. Other species of *Leuckartiara* with *Perigonimus*-like polyps that are not *L. octona* are occasionally collected in our area. The shape of the apical projection on *Leuckartiara* and other pandeid species is rather plastic and, tempting though it may be, is not the best diagnostic character to use when trying to make identifications. Color photograph in Wrobel and Mills 1998 and 2003, p. 27.

Neoturris breviconis (Murbach and Shearer, 1902). Medusa (hydroid unknown). Known from both the North Pacific and North Atlantic, occurs on the West Coast from the Bering Sea to Monterey Bay. Color photograph in Wrobel and Mills 1998 and 2003, p. 28.

Neoturris fontata (Bigelow, 1909). Medusa (hydroid unknown). Medusa collected only once, at the surface near the coast, Baja California (Bigelow 1909, Mem. Mus. Comp. Zool. Harvard 37: 1–243, pls. 1–48; Kramp 1968, p. 49).

Neoturris pelagica (A. Agassiz and Mayer, 1902). Medusa (hydroid unknown). North and South Pacific, including coast of California; rare.

Neoturris sp. (undescribed). Medusa (hydroid unknown) that corresponds more or less to *N. pileata* (Forsskål, 1775) except for its enormous size (to 80 mm tall, whereas *N. pileata* [see hydromedusa plate 56G] is described as 40 mm tall) and the very broad, distinctive, tablike diverticula off its radial canals has been collected infrequently offshore in southern California (C. E. Mills, unpublished observations); a record of *"N. pileata"* off Vancouver Island (see Kramp 1968, p. 50) may be the same species.

Pandea conica (Quoy and Gaimard, 1827). Medusa (hydroid unknown). With characteristic, usually pointed bell, to 21 mm high, a shelf species perhaps, but occasionally encountered near shore in California; found in the Atlantic, Pacific, and Mediterranean (Kramp 1961, 1968). Remarkable color illustration of hydroid and medusa from Naples in Brinckmann-Voss 1970, plate 11.

**Pandea rubra* Bigelow, 1913. Medusa (hydroid unknown). A larger (to 75 mm high and wide) flat-topped deep sea species that occurs off California (as well as in the Atlantic and Antarctic) with characteristic deep red gut, gonads, tentacles and subumbrella; unlikely to be found near shore (compare with *P. conica*) (Kramp 1961, 1968).

* = Not in key.

Stomotoca atra L. Agassiz, 1862. Medusa (hydroid unknown). A common near-shore medusa on the entire West Coast that swims in a sinusoidal pattern trailing its two long tentacles, feeding primarily on other small hydromedusae (Mills 1981). Many have attempted to raise its hydroid in the lab: the stolons elongate, but hydranths do not develop (Volker Schmid pers. comm.); the hydroid may be symbiotic on another organism. It is unlikely that our temperate West Coast *S. atra* is conspecific with the Papua New Guinea medusa of the same name. Color photograph in Wrobel and Mills 1998 and 2003, p. 28.

PROBOSCIDACTYLIDAE

Hydroids of the various species of *Proboscidactyla* strongly resemble each other and are differentiated largely on the basis of medusoid characters (Millard 1975). The family has been classified among the Limnomedusae by several authors (e.g., Kramp 1961; Naumov 1969; Millard 1975; Bouillon 1985, 1995a). Following Petersen (1990), Schuchert (1996), and others, we assign it to the Anthoathecata because of the presence of a stolon system, desmoneme cnidocysts, and the absence of statocysts in the medusae. Gastrozooids in all species of *Proboscidactyla* are arranged in a circle around the rim of the tube of a sabellid polychaete host. The two tentacles of each hydranth are directed toward the opening of the tube, and the asymmetrically placed pad of cnidocysts on the hypostome is oriented away from it. Polyps are active, securing food from the tentacles of the sabellid or consuming spawned eggs of the host. In bending over periodically towards the central axis of the polychaete tube, with the two tentacles extended and the hypostome resembling a human head, a hydranth resembles a person praying. Nonfeeding polyps sometimes occur some distance from the tube rim. The association of *Proboscidactyla* spp. with its polychaete substrate is obligatory: planulae settle and develop only on the worm tube (Hand 1954—see below; Millard 1975; Rees 1979—see below).

Proboscidactyla circumsabella Hand, 1954. Hydroid and medusa. Hydroid found at Pacific Grove, on tubes of the sabellid *Pseudopotamilla ocellata* (and rarely on *P. intermedia*), on rocks at low tide; medusae known from Monterey Bay (see Hand and Hendrickson 1950, Biol. Bull. 99: 74–87 and Hand, 1954, Pacific Sci. 8: 51–67).

Proboscidactyla flavicirrata Brandt, 1835. Hydroid and medusa. A northern species occurring from China and Japan to central Oregon, where it is rare. Hydroid known from Friday Harbor commensal on the sabellids *Schizobranchia insignis* and *Pseudopotamilla ocellata*. For life cycle, see Hand 1954, Pac. Sci. 8: 51–67 and Rees 1979, Can. J. Zool. 57: 551–557; for host specificity and description of larvae settling on sabellid worm tubes, see Campbell 1968, Pac. Sci. 22: 336– 339 and Donaldson 1974, Biol. Bull. 147: 573–585; for medusa feeding behavior and diet, see Mills (1981) and Costello and Colin (2002). Photograph in Wrobel and Mills 1998 and 2003, p. 38.

Proboscidactyla occidentalis (Fewkes, 1889). Hydroid and medusa. Hydroids on tubes of sabellids (*Potamilla neglecta* and *Pseudopotamilla intermedia*) from a kelp holdfast, La Jolla, 12–15 m; medusae known from Santa Cruz Island, La Jolla, and San Diego Bay (see Hand 1954, Pac. Sci. 8: 51–67).

PROTIARIDAE

**Protiara* sp. Medusa (hydroid unknown). Two medusae collected in July in Bodega Bay (Rees 1975, p. 252a) and several others collected May through July in Yaquina Bay (1969–1974, R. J. Larson, personal communication). The Oregon specimens reached 5 mm in bell height and appear to be an undescribed species (see hydromedusa plate 54E) (R. J. Larson, personal communication).

RATHKEIDAE

Rathkea octopunctata (M. Sars, 1835). Hydroid and medusa. Synonyms in Schuchert (1996, p. 59). Medusa known from Alaska to central California; the miniscule hydroid, seldom seen, is described by Schuchert (1996). The medusae go through a period of asexually producing more medusae from the manubrium walls before sexual gonads develop in the same location. Reported from around the world. Color photograph in Wrobel and Mills 1998 and 2003, p. 28.

STYLASTERIDAE

Stylantheca porphyra Fisher, 1931 (=*Allopora porphyra*). Hydroid. Colonies forming vivid purple calcareous encrustations varying in size from tiny patches to large sheets (Haderlie et al. 1980). On exposed, rocky coasts, Monterey Bay and vicinity, low intertidal (Cairns 1983, Bull. Mar. Sci. 33: 427–508 (taxonomy); Alberto Lindner pers. comm.). The commensal polychaete *Polydora alloporis* forms distinctive paired holes in the colony.

**Stylaster californicus* (Verrill, 1866) (=*Allopora californica*). Hydroid. The common sublittoral, branched representative of the alloporas, frequently seen by snorkelers and divers at Carmel, color ranging from orange to pink into purple. See Ostarello 1973, Biol. Bull. 145: 548–564 (natural history); color photograph in Haderlie et al. 1980, 3.17, plate 18. Unpublished molecular work by Alberto Lindner and Steve Blair indicates that this branched form is conspecific with *S. porphyra,* above, and possibly with other species further north; the *S. californicus* name has precedence (pers. comm.).

ORDER CAPITATA

CANDELABRIDAE

Candelabrum fritchmanii Hewitt and Goddard, 2001. Hydroid. Hydranths large (total body length to 100 mm when relaxed, to <20 mm when disturbed or contracted), with clasper tentacles attached to developing embryos in the blastostyle-bearing region, at least during the reproductive season. Colony attached to hard substrate by laterally flattened, basal hydrorhiza (this often with short, tentacular processes); naked attachment tentacles with chitinous pads also arise from the hydranth base. Under intertidal boulders in southern Oregon. Feeds on idoteid isopods and small gammarid amphipods; life cycle includes an actinula. See Hewitt and Goddard 2001, Can. J. Zool. 79: 2280–2288. *Note:* Hand and Gwilliam (1951, J. Wash. Acad. Sci. 41: 206–209) described solitary *Candelabrum* sp. from Pigeon Point, San Mateo Co., California. These specimens are similar to solitary *C. fritchmanii*, but owing to their lack of reproductive structures, cannot be specifically identified based on morphological characters alone.

CLADONEMATIDAE

The medusae of *Cladonema* are benthic, adhering to substrates by specialized, adhesive tentacles. The hydroids are frequently introduced accidentally to aquaria (Brinckmann-Voss 1970) and

* = Not in key.

can be kept for long periods (as many as 30 years, Russell 1953, p. 108). The medusae are exceptionally long-lived (several months) for such small species. The taxonomy of the genus is confused (Rees 1979—see below). In coastal California, two groups of species are distinguishable based on the hydroids: *Cladonema californicum* and *C. radiatum* (polyps with two whorls of tentacles, one capitate and the other filiform), and *Cladonema myersi* and *C. pacificum* (polyps with capitate tentacles only). Two different groups are recognized from the medusae: *C. californicum* in one, and *C. myersi, C. radiatum* and *C. pacificum* in another (Rees 1949—see below; Kramp 1961; Rees 1979, 1982—see below; Hirohito 1988). A combination of characters thus distinguishes the three species.

Cladonema californicum Hyman, 1947 (*californica* is a misspelling). Hydroid and medusa. For life cycle, see Rees 1979, J. Nat. Hist. 13: 295–302. Medusae present all year clinging to shallow eelgrass or *Ulva* in bays and harbors (see Hyman 1947, Trans. Am. Microsc. Soc. 66: 262–268). The medusae feed on benthic fauna associated with eelgrass and seaweed, capturing prey passively while remaining attached to the plants, but they swim actively when disturbed. Medusa found from British Columbia to Long Beach; hydroid known from Bodega Harbor. For lab culture, feeding, carbon, and nitrogen budgets, see Costello 1988, J. Exp. Mar. Biol. Ecol. 123: 177–188; Costello 1991, Mar. Biol. 108: 119–128; Costello 1998, J. Exp. Mar. Biol. Ecol. 225: 13–28. Color photograph in Wrobel and Mills 1998 and 2003, p. 29.

Cladonema myersi Rees, 1949. Hydroid and medusa. Hydroids on coralline algae; can be kept in aquaria for long periods (see Rees 1949, Proc. Zool. Soc. London 119: 861–865). Described from La Jolla, where the hydroid, releasing medusae, was found in 1934.

Cladonema pacificum Naumov, 1955 (=*C. uchidai* Hirai, 1958; see Hirohito 1988 for its complex taxonomic history). Hydroid and medusa. Found in display tank at the University of California, Berkeley, with material in the tank from San Francisco Bay and presumed to occur there (Rees 1982, Pac. Sci. 36: 439–444). Originally described from the Sea of Japan. An introduction from east Asia (Rees 1982 above).

Cladonema radiatum Dujardin, 1843. Hydroid and medusa. Synonyms in Schuchert (1996, p. 131). European species common amongst the eelgrass *Zostera* in Padilla Bay, Washington, adjacent to oil refineries on March Point, and likely to occur elsewhere on the West Coast because of frequent tanker traffic to refineries up and down the West Coast. Spectacular color illustration of hydroid and medusa in Brinckmann-Voss 1970, plate 5. Introduced.

CORYMORPHIDAE

Corymorpha palma Torrey, 1902. Hydroid. Synonyms in Hochberg and Ljubenkov (1998, p. 13). We follow Petersen (1990) and Schuchert (1996) in assigning this species to *Corymorpha*. In being an easy species to cultivate in the laboratory, aspects of its behavior, developmental biology, associations with algae, and statocysts have been investigated (see Haderlie et al. 1980 and Hochberg and Ljubenkov 1998, for references; color photograph in Haderlie et al., 3.4, P15). A southern species ranging at least north to Santa Barbara Channel, lower intertidal to 60 m; occurring where currents are moderate in turbid bays and estuaries, and on muddy bottoms offshore (Fraser 1937; Hochberg and Ljubenkov 1998).

Euphysa spp. Hydroid and medusa. A group of boreal (North Pacific, North Atlantic, and Arctic) species that are commonly found as far south as Washington and occasionally are collected at least to central Oregon (R. J. Larson unpublished observations). Discussion of synonomies and northeast Pacific species in Arai and Brinckmann-Voss (1980: 6–9). *Euphysa tentaculata* medusae have only three tentacles at maturity (4–6 mm bell height); *E. flammea* and *E. japonica* both have four tentacles at maturity (about 1 cm tall) and are indistinguishable at that point. *E. flammea* has only one tentacle in the young stages, whereas *E. japonica* has four already at very small size. Some species of *Euphysa,* including *E. ruthae* near Friday Harbor, have interstitial polyps (see Norenburg and Morse 1983, Trans. Am. Microsc. Soc. 102: 1–17). Color photograph in Wrobel and Mills 1998 and 2003, p. 31.

Euphysora bigelowi Maas, 1905. Hydroid and medusa. Synonyms in Hochberg and Ljubenkov (1998, p. 16). Hydroid raised in lab from mature medusae collected in Monterey Bay (see Sassaman and Rees 1978, Biol. Bull. 154: 485–496). Typical of species of this family, the oral tentacles not distinctly capitate but may be thickened at their tips, especially in young polyps (Sassaman and Rees 1978; Petersen 1990). Hydroid generally found on soft bottoms, anchoring rootlets with inflated tips being used for attachment. Reproducing asexually with part of the base of the parental polyp detaching, developing tentacles, and breaking free (Hochberg and Ljubenkov 1998). Period of medusa liberation prolonged due to asynchronous development of the gonophores (Sassaman and Rees 1978). Assigned to *Corymorpha* by Sassaman and Rees (1978), Petersen (1990), and Cairns et al. (2002), but we refer it to *Euphysora* (Kramp 1961, 1968; Hochberg and Ljubenkov 1998, Bouillon et al. 2004). Indo-Pacific and Mediterranean.

*Unidentified corymorphid. A tiny (2–3 mm), orange-tinted polyp (see hydroid plate 44J), similar to the European *Corymorpha nutans* M. Sars 1835 collected from soft mud at Point Richmond in 1955 by Meredith Jones and again (if the same species) by James Carlton in Lake Merritt, Oakland, in 1967 (Cohen and Carlton 1995, p. 33).

CORYNIDAE

Coryne eximia Allman, 1859 (=*Syncoryne eximia*). Hydroid and medusa. Additional synonyms in Schuchert (2001b, p. 773). Hydroid easily kept in laboratory. See Schuchert (2001b) for differences between hydroid and medusa stages of *C. eximia* and *C. japonica*. Rocky intertidal and subtidal zones, Alaska to Monterey Bay, 0–18 m (Fraser 1937, 1946). Some reports of *C. eximia* could be *C. cliffordi* (Brinckmann-Voss 1989), a similar species known only from British Columbia (Schuchert 2001b).

Coryne japonica (Nagao, 1962) (=*Stauridiosarsia japonica*). Hydroid and medusa. Additional synonyms in Schuchert (2001b, p. 757). Known from Bodega Harbor and adjacent outer coast (Rees 1975); North and South Pacific, intertidal and shallow subtidal, on rocks and shells. See Arai and Brinckmann-Voss 1980; Schuchert 2001b.

Coryne sp. (undescribed). Hydroid and medusa. Large showy unbranched colonies of polyps (to 6 cm tall) growing on floating wood nearly always within 2–3 cm of the surface at Alameda Point, eastern shore of San Francisco Bay; large hydranths bear as many as 80 medusa buds at one time. Medusae grown in culture to maturity in 2 to 3 weeks, distinguished by bubblelike vesicles on the exumbrella (J. T. Rees unpublished observations). Probably an introduced species that is either undescribed or yet to be matched to a known species elsewhere in the world.

* = Not in key.

Dipurena bicircella Rees, 1977. Hydroid and medusa. Larger, mature polyps occurring at center of colony; smaller polyps with fewer or no medusa buds at periphery. Adult medusae sluggish swimmers, spending most of their time on the bottom in culture. On granite rock and shell, 3–10 m in Horseshoe Cove, Bodega Head (Rees 1977, Mar. Biol. 39: 197–202). See Schuchert (2001b) for comparison with other species of *Dipurena*.

Dipurena ophiogaster Haeckel, 1879. Hydroid and medusa. Hydroid (see hydroid plate 42F) grows on algae, barnacles and rock in Europe (see Schuchert 2001b, p. 803). Medusae with three or four gonads on the manubrium (McCormick 1969a, b; R. J. Larson unpublished observations) identified as *D. ophiogaster* in Yaquina Bay; and medusae without description identified as *D. ophiogaster*? in Bodega Harbor (Rees 1975, p. 252a), but this medusa is easily confused with *D. reesi*. *D. ophiogaster* is known from a variety of locations in both the Pacific and Atlantic Oceans (see Schuchert 2001b).

Dipurena reesi Vannucci, 1956. Hydroid and medusa. Barely detectable hydroid (see hydroid plate 42G) grows on rock and shell in Europe (see Schuchert 2001b, p. 805). Medusa reported from southern California and Mexico (known also from Brazil, Mediterranean and Bay of Biscay). Difficult to distinguish from *D. ophiogaster* (see Schuchert 2001b).

Sarsia tubulosa (M. Sars, 1835). Hydroid and medusa. As *Syncoryne mirabilis* (Agassiz, 1862) in Torrey (1902) and Fraser (1911, 1937, 1946), but that name, originally used for a medusa from New England, appears to have been applied to a complex of corynid species and is best not used for West Coast material pending further studies. In bays and harbors, Alaska to southern California, 0–22 m (Fraser 1937, 1946). Identifications questionable due to many similar species; see Miller 1982, J. Exp. Mar. Biol. Ecol. 62: 153–172 (species of Friday Harbor, including *S. tubulosa*), but see also Schuchert (2001b) for critical discussion and synonomies. Medusa feeding behavior and diet reported by Costello and Colin (2002) may represent more than one species, which may or may not be *S. tubulosa*. Present in San Francisco Bay in 2000 (J. T. Rees unpublished collection); likely introduced.

**Sarsia* spp. and *Coryne* spp. Species of *Sarsia* and *Coryne* are difficult to identify because of a lack of morphological characters (Brinckmann-Voss 1985, Can. J. Zool. 63: 673–681; Schuchert 2001b). Two unnamed species of the *"Sarsia/Coryne eximia"* group occur in our area, *Coryne* sp. A and B (Rees 1975). The *"eximia"* group, now referred to *Coryne,* comprise medusae with a short manubrium; the *"tubulosa"* group, now referred to *Sarsia,* include medusae with a long manubrium. Rees (1975) reports at least five unidentified species of *"Sarsia"* (includes *Coryne* by present generic definitions) present in the plankton in Bodega Bay. Color photograph in Wrobel and Mills 1998 and 2003, p. 29.

HALIMEDUSIDAE

This family was assigned to the Order Filifera (Bouillon 1985) prior to life-cycle studies. The hydranths have capitate tentacles (Mills and Miller 1987; Wrobel and Mills 1998; Mills 2000), indicating that the Halimedusidae should be assigned to the Capitata (Mills 2000).

Halimedusa typus Bigelow, 1916. Hydroid and medusa. Hydroid reared in the laboratory. Hydranths feed on nematodes and rotifers; their solitary condition and minuteness make them inconspicuous in nature (see Mills 2000, Sci. Mar. 64 [Suppl. 1]: 97–106). Medusae occur at least in Yaquina Bay, Coos Bay, Humboldt Bay, and Bodega Bay and Bodega Harbor. Color photograph in Wrobel and Mills 1998 and 2003, p. 26.

HYDROCORYNIDAE

Hydrocoryne bodegensis Rees, Hand and Mills, 1976. Hydroid and medusa. Polyps with large hydranths (0.5–6.0 cm high, depending on state of contraction); these move with the current, swinging like maces through the water and along the substrate, quickly contracting when disturbed. They feed on relatively large (2–4 mm) gammarid amphipods and other macrobenthic crustaceans (see Rees et al. 1976, Wasmann J. Biol. 34: 108–118). Intertidal and subtidal on jetty at entrance to Bodega Harbor, on rock faces exposed to moderately strong water movements; occasionally on kelps; medusa in Bodega Harbor and Bodega Bay.

MARGELOPSIDAE

Climacocodon ikarii Uchida, 1924. Hydroid and medusa. An oceanic species, with hydroids free-living in the plankton; occasionally collected near shore in central California and central Oregon. Polyps highly differentiated, budding medusae, which are released but do not grow much beyond 2 mm, making them among the smallest of the hydromedusae (see Uchida 1924, Japanese J. Zool. 1: 59–65).

MOERISIIDAE

Moerisia sp. Hydroid and medusa. Although this species was assigned to *Moerisia lyonsi* Boulenger, 1908 by Cairns et al. (2002), both the medusa and polyp in California have certain substantial differences from that species, as noted by Rees and Gershwin (2000), which prevent a positive species identification. It may also be conspecific with material from the Chesapeake Bay region identified as *M. gangetica* Kramp, 1958 by Petersen (1990). A study of variability in *Moerisia* is needed: if a single species, it is highly morphologically variable. Hydroid found on floats in low-salinity rivers and sloughs feeding into San Francisco Bay, reproducing asexually several ways, including frustulation and formation of podocysts, from which hydranths arise. Hydranth tentacles appear filiform but are moniliform, sometimes with a slightly capitate tip. Hydroids of this species, from the Petaluma River in San Francisco Bay, were incorrectly assigned to *Maeotias* by Mills and Sommer (1995); found in same location during 2004 on tubes of the polychaete *Ficopomatus enigmaticus*.

PENNARIIDAE

**Pennaria disticha* Goldfuss, 1820 (=*Halocordyle disticha*, =*Pennaria tiarella* [Ayres, 1854]). Hydroid and ephemeral medusa (see hydromedusa plate 52J), which sometimes release their gametes without ever being released from the hydroid colony, other times swim freely for a few hours (Mayer 1910). Reported from San Francisco Bay as *Pennaria tiarella* by Fraser (1937) without a collection date; then reported as *Pennaria* sp. on fouling panels at Mare Island, SF Bay, in 1944–1947; no further records (Cohen and Carlton 1995, Appendix 2, p. 1). See hydroid plate 52J, 52K.

POLYORCHIDAE

Polyorchis haplus Skogsberg, 1948. Medusa (hydroid unknown). Medusae found from Bodega Harbor to Scripps Pier,

* = Not in key.

La Jolla; rare. See Rees and Larson 1980, Can. J. Zool. 58: 2089–2095 (morphological variation). Color photograph in Wrobel and Mills 1998 and 2003, p. 30.

Polyorchis penicillatus (Eschscholtz, 1829). Medusa (hydroid unknown; see Brinckmann-Voss 2000, Sci. Mar. 64 [Suppl. 1]: 189–195 for retraction of discovery of "polyp of *P. penicillatus*"). Medusae found from Aleutian Islands to Sea of Cortez, primarily in protected bays. Once locally abundant throughout their range, they have disappeared or substantially decreased in numbers in the past several decades from highly urbanized or otherwise developed areas, especially in California. Medusae feed both in the water column and on the bottom, spending much of their time perched on their tentacles on the sea floor (Mills 1981). See Arai and Brinckmann-Voss (1980) and Rees and Larson 1980, Can. J. Zool. 58: 2089–2095 for morphological variability and discussion of the synonymy between *P. montereyensis* Skogsberg, 1948 and *P. penicillatus*. A number of scientists have devoted many hours to trying to culture the polyp of this charismatic species, with no success, leading us to imagine that it is likely symbiotic on or in some other organism. Newly released medusae, 1–2 mm in diameter, occur for example around marina floats heavily coated with fouling organisms in San Francisco Bay and Bodega Harbor and above a mud-bottom with abundant eelgrass and common infaunal bivalves, suggesting that a cryptic polyp is frustratingly close by. See Gladfelter 1972, Helgol. wiss. Meeresunters. 23: 38–79 (locomotor system); Haderlie et al. 1980 (general review, literature, see color photograph 3.8, plate 16, as *P. montereyensis*). Color photograph in Wrobel and Mills 1998 and 2003, p. 30.

Scrippsia pacifica Torrey, 1909. Medusa (hydroid unknown). These magnificent medusae are usually born in mid-winter, reaching adulthood in the summer months, when they are occasionally seen in large numbers in central California bays, at the surface or washed up on ocean beaches. They have been seen offshore on the bottom from about 20 m in La Jolla (by scuba divers) to as deep as 367 m in Monterey Bay (by ROV); their range is from northern California to Baja California. Color photograph in Wrobel and Mills 1998 and 2003, p. 30.

PORPITIDAE

Velella velella (Linnaeus, 1758). Hydroid and medusa. "By-the-wind sailor." Colonies polymorphic, deep blue, floating on the sea surface worldwide. Occasionally washed ashore across the region (massive strandings can be from British Columbia to central California) in large numbers, spring and summer (Alvariño 1971; Arai and Brinckmann-Voss 1980, and earlier papers by Edwards, Mackie, and others, cited therein). Color photograph in Wrobel and Mills 1998 and 2003, p. 31. Although released from the floating hydroid in copious numbers, the medusae are rarely collected in the field.

PROTOHYDRIDAE

Protohydra leuckarti Greeff, 1868. Hydroid only. Microscopic solitary polyp known mostly from Europe, with occasional sightings elsewhere including Puget Sound (1950s—see Wieser 1958, Pac. Sci. 12: 106–108; 1970s and 2005, C. E. Mills and E. N. Kozloff unpublished observations). This tentacleless hydroid (see plate 49R, 49S) is less than 1 mm in length and occurs in organically rich, sandy mud or mats of algae in brackish water and feeds on nematodes, harpacticoid copepods, and ostracodes. It is likely to be found elsewhere on the Pacific coast as interstitial meiofauna in the low intertidal, a community that has rarely been closely investigated in our region.

TUBULARIIDAE

Hybocodon prolifer L. Agassiz, 1862. Hydroid and medusa. Synonyms in Schuchert (1996, p. 113). Hydroid with stolons often buried in sponges. Hydranths pink. Although solitary, several polyps may occur together; branched hydrocauli observed under cultivation (Petersen 1990; Schuchert 1996). Medusae with asymmetrical umbrella produce additional medusae from the one well-developed tentacle bulb; the same individuals later reproduce sexually, at which time eggs develop into actinulae, still attached to the manubrium. Medusa incorrectly recorded as *"Sarsia prolifer"* in Yaquina Bay (McCormick 1969a, b).

Pinauay crocea (L. Agassiz, 1862) (=*Ectopleura crocea*, =*Tubularia crocea*). Hydroid. Additional synonyms in Schuchert (1996, p. 107), genus *Pinauay* proposed by Marques and Migotto 2001, Pap. Avulsos Zool. (São Paulo) 41(25): 465–488, leading to the sequential (as it passed through *Ectopleura*) demise of one of the most well-known names (*Tubularia crocea*) in the hydroid and fouling literature. *Pinauay,* which means "water palm tree" in the pre-Columbian Tupi language of Brazil (because this hydroid, like the other "Tubularias," looks like a palm tree underwater), is pronounced "pin-áw-wa-i." A primary fouling species with a wide distribution, mainly in estuaries (Torrey 1902; Petersen 1990). Colonies forming conspicuous clusters on pilings and floats in bays and harbors. Gulf of Alaska to southern California, low tide to 40 m (Fraser 1937; Haderlie et al. 1980—see color photograph 3.3, p. 14). Introduced on ship bottoms from the North Atlantic.

Pinauay marina (Torrey, 1902) (=*Ectopleura marina,* =*Tubularia marina*). Hydroid. Colonies on the lee side of rocks exposed to breakers on the open seacoast; active during winter (Haderlie *et al*. 1980—see color photograph 3.2, plate 14). More delicate and sparse than *P. crocea*. British Columbia to California, lower intertidal to 37 m (Torrey 1902; Fraser 1937; Petersen 1990).

Tubularia harrimani Nutting, 1901. Hydroid. Characterized by having well-developed tentacles on the gonophores. Alaska to Monterey Bay (Fraser 1937). Sometimes found at Pescadero Point, on Monterey Peninsula before 1954 (Light et al. 1954, p. 32); present status in our area unknown.

ZANCLEIDAE

Zanclea bomala Boero, Bouillon and Gravili, 2000. Hydroid and medusa. Hydroid on unidentified bryozoan, with reticulate hydrorhiza growing under the bryozoan skeleton. Medusae released with two tentacles, but mature with four tentacles. Bodega Harbor, shallow water. See Boero et al. 2000, Italian J. Zool. 67: 93–124. There are scattered records of *Z. costata* Gegenbauer, 1856 in central California, including Rees (1975), who reports collecting a *"Z. costata"* medusa in a plankton tow in Bodega Harbor and also a zancleid polyp on floating docks in Bodega Harbor on a *Membranipora* colony, and a note from Ralph Smith that *Z. costata* is found "on pink bryozoa under boulders, Schuster's Rock (Doran Beach). In their zancleid review, Boero et al. caution that *Z. costata* is known with certainty only from the Mediterranean and that all other records must be confirmed by a study of the cnidocysts. Since two zancleids have now been described from Bodega Harbor, both associated with bryozoans, we remove *Z. costata* from our species list until such time as its presence on the West Coast is verified. Young *Z. bomala* medusae are nearly identical to those of *Z. costata*.

Zanclella bryozoophila Boero and Hewitt, 1992. Hydroid and medusa. Originally in *Zanclella*, synonymized with *Zanclea* (Schuchert 1996, p. 93), separated out again by Boero et al. (2000—see entry above). Hydroid epizoic on the bryozoan *Schizoporella* in shallow subtidal and protected by the bryozoan surface. Believed to feed on material gathered by the bryozoan lophophore. Diet microphagous, with hypostome and tentacles causing no retraction of the host's lophophores. Medusae, released with mature gonads, live only a few hours, sometimes spawning without actually being released from parent hydroid. Known only from the north jetty of Bodega Harbor. See Boero and Hewitt 1992, Can. J. Zool. 70: 1645–1651.

HYDROZOA SUBCLASS LEPTOTHECATA (also known as LEPTOMEDUSAE and THECATA)

ORDER CONICA

AEQUOREIDAE

There seem to be at least two species of *Aequorea* on the West Coast of North America; a variety of names are available, and final identification awaits molecular genetic studies. The name *Aequorea victoria* (below) was assigned to the smaller, common, nearshore representative of the two obvious species by Arai and Brinckmann-Voss (1980), but this species, the source of both green-fluorescent protein (GFP) and aequorin, a bioluminescent protein, has also been called *A. aequorea* and *A. forskalea* in the literature. A much larger species of *Aequorea* is more oceanic off Washington, Oregon, and California, but nearshore in Alaska. These large offshore individuals in California, which occasionally make it to the coastline, seem to agree with *A. coerulescens* (below). They may or may not be the same as those in Alaska designated *A. aequorea* var. *albida* by Bigelow (1913, Proc. U.S. Natl. Mus. 44: 1–119).

Aequorea ?coerulescens (Brandt, 1835). Medusa (hydroid unknown). Very large *Aequorea* with large numbers of radial canals occasionally occur along the West Coast; these seem to be referable to this species, which was originally described from the open ocean 35°N, 144°W. This name is also used for some *Aequorea* medusae in Japan.

Aequorea victoria (Murbach and Shearer, 1902). Hydroid and medusa. Hydroid known mostly from lab culture (Strong 1925, Publ. Puget Sound Biol. Station 3: 383–399), where it grows easily. Medusae from Alaska to California, less abundant off Oregon and California than in Alaska, British Columbia, and Washington. This medusa was the source of the now laboratory-produced luminescent and fluorescent proteins aequorin and GFP. The taxonomy of this species remains confusing: *A victoria* may or may not be conspecific with *A. aequorea* (Forsskål 1775) and/or *A. forskalea* Péron and Lesueur, 1809 (see http://faculty.washington.edu/cemills/Aequorea.html). For medusa feeding behavior and diet, see Costello and Colin (2002). Color photograph in Wrobel and Mills 1998 and 2003, p. 32.

AGLAOPHENIIDAE

Aglaophenia inconspicua Torrey, 1904. Hydroid. Colonies small (35–40 mm), delicate, on algae. A southern species occuring as far north as Oregon, 0–154 m (Fraser 1937, 1946).

**Aglaophenia latirostris* Nutting, 1900. Hydroid (see hydroid plate 44E, 44F). Common on rocks and large red and brown algae from the low intertidal to 35 m, this species shares the common name "ostrich plume hydroid" with *A. stuthionides*. These robust hydroids are frequently seen cast ashore on beaches after storms. *A. latirostris* may have prominent reproductive structures called corbulae, containing the reduced meduoids (see color photograph in Haderlie et al. 1980, 3.15, plate 18); if ripe, these will produce planulae readily when left in the sun for approximately an hour (Light et al. 1954, p. 33). Fraser (1937, 1948) recorded it from San Pedro, Santa Barbara, and San Francisco Bay, with an overall range from British Columbia to Central America,

Aglaophenia struthionides (Murray, 1860). Hydroid. Synonyms in Fraser (1937, p. 180). This is a large (about 6.5 cm), conspicuous species in the lower intertidal and shallow subtidal, sometimes known as the "ostrich plume hydroid," a common name that it shares with *A. latirostris*. Exposed rocky shores. Alaska to southern California, low tide to 160 m (Fraser 1937, 1946). Haderlie et al. 1980 note that the nudibranch *Dendronotus subramosus* "often occurs on and closely resembles this hydroid in appearance"; see also color photograph 3.14, plate 18 (Haderlie et al. 1980).

**Aglaophenia epizoica* Fraser, 1948. Hydroid. A subtidal species, with large colonies (20 cm or more) and long corbulae. Abundant in the Channel Islands region (see Fraser 1948). A wealth of material of this species exists in collections from Allan Hancock Pacific Expeditions at the Santa Barbara Museum of Natural History. Santa Barbara to Baja California, 15–150 m.

**Aglaophenia* spp. Hydroid. Several other species of this genus have been reported from our region. See Fraser (1937, 1948) for records, and Cairns et al. (2002) for names.

BLACKFORDIIDAE

Blackfordia virginica Mayer, 1910. Hydroid and medusa. Hydroid colonies tiny (0.5 mm tall), in brackish waters; on introduced Atlantic barnacle *Amphibalanus improvisus,* attached to floats in rivers and sloughs feeding into San Francisco Bay. Medusae collected in tributaries to San Francisco Bay and Coos Bay (Mills and Rees 2000). Introduced, original provenance perhaps Ponto-Caspian; earliest collections on the West Coast are of medusae in the Napa and Petaluma Rivers in 1970 and 1974 (as *"Phialidium,"* which they closely resemble).

CALYCELLIDAE

Calycella syringa (Linnaeus, 1767). Hydroid. Synonyms in Cornelius (1995a, p. 186). A stolonal epibiont on stems of other hydroids (e.g., *Tubularia*, *Hydrallmania*, *Lafoea*), as well as algae and similar substrates (Hochberg and Ljubenkov 1998). Tolerant of brackish water (Cornelius 1995a). Alaska to Baja California, intertidal to 300 m (Fraser 1937, 1946; Hochberg and Ljubenkov 1998). [*Calicella* Hincks, 1861 is not the same as *Calycella* Hincks, 1864, but it is instead a junior synonym of *Lafoea* Lamouroux, 1821; the specific name *syringa* has occasionally been combined with the genus *Calicella* in error.]

* = Not in key.

EIRENIDAE

Eirene mollis Torrey, 1909. Medusa (hydroid unknown). This West Coast species is rarely reported, possibly because it is easily overlooked among the similar, but much more abundant *Eutonina indicans* (as noted by Arai and Brinckmann-Voss, 1980). Its range is at least British Columbia to San Diego.

Eutonina indicans (Romanes, 1876). Hydroid and medusa. North Pacific and North Atlantic; Bodega Harbor, on *Zostera*, crabs, and rocks, shallow water (see Rees 1978, Wasmann J. Biol. 36: 201–209). Operculum sometimes shed in older colonies (Cornelius 1995a). Medusae abundant in summer plankton and may litter ocean beaches where the gelatinous peduncle shows up as a colorless, nipplelike piece of jelly. Color photograph in Wrobel and Mills 1998 and 2003, p. 33. It seems possible that the rarely reported *Eutimalphes brownei* medusa of Torrey (1909) (collected at that time in substantial numbers in San Diego Bay) is a junior synonym of *E. indicans*.

HALECIIDAE

Halecium spp. Hydroid. Several species of this diverse and difficult genus, including *Halecium annulatum* Torrey, 1902, *H. corrugatum* Nutting, 1899, and *H. kofoidi* Torrey, 1902 have been reported from our area. Identification is difficult or impossible unless gonophores are present. See Fraser (1937, 1946) for accounts, and Cairns et al. (2002) for nomenclature.

HALOPTERIDIDAE

Antennella avalonia Torrey, 1902. Hydroid. Synonyms in Schuchert (1997 [see below], p. 18). This species is considered to be of doubtful validity; possibly conspecific with the more cosmopolitan *A. secundaria* (Gmelin, 1791) by Schuchert (1997, Zool. Verh. Leiden 309: 1–162), but could also be a California regional species. Santa Catalina Island and southward, 4–64 m (Fraser 1937, 1946).

Monostaechas quadridens (McCrady, 1859). Hydroid. Synonyms in Hirohito (1995, pp. 249, 251) and Schuchert (1997, p. 130). A warm-water species, sometimes epizoic on other hydroids. San Francisco Bay and southward, 5–84 m (Fraser 1946, 1948).

KIRCHENPAUERIIDAE

Kirchenpaueria plumularioides (Clark, 1877) (=*Plumularia plumularioides*). Hydroid. Specific name misspelled *plumularoides* in Fraser (1937, 1946). Small colonies (30 mm), growing in clusters, lacking lateral nematothecae. Bering Sea to San Diego, intertidal to 46 m (Fraser 1946).

LAFOEIDAE

**Filellum serpens* (Hassall, 1848). Hydroid. Alaska to San Diego, from low tide to160 m (Fraser 1937); also reported from the Atlantic and Arctic Oceans (Cairns *et al.* 2002).

**Lafoea dumosa* (Fleming, 1820). Hydroid. Alaska to San Pedro, from low tide to 110 m (Fraser 1937); also reported from the Atlantic and Arctic Oceans (Cairns et al. 2002).

LAODICEIDAE

Laodicea sp. Hydroid and medusa. Occasional medusae referable to the genus *Laodicea* have been collected in our area (Rees 1975, p. 2523b). Their specific identification is not known; the polyp of *L. undulata* is shown in Russell (1953, p. 238).

Ptychogena californica Torrey, 1909. Medusa (hydroid unknown). San Diego to the Bering Sea; possibly a young stage of *P. lactea* (see Arai and Brinckmann-Voss 1980, p. 83).

Ptychogena lactea A. Agassiz, 1865. Hydroid and medusa. San Diego to the Bering Sea, Arctic. Naumov (1969, p. 322) ascribes a deep water hydroid (250–520 m) to this species because they have the same general distribution. Color photograph in Wrobel and Mills, 1998 and 2003, p. 33.

* = Not in key.

LOVENELLIDAE

Eucheilota bakeri (Torrey, 1904) (=*Clytia bakeri*). Hydroid and medusa. Hydroid with stalks to 12 cm tall, epizoic on live gastropod and bivalve shells on sandy beaches, lower intertidal to subtidal; the small medusae sometimes abundant in near-shore plankton, San Francisco to Baja California, surf zone to more than 70 m (Fraser 1937; Haderlie et al. 1980, see color photograph of hydroid 3.9, p16, as *Clytia bakeri*).

MELICERTIDAE

Melicertum octocostatum (M. Sars, 1835). Hydroid and medusa. North boreal circumpolar nearshore species occasionally collected as medusae as far south as central Oregon. Further studies may restore the similar West Coast species *M. georgicum* A. Agassiz, 1862, which has been given junior synonym status by recent authors (Brinckmann-Voss and Arai 1980). Color photograph in Wrobel and Mills 1998 and 2003, p. 33. Hydroid described in Russell (1953, p. 250), but not yet collected on West Coast.

MITROCOMIDAE

Foersteria purpurea (Foerster, 1923). Medusa (hydroid unknown). Rare, possibly deep-water species, known only from British Columbia, where it occurs just off the bottom, and central California, where it has occasionally been found at the surface in Monterey Bay. Color photograph in Wrobel and Mills 1998 and 2003, p. 34.

Mitrocoma cellularia (A. Agassiz, 1865). Hydroid and medusa. The hydroid has been raised in the laboratory (Widmer 2004), but is not known from the field; it resembles those assigned to the catch-all genus *Cuspidella*. The medusae are found from the Bering Sea to southern California, from near shore to deep water (see Raskoff 2000, Scientia Marina, 64 [Suppl. 1]: 151–155); for feeding behavior and diet see Costello and Colin (2002). Color photograph in Wrobel and Mills 1998 and 2003, p. 34.

PHIALELLIDAE

Phialella fragilis (Uchida, 1938). Hydroid and medusa. Hydroid on mussels (*Mytilus*) on floating docks, with colonies best developed near edge of the shell beside the inhalant and exhalant currents. Occasionally on the same shells as *P. zappai* and having similar ecological requirements. Medusa to 10 mm. Rarely collected; known only from Japan and Bodega Harbor (Boero 1987). Possibly introduced.

Phialella zappai Boero, 1987. Hydroid and medusa; *Phialella* sp. in Boero (1987) and *Phialella* n. sp. in Rees (1975) are *P. zappai* (F. Boero pers. comm.). Hydroid on mussels (*Mytilus*) on floating docks and difficult to distinguish from *P. fragilis* without 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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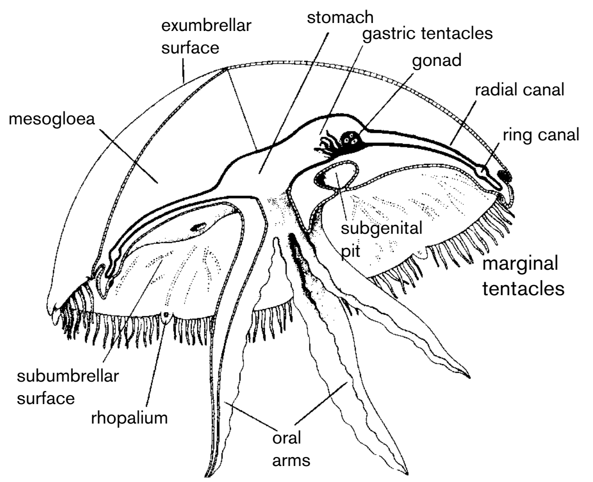


PLATE 61 Scyphozoa. Scyphomedusan structure, diagrammatic (modified after Naumov from Bayer and Owre, *The Free-Living Lower Invertebrates*, 1968; used with permission of The MacMillan Company).

Scyphozoa: Scyphomedusae, Stauromedusae, and Cubomedusae

CLAUDIA E. MILLS AND RONALD J. LARSON

(Plates 61–63)

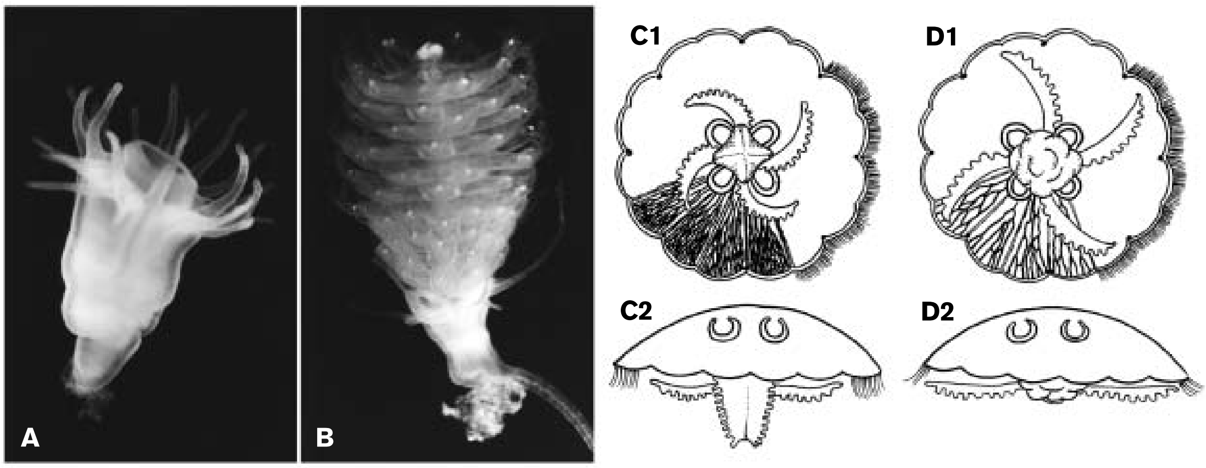
The relatedness of the 200 worldwide species of scyphozoan jellyfish (Mianzan and Cornelius 1999) known as semaeostome medusae, rhizostome medusae, coronate medusae, stauromedusae, and cubomedusae remains unclear (Dawson 2004b, Marques and Collins 2004). Here we use the names for the three jellyfish 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, 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.



Aurelia labiata
scyphistoma

Aurelia labiata
strobilating polyp

Aurelia labiata

Aurelia sp.1

PLATE 62 *Aurelia* spp. A, *Aurelia labiata*. scyphistoma; B, *Aurelia labiata*. strobilating polyp; C1, C2, *Aurelia labiata* (oral and side views); D1, D2, *Aurelia* sp. 1 (oral and side views) (all images by Claudia E. Mills).

Many of the medusae discussed in this section are large and awkward to study whole under a microscope. Preservation for morphological purposes should be done in 5% to 10% percent buffered formalin; specimens or portions of specimens for molecular studies should be preserved in >70% ethanol and stored in a refrigerator or freezer (Dawson 2004b).

Beautiful color images of most of the scyphomedusae in this key can be found on the Internet. See especially http:// jellieszone.com/scyphomedusae.htm and http://divebums.com/main.html for particularly nice photographs taken mostly in California. Caution must be exercised in the accuracy of web identifications of some of the species; use keys such as this one for the authoritative name for a species.

Families used in the species list are from Cairns et al. (2002).

Glossary of Scyphozoa

ABORAL the side of the jellyfish opposite to that on which the mouth opens (the upper surface of the bell in pelagic species).

CALYX the flaring bell-like portion of a stauromedusa, containing the gonads, central manubrium and marginal tentacle clusters.

CNIDOCYST (=**NEMATOCYST**) stinging organelle characteristic of the Cnidaria, consisting of a double-walled capsule containing fluid and a long tubule that everts and straightens when the capsule discharges upon stimulation; used for prey capture, defense and attachment (also inaccurately called "stinging cell").

CNIDOCYST VESICLES round, white, cnidocyst-filled structures visible through the calyx wall of some species of stauromedusae.

EXUMBRELLA the outer, aboral, surface of a jellyfish "bell."

GONADIAL SACS the many round structures that fill the gonads of stauromedusae (also called "genital sacs," "vesicles," or "follicles").

LAPPET one of the lobes separated by clefts at the margin of a pelagic scyphomedusa.

MANUBRIUM central stomach structure that attaches to the center of the subumbrella.

MARGINAL ANCHOR marginal structure between tentacle clusters in some species of stauromedusae; lacking any special sensory capabilities, these are morphologically merely reduced tentacles (sometimes called "rhopalioids").

ORAL the side of the jellyfish to which the mouth opens.

ORAL ARM feeding and prey capture structure attached to the manubrium and surrounding the mouth. On a scyphomedusa, there are nearly always several (usually four in semaeostome and eight in rhizostome medusae) oral arms surrounding the mouth; they may be simple or frilly and membranaceous, or very complicated and fleshy; digestion often begins while prey are still within the oral arms.

PLANULA (plural planulae) microscopic, egg-shaped or subcylindrical larva that develops from a cnidarian egg.

RADIAL CANALS circulatory canals on the subumbrellar surface of a jellyfish emanating from the mouth toward the bell margin; these may be simple or may branch one or more times.

RHOPALIUM (plural rhopalia) one of the numerous marginal sense organs in clefts between lappets at the margin of a scyphozoan bell. Rhopalia usually have a gravity receptor (statocyst) and one or more "eyes" (ocelli). Cubomedusae are very sensitive to light and have multiple eyes, some with large lenses, on each rhopalium.

SCYPHISTOMA the asexual benthic (bottom-living) polyp stage of semaeostome and rhizostome scyphomedusae. These are often capable of reproduction by fission or pedal laceration and also metamorphose so as to produce stacks of tiny jellyfish (ephyrae) that break loose one by one (a process known as strobilation) and mature in the plankton, usually over several months.

STALK elongate portion at the aboral end of a stauromedusa, with which it attaches to rock, eelgrass, or seaweed.

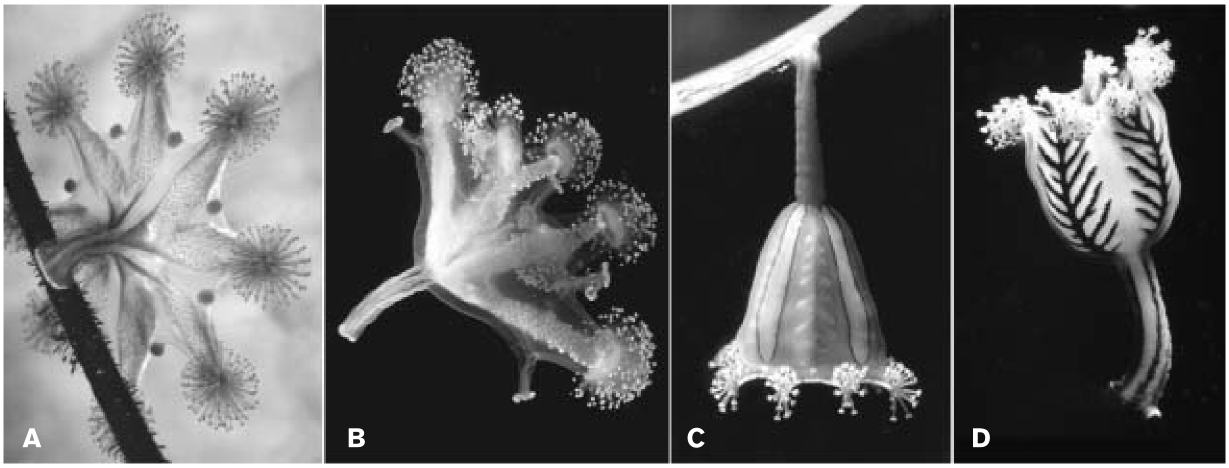
STROBILATION asexual process in which a semaeostome scyphistoma absorbs its tentacles and produces instead a stack of developing jellyfish by transverse fission (the parent polyp and the resulting jellyfish are all the same sex, either male or female, and thus are clones). The base of the polyp remains attached to the substratum and grows new tentacles when strobilation is complete.

SUBUMBRELLA the inner, or underneath, surface of a jellyfish "bell".

VERMIFORM wormlike.

Key to the Scyphomedusae, including the attached Stauromedusae

1. Free-swimming bell-like forms, usually greater than 1 cm . . . . Semaeostomeae 2
— Small, inconspicuous, attached medusoid forms having a stalk and calyx with eight marginal clusters of short, knobbed tentacles. . . . . Stauromedusae 8
2. With 24 or fewer marginal tentacles 3
— With more than 24 tentacles, too numerous to easily count 5
3. With eight marginal tentacles alternating with eight rhopalia; color magenta, brown, and blue, combining to form a striking deep purple pattern on the pale whitish exumbrella composed of an apical ring and 16 radiating streaks . . . . *Chrysaora colorata*
— With 24 marginal tentacles, alternating in groups of three with eight rhopalia 4
4. Basic color of the exumbrella dark amber, darkest near the margin, sometimes with a fainter radiating starlike pattern; oral arms strongly spiraled in a screwlike manner; subumbrella without 16 radiating dark streaks. . . . . *Chrysaora fuscescens*
— Basic color of the exumbrella whitish and pale, with 16 dark brownish streaks radiating outward from a broad central ring; between the 16 steaks are usually found 32 dark crescents of pigment near the margin; oral arms twisted, but not in a tight spiral; subumbrella pale with 16 radiating dark streaks . . . . *Chrysaora melanaster*
5. Bell opaque whitish, although sometimes infused with pink, lavender, tan, or yellow; four horseshoe-shaped gonads visible from the exumbrellar side; tentacles originating at the bell margin and very small and numerous; four moderately frilly, mostly transparent, oral arms 6
— Bell mostly pigmented in tones of brown, red, or yellow; tentacles originating from the subumbrellar surface; oral arms extensively frilly, complicated, and prominent. 7
6. Bell margin scalloped into 16 lobes, separated into pairs by eight rhopalia; with a large conical manubrium that is one fifth to nearly one half as long as the bell is wide, at the center of the subumbrella, with oral arms attached to this structure; the oral arms each about two thirds to three quarters as long as the bell radius, frequently bent in a counterclockwise direction, or straight; radial canals numerous and many times branched in larger specimens; lavender or white planula larvae brooded on the manubrium in females (plate 62C) . . . . *Aurelia labiata*
— Bell margin scalloped into 16 lobes, separated into pairs by eight rhopalia; with a short rounded manubrium that is less than one sixth the bell diameter, at the center of the subumbrella with oral arms attached to this structure; the oral arms each about four fifths to nine tenths as long as the bell radius, straight; radial canals moderately numerous and branched; white, ochre, or orange planula larvae brooded on the manubrium in females (plate 62D) . . . . *Aurelia* sp. 1
7. With eight rhopalia; with eight clusters of up to 150 tentacles each, arranged in up to four rows originating from deep under the bell in U-shaped bases that are evident from the top of the bell; color usually yellowish-brown to reddish-brown to brick red; bell to about 1 m diameter, but usually much less . . . . *Cyanea capillata*
— With 16 rhopalia; with 16 linear groups of up to 25 tentacles each in a single row that originate on the subumbrella just inside of the bell margin; the umbrella is usually transparent to milky white, with a bright egg-yolk-yellow center; bell to about 60 cm diameter. . . . . *Phacellophora camtschatica*
8. Animal goblet-shaped, like glass stemware, with flared calyx of approximately equal length to stem; up to 4 cm long 9
— Animal mostly tubular; calyx flaring near the apex, stalk flaring near the base; up to 2 cm long (rare and inconspicuous) 13
9. Calyx broader than it is tall, widely open like a martini glass, with eight well-developed, equally spaced, marginal arms or lobes, each with a terminal cluster of up to 250 knobbed tentacles; tentacles all alike and without cushionlike swellings at their bases 10
— Calyx longer than it is broad, more or less wine glass-shaped, with eight poorly developed arms or lobes, each with a terminal cluster of up to 30 tentacles; the outermost tentacles in each cluster with cushionlike swellings at their bases. 11
10. Eight prominent coffee bean–shaped marginal anchors alternate with eight arms terminating in clusters of up to 130 tentacles; gonads extend the full length of each arm, each with 200–300 gonadial sacs, irregularly, but tightly packed, with as many as 10–22 abreast in the broadest part of each gonad; with a few white cnidocyst vesicles lined up adjacent to each gonad out near the tip of each arm; color variable in shades of green, brown, olive, yellow, orange, pink, purple; found in protected or semi-exposed waters (plate 63A) . . . . *Haliclystus* sp. (undescribed species)
— Eight elongate, trumpet-shaped marginal anchors alternate with eight arms terminating in clusters of up to 250 tentacles; gonads extend the full length of each arm, each with 80–120 gonadial sacs, irregularly packed, with two to eight (usually four to six) abreast in the broadest part of each gonad; with a few white cnidocyst vesicles irregularly arranged along the outer edges of each gonad, especially on the distal half; color usually golden brown or tan, occasionally greenish; found in protected bays (plate 63B) . . . . *Haliclystus salpinx*
11. Stalk gradually flaring into the calyx as in a trumpet or distinctly demarcated like a goblet; with eight marginal clusters of 15–25 tentacles and with single row of white cnidocyst vesicles along the margin between the tentacle clusters; overall color usually green to yellow-green or red, with four distinctive, linear paler "windows" on the exumbrella; found in protected waters (plate 63C). . . . . *Manania handi*
— Stalk distinctly demarcated from the calyx as in a goblet; with eight marginal clusters of 15–30 tentacles; color usually cream to tan or some shade of red, but without the distinctive four linear stripes on the exumbrella; found on the open coast in areas of considerable wave action. 12
12. Calyx and stalk usually dark red, but varying from tan to



Haliclystus sp. (*"sanjuanensis"*) | *Haliclystus salpinx* | *Manania handi* | *Manania distincta*

PLATE 63 Stauromedusae. A, *Haliclystus* sp. *"sanjuanensis"*; B, *Haliclystus salpinx*; C, *Manania handi*; D, *Manania distincta* (photographs A–C by Claudia E. Mills; photograph D by Ronald J. Larson).

magenta, with eight marginal clusters of 15–30 tentacles and with distinctive, contrasting patches of white subumbrellar cnidocyst vesicles between the pairs of tentacle clusters . . . . *Manania gwilliami*

— Calyx and stalk usually light tan to cream in color, with up to 26 tentacles in each of eight marginal clusters; with a distinctive dark brown herringbone pattern on the calyx that extends down the stalk as four dark lines (plate 63D) . . . . *Manania distincta*

13. Vermiform, with small flared calyx and flared base; with eight groups of about 25 tentacles alternating with eight small single tentacles; color purple with small white spots . . . . *Kyopoda lamberti*

— Vermiform, with a long tubular calyx demarcated by a constriction from a very short flared stalk; with eight groups of eight to 12 tentacles alternating with four rudimentary solid structures at the calyx margin; color greenish-brown with minute white flecks . . . . Undescribed genus and species ("*Stenoscyphopsis vermiformis*" of Gwilliam 1956)

List of Species

CUBOMEDUSAE

CARYBDEIDAE

**Carybdea* sp. The only cubomedusa (box jelly) known from the West Coast of North America, can be common during autumn in the surf zone just inside the kelp beds at Santa Barbara. This medusa, bell to 4 cm tall, has also been collected at Redondo Beach, Malibu, and La Jolla, all in Southern California. Previously known in the West Coast literature as the Western Pacific *C. rastoni* Haacke, 1886, and the Atlantic *C. marsupialis* (Linnaeus 1778), ours is an undescribed species (L. Gershwin personal communication 2005, based on specimens collected at Redondo Beach). See Larson and Arneson, 1990; color photograph in Wrobel and Mills 1998 and 2003, p. 48.

* = Not in key.

STAUROMEDUSAE

DEPASTRIDAE

Manania distincta (Kishinouye, 1910). Northern Japan to Oregon, along the open coast in areas of wave action; to about 4 cm long. Very few specimens have been collected in the eastern Pacific (see Larson and Fautin 1989). Color photograph in Wrobel and Mills 1998 and 2003, p. 49.

Manania gwilliami Larson and Fautin, 1989. Vancouver Island and from northern California to Baja, California, this species probably occurs along the entire West Coast; to about 4 cm long. Attached to rocks and algae in surf-swept areas; very cryptic near coralline algae (so much so that the animal is essentially invisible when a color photograph is converted to black and white).

Manania handi Larson and Fautin, 1989. Known from Vancouver Island, Washington, and central California, attached to *Zostera* or algae in semiprotected subtidal habitats; to about 4 cm long. Often with *Haliclystus*; uncommon. Color photograph in Wrobel and Mills 1998 and 2003, p. 50.

KYOPODIIDAE

Kyopoda lamberti Larson, 1988. British Columbia and Southern California in the subtidal on cobble with, or nearby, crustose coralline algae in areas of wave surge. Extremely cryptic (to about 2 cm long), and thus probably occurs along much of the North American coast.

LUCERNARIIDAE

Haliclystus salpinx Clark, 1863. Known mostly from the North Atlantic, and on the Pacific coast from only from a small number of isolated bays in the San Juan Islands (Washington) and southern Vancouver Island, this boreal species, to about 3 cm, might be expected to be found elsewhere on the West Coast (unless it was introduced locally in early coastal exploration and shipping); its trumpet-shaped marginal anchors are distinctive.

Haliclystus sp. (=*H. "sanjuanensis," nomen nudum*). Hirano (1997), having studied *Haliclystus* from all over the world, concluded that West Coast material from at least British Columbia to California is an undescribed species (it had been previously called *H. auricula, H. octoradiatus, H. stejnegeri,* and *H. sanjuanensis*). It is the same as *H. "sanjuanensis,"* which is, however, an unpublished manuscript name (Gellerman 1926) and thus not available despite its occasional appearance in the literature (Guberlet 1936, 1949; Hyman 1940b). Look closely to distinguish the superficially similar *H. salpinx* (see above). Color photograph in Wrobel and Mills 1998 and 2003, p. 49.

**Haliclystus* sp. (=*H. "californiensis"* of Gwilliam 1956). This unpublished manuscript name (Gwilliam 1956) applies to a single specimen of about 2 cm, found by Paul Silva at 29 m, off Christy Cove on Santa Cruz Island. The species is distinct in having a very short stalk topped by a calyx that is wide open at the top, but very elongate, nearly tubular, at the base.

Undescribed genus and species (*"Stenoscyphopsis vermiformis"* of Gwilliam 1956). This unpublished manuscript name (Gwilliam 1956) applies to eight specimens, found only once in 1952, on *Macrocystis* off the Hopkins Marine Station in Pacific Grove. Gwilliam stated that this species (to about 1.5 cm long) was extremely cryptic, matching the color of the seaweed; he was unable to find it again.

SEMAEOSTOMEAE SCYPHOMEDUSAE

CYANEIDAE

Cyanea capillata (Linnaeus, 1758). The "lion's mane," especially abundant from Washington northward to the Bering Sea (and in the Atlantic) in the summer and fall, this cold-water species is less numerous off Oregon and only occasionally seen in northern California. Usually <50 cm in diameter. Color photograph in Wrobel and Mills 1998 and 2003, p. 54.

PELAGIIDAE

**Chrysaora achlyos* Martin, Gershwin, Burnett, Cargo, and Bloom, 1997. This species can be enormous, with oral arms extending as much as 6 m beyond the 1 m diameter bell; it has a dark purple, nearly black, umbrella and was seen along the coast of Southern California and Baja, California, in 1989, 1999, and 2005. Where it occurs most years (when it is not found off California) is not known.

Chrysaora colorata (Russell, 1964). Formerly known as *Pelagia colorata* (see Gershwin and Collins 2002) and often misidentified as *P. noctiluca* (see below a separate species of worldwide distribution, found usually south of California in the eastern Pacific). The apparently oceanic *C. colorata* reaches about 70 cm in diameter and regularly washes ashore on the beaches of Southern California and is occasionally found as far north as San Francisco Bay and Bodega Bay; most sightings are in the late spring. Color photograph in Wrobel and Mills 1998 and 2003, p. 54.

Chrysaora fuscescens Brandt, 1835. This is the common central California and Oregon species of *Chrysaora,* which may occur in shoals just offshore and stranded on beaches. It can be found from the Gulf of Alaska to Mexico and usually has up to about 30 cm bell diameter. There is much confusion in the literature about the name of this animal, which has frequently been referred to as *C. melanaster*, a separate species (see below). Other names used in the literature for this species include *C. helvola* Brandt, 1838 and *C. gilberti* Kishinouye, 1899, both junior synonyms of *C. fuscescens* (see Larson 1990; color photograph in Wrobel and Mills 1998 and 2003, p. 53).

Chrysaora melanaster Brandt, 1835. Although this name is frequently seen in the older California literature, it properly belongs to a more strongly patterned species (to 60 cm diameter) found commonly in Alaska and perhaps British Columbia and occasionally drifting to the south at least as far as Oregon, perhaps with rare sightings in California (see Larson 1990; color photograph of underside in Wrobel and Mills 1998 and 2003, p. 53).

**Pelagia noctiluca* (Forsskål, 1775). An oceanic warm water species of all seas most likely to be encountered south of the range of this book, distinguished by its 16 marginal lappets, with eight tentacles alternating with eight rhopalia around the margin, and conspicuous exumbrellar "warts." *P. noctiluca* is a small scyphomedusa, generally not exceeding 9 cm in diameter; color photograph in Wrobel and Mills 1998 and 2003, p. 54.

ULMARIDAE

**Aurelia aurita* (Linnaeus, 1758; occasionally as *Aurellia*). This species, which may reach 50 cm in diameter, is apparently endemic to the North Atlantic and Baltic (see Gershwin 2001 and Dawson 2003, 2004a). It is characterized by eight, rather than 16, marginal lobes and unbranched, rather than anastomosing, adradial canals. Despite the common use of this name in West Coast literature, *A. aurita* is not known from the American Pacific coast.

Aurelia labiata Chamisso and Eysenhardt, 1821. Originally described from the San Francisco area, this once largely forgotten name is the correct one for a Northeast Pacific endemic species (to about 40 cm diameter) that includes most of the *Aurelia* on the West Coast, from central California to Oregon, with a northern variant extending to Alaska which appears to be an evolutionarily distinct lineage (Gershwin 2001; Dawson and Jacobs 2001; Dawson 2003, 2004a). Some specimens in Alaska with brown marginal pigment correspond to another apparently valid species, *Aurelia limbata* Brandt, 1835. *Aurelia* typically occurs in large aggregations, rather than singly, although the mechanisms for keeping such aggregations together are unknown. Color photograph in Wrobel and Mills 1998 and 2003, p. 55.

Aurelia sp. 1 (of Dawson 2003, 2004a, b). *Aurelia* medusae in Southern California are morphologically different but of similar size to those further north (Gershwin 2001) and have been shown using molecular techniques (Dawson and Jacobs 2001; Dawson 2003, 2004a, b) to be a separate species of worldwide distribution, including Los Angeles to San Diego, Tokyo Bay, and northern Japan, Australia, Atlantic and Mediterranean coasts of France, and probably also in south San Francisco Bay. This species may have been widely distributed by ships. Color photograph in Wrobel and Mills 1998 and 2003, p. 55 (top).

Phacellophora camtschatica Brandt, 1835. Occurs in the Pacific from Kamchatka to Alaska to Chile, but is more common at higher latitudes; also known from the North and South Atlantic and Mediterranean. Occasionally seen in bays in California and Oregon; to about 60 cm bell diameter. Color photograph in Wrobel and Mills 1998 and 2003, p. 55.

* = Not in key.

RHIZOSTOMEAE SCYPHOMEDUSAE

MASTIGIIDAE

**Phyllorhiza punctata* von Lendenfeld, 1884. An introduced Indo-Pacific species known also from Hawaii, the western tropical Atlantic, and the Mediterranean, and occasionally seen in Southern California in San Diego Bay and Mission Bay (Larson and Arneson 1990); bell to about 50 cm diameter. Color photograph in Wrobel and Mills 1998 and 2003, p. 57.

RHIZOSTOMATIDAE

**Stomolophus meleagris* L. Agassiz, 1862. Coastal species of the warm Atlantic, Caribbean, and Gulf of Mexico; occasionally collected in the Pacific from Southern California and the Gulf of California to Ecuador; bell to about 20 cm diameter. Color photograph in Wrobel and Mills 1998 and 2003, p. 57.

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Anthozoa

DAPHNE G. FAUTIN AND CADET HAND

(Plates 64–68)

Anthozoa, the largest class of cnidarians, including the familiar sea anemones and corals, contains more than 6,000 species. The most diverse anthozoan fauna is in the coral-reef areas of tropical and subtropical seas, where representatives occur of some orders not found from central California to Oregon. Some tropical anthozoans are also much more massive than those on the shores of California and Oregon, but on some shores of the northeast Pacific, anthozoans dominate space, so animals of this class play a prominent role in the ecology of both tropical and temperate seas.

Unlike cnidarians of the other classes, anthozoans do not possess a medusa phase. Thus the anthozoan polyp reproduces sexually and, in most species, asexually as well. Gametes are derived from the endoderm and develop in the mesenteries. In most species, gametes are spawned through the mouth into the sea, where fertilization takes place and a planktonic planula larva develops. Ultimately, it metamorphoses and settles onto or into the substratum. Several species of local anemones, by contrast, brood their young. In *Epiactis ritteri,* for example,

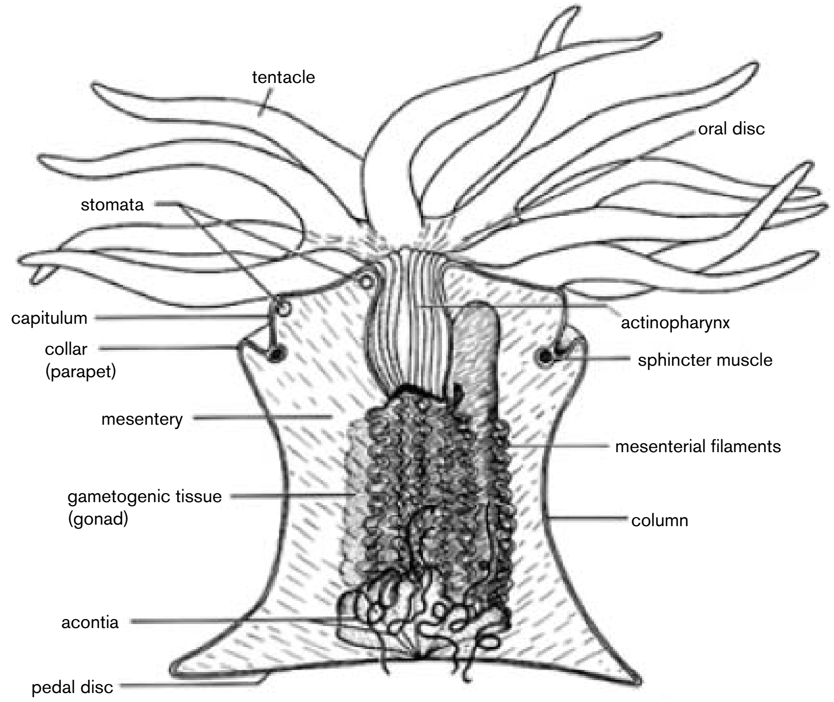


PLATE 64 Diagrammatic longitudinal section of a sea anemone (drawing by Emily Reid).

freely spawned sperm seem to find their way into the coelenteron of a female, where the eggs are fertilized and develop. The small anemones that are released settle down directly, without having passed through a dispersal stage. Likewise, in *E. prolifera,* development is direct, but the young develop attached to the outside of the parent's column and simply crawl off when mature. It appears that these sexually produced young are being budded, but *Epiactis,* like most anemones, does not reproduce asexually, to the best of our knowledge.

Among the local sea anemones that undergo asexual reproduction are *Diadumene lineata* and *Metridium senile*. In the process known as "pedal laceration," little bits rip from the edge of the pedal disc of an individual of *M. senile* as it remains in one spot or as it glides along the substratum, a daughter anemone developing from each bit of tissue. Thus dense clones of the animals develop, with the original individual encircled or trailed by its genetically identical progeny. Clones are also characteristic of *Anthopleura elegantissima,* which propagates asexually by longitudinal binary fission (as does *D. lineata*), and of *Nematostella vectensis*, which propagates asexually by transverse binary fission.

Most local anthozoans belong to the subclass Hexacorallia (or Zoantharia). Hexacorallians are characterized by simple or branched hollow tentacles that are typically numerous, often a multiple of six in number. Sea anemones, members of the hexacorallian order Actiniaria, are the most diverse intertidal anthozoans in Central California. All sea anemones are solitary (although they may be clonal), whereas at least some members of most other orders are colonial (that is, clonemates are physically attached to one another). Another difference between sea anemones and hexacorallians of most other orders is that anemones lack skeletons.

Plate 64 illustrates the anatomy of a typical sea anemone. Its form is that of an animal attached by its base; *Flosmaris grandis* (plate 66) illustrates a typical burrowing anemone. At the basal end of the body column is the pedal disc, the site of attachment of the polyp to the substratum, or, in most burrowing anemones, the bulbous physa. In species in which the column is divisible into regions that differ morphologically, the scapus is just distal to (above) the physa or the pedal disc; the scapus is typically the longest region of the column. Distal to it is the scapulus and/or the capitulum. The column may have a collar (parapet) in its distal part and bear protuberances of various sorts; verrucae (Latin for warts) are present on many anemones of California and Oregon (plate 65). Hollow tentacles used in food capture and ingestion are arrayed in circlets and/or radial rows on the oral disc.

In anemones of some taxa, below the edge of the oral disc, at the top of the column, is a circle of small tentaclelike structures termed "marginal spherules"; when inflated, these are used in aggression (see, for example, Francis 1973b). The top of the column can be drawn over the tentacles through contraction of the circularly arrayed sphincter muscle. The slitlike form of the mouth, which is in the center of the oral disc, reflects the biradial symmetry of an anthozoan polyp. The long axis of the mouth is termed the "directive axis." The mouth leads into the actinopharynx (gullet), a tube of tissue that opens into the body space, the coelenteron.

The coelenteron is divided by numerous radially arrayed longitudinal sheets of tissue (mesenteries) that extend from the column wall and some of which attach at their opposite edge to the actinopharynx. (Mesenteries have also been called septa, a term that should be reserved for the calcareous partitions of scleractinian corals that are flanked and secreted by the mesenteries.) The edges of the mesenteries are thickened into mesenterial filaments, which bear gland cells that serve in digestion, and cilia that keep the fluids within the coelenteron moving. Gametes develop in some or all of the mesenteries. Extending from the lower edge of some mesenteries of certain taxa are threadlike structures, acontia. Acontia can be emitted though the mouth or through pores in the column wall (cinclides), presumably as a defense.

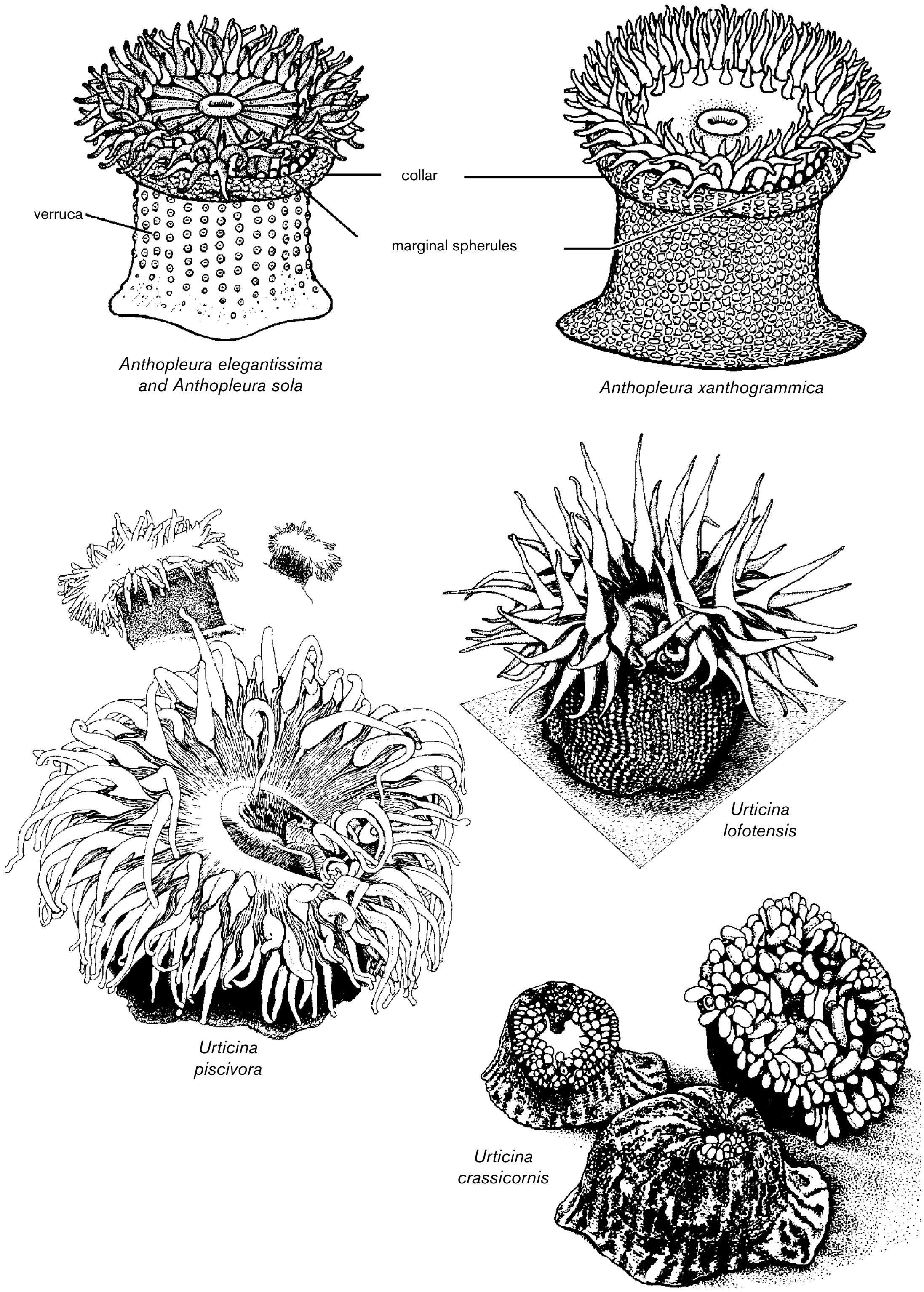


PLATE 65 Large sea anemones. Individuals of some species may exceed 500 mm in diameter, and most individuals of these species (except for *A. elegantissima*) reach 100 mm. All are members of family Actiniidae. Appearance of the species *Anthopleura elegantissima* and *A. sola* can be so similar they were long considered to belong to a single species. However, *A. elegantissima* is clonal whereas the larger *A. sola* is solitary. The two also differ in habitat. *Anthopleura xanthogrammica,* which can grow to a diameter of 500 mm, is typically somewhat smaller—about the same size as *A. sola,* with which it can be confused. These drawings are semidiagrammatic to emphasize the differences between them (Original drawings by Vicki B. Pearse, redrawn by Mildred Waltrip). Members of the genus *Urticina* are typically red in color. One of the largest anemones on this coast, *Urticina piscivora* has a column that is solid velvety-red and tentacles that are all either pink or white (Drawing by Steven Sechovec). The white verrucae and pigment spots of *U. lofotensis* may run together when the animal contracts, giving it a red-and-white-striped appearance (Drawing by Steven Sechovec). Some individuals of *Urticina crassicornis* are mottled with green, and the rare one may lack red altogether (drawing by Steven Sechovec).

SYMBIOTIC ALGAE

Daphne G. Fautin

Individuals of the sea anemones *Anthopleura elegantissima, A. sola,* and *A. xanthogrammica* typically posses zooxanthellae. These dinoflagellates live within cells of the endoderm, the inner cell layer of anemones. Several plant cells may live within one animal cell (Shick 1991). In *Anthopleura,* they are densest at the distal end and diminish in density proximally (that is, toward the base). Nearly all species of reef-forming corals are also zooxanthellate, as are giant clams, some foraminiferans, many species of tropical sea anemones, and some other tropical cnidarians. Outside the tropics and subtropics, some New Zealand anemones are also zooxanthellate (Buddemeier and Fautin 1996).

Zooxanthellae were once considered to belong to a single species, *Symbiodinium microadriaticum,* which was described from a tropical jellyfish. It is now known that there are many taxa of zooxanthellae and that there is not a simple 1:1 relationship between taxa of hosts and algal symbionts (e.g., Kinzie 1999). According to LaJeunesse and Trench (2000), some individuals of *A. elegantissima* in central and southern California possess simultaneously zooxanthellae of two species, *S. muscatinei* and *S. californium*.

A large proportion of the carbon fixed by the zooxanthellae through photosynthesis may be translocated to the animal, a process that was first demonstrated in *A. elegantissima* (see Muscatine and Hand 1958). Thus, although the host cnidarian cannot digest its symbiotic algae, it does benefit nutritionally from them. The symbiosis is mutualistic, the algae taking up products of the host's metabolism (Shick 1991). In a manner that is not understood, possession of zooxanthellae allows precipitation of massive calcium carbonate skeletons by reef-forming corals and giant clams (Gattuso et al. 1999). Calcification is also enhanced in zooxanthellate foraminiferans.

Individuals of *A. elegantissima, A. sola,* and *A. xanthogrammica* living in the dark, e.g., in caves (as in Oregon and Washington), under piers (as on the old Cannery Row of Monterey), or even under overhangs or deep in tide channels, lack symbiotic algae (Secord and Muller-Parker 2005). Such animals may be white rather than the typical green color; animals that live in dim light have low densities of zooxanthellae and most are intermediate in color. The green color, however, is not that of the algae, but is produced by the animals (Pearse 1974). The pigment functions to block potentially harmful radiation (Shick 1991).

Symbiotic algae affect not only the biochemistry but also the behavior of their host anemones. Individuals of *A. elegantissima* with zooxanthellae move toward light whereas those lacking them do not (Pearse 1974). Some tropical anemones possess outgrowths of their bodies in which zooxanthellae are concentrated and that extend during daylight and retract at night (Gladfelter 1975).

In addition to or instead of zooxanthellae, some individuals of *A. elegantissima* and *A. xanthogrammica* north of San Francisco possess unicellular symbiotic green algae, called zoochlorellae (Muscatine 1971, Lewis and Muller-Parker 2004). Anemones that contain mainly or only zoochlorellae tend to occur in places with lower light levels than those with mainly or only zooxanthellae (Secord and Augustine 2000). Zoochlorellae may live in the same cells as the zooxanthellae (Muller-Parker, personal communication). An individual zoochlorella cell photosynthesizes at a lower rate than an individual zooxanthella cell, and much more carbon is translocated to the anemones from zooxanthellae than from zoochlorellae (Verde and McCloskey 1996, Engebretson and Muller-Parker 1999).

Stress can disrupt the animal-alga symbiosis. Atypically high or low temperature, salinity, or sunlight, high UV insolation, or noxious chemicals can result in the break-down of the symbiosis. This phenomenon is termed "bleaching" because in corals it results in the normally brownish animal appearing white. The transparent tissue of the coral animal allows sunlight to reach the zooxanthellae, the color of which is usually perceived; when algae are absent, the white calcium carbonate skeleton is visible through the animal tissue. Bleaching is often explained as the host expelling the algae, but it is unclear whether that is happening or whether the dinoflagellates initiate the break-down in the symbiosis. Initiation probably varies with the stress and the species involved. Animals may reacquire zooxanthellae, so bleaching is not invariably lethal. In fact, a low level of algal loss appears to be normal (e.g., Fitt et al. 1997, 2000). Such "background bleaching" may be a mechanism of changing symbiotic partners (Buddemeier and Fautin 1994). *Anthopleura elegantissima, A. sola,* and *A. xanthogrammica* appear to be far less susceptible to bleaching than is typical of tropical animals. Moreover, individuals living in dark places appear not to suffer from their lack of symbiotic algae.

The flagellated, motile phase of the zooxanthella life cycle is poorly understood. Some species of cnidarians transmit the algae in their eggs (Fadlallah 1983), but others, such as *A. elegantissima* and *A. xanthogrammica,* do not (Siebert 1974), which obliges larval or juvenile animals to acquire their symbiotic algae from the environment (Schwarz et al. 2002), just as bleached animals presumably do. It is thought that algae may be concentrated in the feces of predators of anemones, such as nudibranchs (Muller Parker 1984), which thereby serve as vectors.

Members of most species of order Zoanthidea, also called Zoanthiniaria, propagate asexually, and the progeny remain tightly or loosely connected to one another. The tentacles of each polyp arise only at the margin. Grains of sand and other hard objects of similar size may be incorporated into the body wall. Zoanthids are mostly tropical; the lone local species, *Epizoanthus scotinus,* is subtidal in California and Oregon but may be intertidal in Washington.

Animals of order Corallimorpharia are commonly termed sea anemones but are actually more like scleractinian corals, except they lack a skeleton. Among the distinguishing features that can be seen in the lone local intertidal representative of this taxon, *Corynactis californica,* are the very large nematocysts (to more than 100 µm in length).

The stony corals, order Scleractinia, are represented in the local intertidal fauna by the solitary orange cup-coral, *Balanophyllia elegans*.

The tube anemones constitute order Ceriantharia. Almost exclusively subtidal, these animals have a ring of short tentacles immediately around the mouth and a ring of long tentacles at the margin of the oral disc. There are few cerianthid species in the world, and the only one locally is rarely found intertidally.

Members of the subclass Octocorallia (or Alcyonaria) are predominantly colonial, and each polyp has eight hollow tentacles that are pinnately branched.

Key to Subclasses of Anthozoa

1. Each polyp with eight, pinnately branched tentacles; polyps typically connected with one another in a colony . . . . . Subclass Octocorallia (Alcyonaria) (end of this section)
— Each polyp with simple (nonbranched) tentacles, which typically number more than eight . . . . Subclass Hexacorallia (Zoantharia), below

Key to Orders of Subclass Hexacorallia (Zoantharia)

1. Polyps solitary—not connected with one another, although they may be very near one another 2
— Polyps connected with one another at base; incorporated into body wall are grains of sand and similar material so animal feels rough; tentacles only at margin of polyp . . . . Order Zoanthidea (=Zoanthiniaria)

Note: Only species that may occur locally and intertidally is *Epizoanthus scotinus* (plate 67).

2. Polyp lives within hard, calcareous exoskeleton or soft, slimy tube 3
— Polyp naked, usually without external covering of any sort, although those of some species may have a cuticular sheath or adherent sand grains, etc. 4
3. Each polyp with two circlets of tentacles—long ones around the margin and short ones around the mouth; column burrowed into mud or sand, ensheathed in a tube . . . . Order Ceriantharia (“tube anemones”)

Note: Only local species that may occur intertidally is *Pachycerianthus fimbriatus*.

— Each polyp with a calcareous exoskeleton . . . . Order Scleractinia (“hard corals”)

Note: Only local intertidal species is the bright orange *Balanophyllia elegans*.

4. Tentacles capitate (knobbed at tip); polyps typically in dense groups, each group of similar color (e.g., orange, pink, lavender, red, brown, or white). . . . . Order Corallimorpharia

Note: Only local intertidal species is *Corynactis californica* (plate 66).

— Tentacles not capitate; polyps in groups or solitary . . . . Order Actiniaria (sea anemones, strictly defined) (below).

Key to Actiniaria

1. Base not attached to substratum or to buried shells or stones; slender, elongate column buried in soft sediments; only oral disc and tentacles protrude, so are the parts typically visible; tentacles 24 or fewer 2
— Base attached to substratum or solid object; 24 or more tentacles except in very young individuals 5

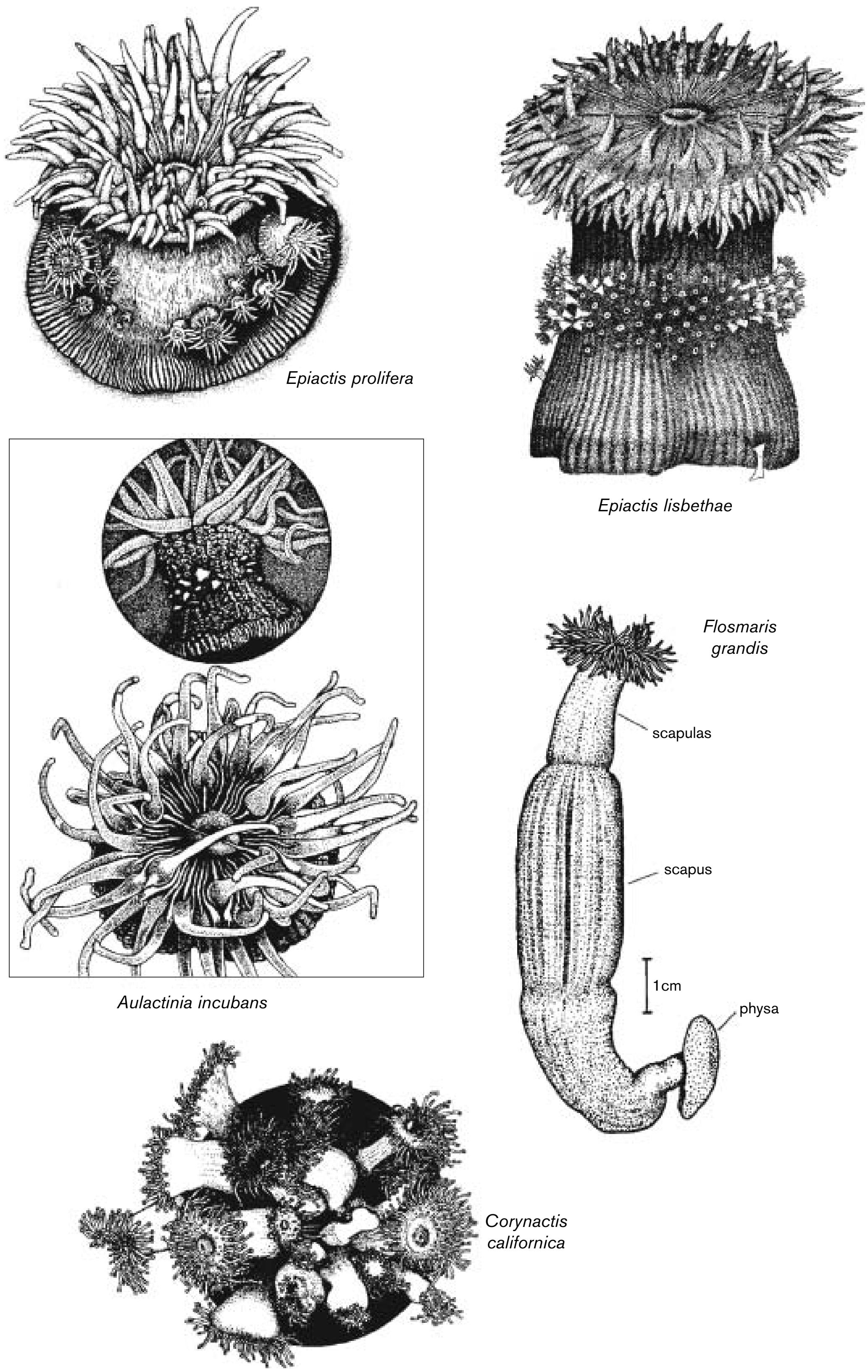
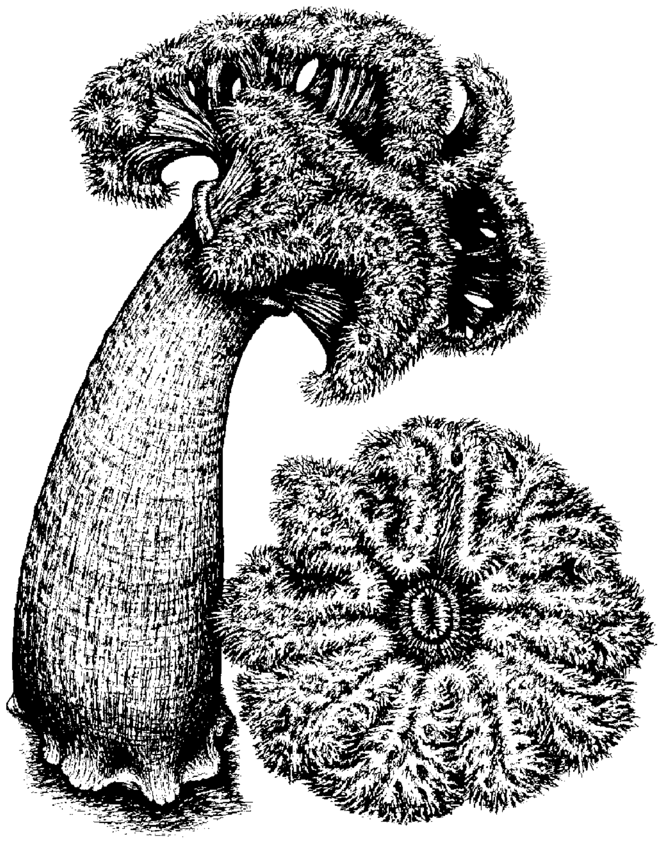
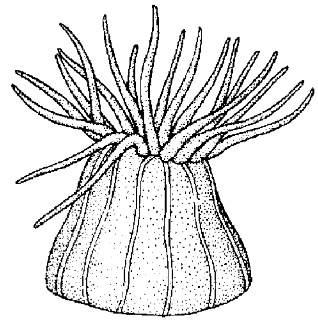


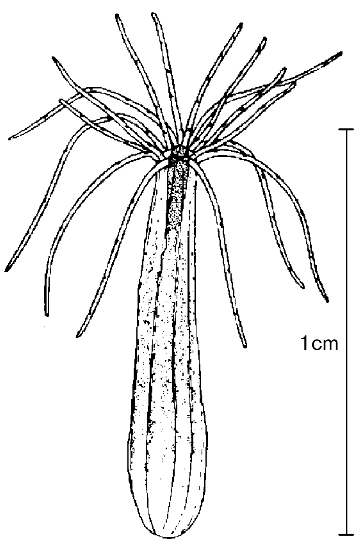
PLATE 66 Some smaller sea anemones. *Epiactis prolifera* rarely exceeds a basal diameter of 30 mm. Its externally brooded young are typically of various sizes (drawing by Steven Sechovec). *Epiactis lisbethae* grows to a maximum basal diameter of 80 mm. The tentacles of this specimen are contracted, but typically the tentacles droop down over the column. The young are all of similar size. The oral disc of *Aulactinia incubans* resembles that of *E. prolifera* and *E. lisbethae*, but the lines on its directive axis run into the mouth. The young of *A. incubans* are brooded internally. Individuals of this species are similar in size to those of *Epiactis* (drawing by Steven Sechovec). *Flosmaris grandis* is a large burrowing species. This drawing illustrates the divisions of the body typical of only some anemones (drawing from Hand and Bushnell 1967). *Corynactis californica* is not a true sea anemone—it is actually a coral without a skeleton. Individual polyps are about 10 mm in diameter (drawing by Steven Sechovec).



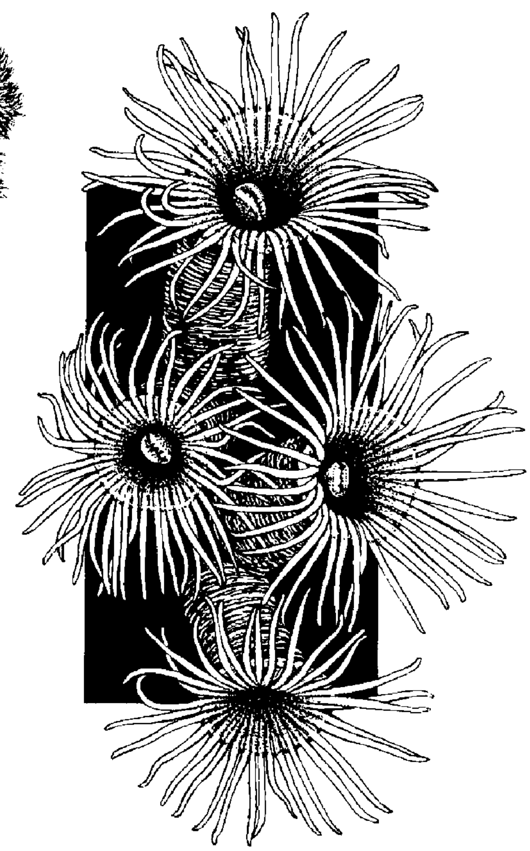
Metridium farcimen



Diadumene lineata



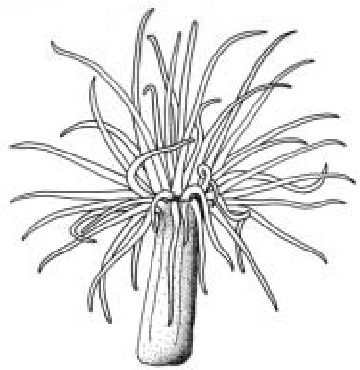
Nematostella vectensis



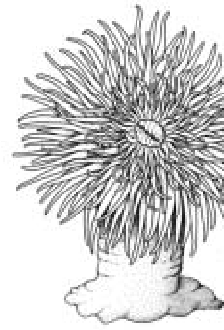
Epizoanthus scotinus

PLATE 67 Sea anemones. The specific name of *Metridium farcimen* refers to its sausagelike appearance. Subtidal individuals may attain nearly a meter in length. Its size, habitat, and highly lobed oral disc are features that distinguish *M. farcimen* from the smaller, intertidal *M. senile* (drawing by Steven Sechovec). *Diadumene lineata,* which rarely is as large as 10 mm across, is probably the most widely distributed species of sea anemone in the world (after Hargitt 1914, redrawn by Emily Reid). Although typically no longer than 10 mm in the field, *Nematostella vectensis* can grow much larger under laboratory conditions (after Crowell 1946, redrawn by Emily Reid). The tentacles of zoanthid *Epizoanthus scotinus* arise only at the margin (drawing by Steven Sechovec).

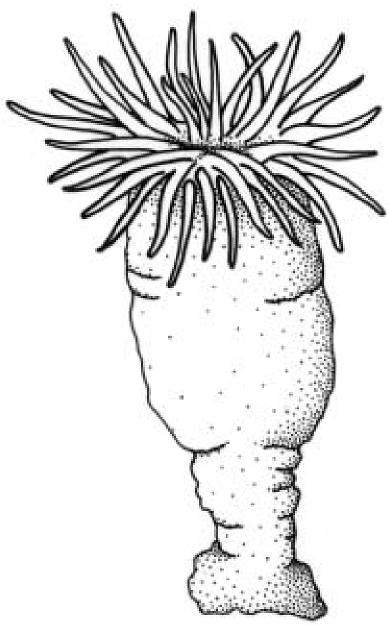
2. Tentacles 10 in number; column to 60 mm long and 6 mm diameter (plate 68) . . . . *Halcampa decemtentaculata*
— Tentacles 12–18 in number 3
3. Tentacles usually 16 in number but vary from 12 to 18; nematosomes (tiny ciliated spheres) circulate in coelenteron; column transparent in expansion, typically 10–15 mm long but can grow to several times that in laboratory (plate 67) . . . . *Nematostella vectensis*
— Tentacles usually 12 in number; column to 50 mm long; no nematosomes 4
4. Column 5–6 mm diameter, opaque, creamy white, with crinkled, cuticular appearance; sand grains attached to column . . . . *Halcampa crypta*
— Column 1–3 mm diameter; divisible into physa, scapus, scapulus, and capitulum; scapus with brownish, well-developed cuticle . . . . *Edwardsia* sp.
5. Tentacles 24 in number, orange (with brown markings in some individuals); column with cuticular sheath (plate 68) . . . . *Cactosoma arenaria*
— Tentacles >24 in number 6
6. With acontia that are extruded through pores or breaks in the body wall, or through the mouth when the animal is disturbed, detached, or handled roughly 7
— Without acontia 15
7. Column translucent or pale white, vermiform (to 500 mm long by 15 mm diameter); burrows in sandy mud with base attached to shells or pebbles (plate 66) . . . . *Flosmaris grandis*
— Neither vermiform nor burrowing 8
8. Margin of oral disc frilled; tentacles short and numerous so there is little tentacle-free area around mouth 9
— Margin of oral disc not frilled; tentacles fewer than 100, so a fairly large area around mouth is tentacle-free; animal typically no more than 20 mm tall, 10 mm diameter; commonly occur in aggregations due to asexual reproduction 10
9. Typically large (to 500 mm long), solitary, and subtidal; oral disc lobed and covered with short tentacles that may number in the hundreds; commonly white, uncommonly salmon, brown, or speckled (plate 67) . . . . *Metridium farcimen*
— Typically small (no more than 50 mm long), living in clusters, and intertidal; oral disc covered with many short tentacles but not lobed or only shallowly so; commonly white, orange, or brown (plate 68) . . . . . . *Metridium senile*
10. Directive tentacles (those nearest each end of mouth slit) with yellow bases; column transparent in extension, but cream, gray, or light green when contracted, commonly with longitudinal white stripes (plate 68) . . . . *Diadumene franciscana*
— Directive tentacles not marked differently from others 11
11. Column some shade of green, commonly with longitudinal single or double stripes of white, yellow, or orange; lives high in intertidal zone (plate 67) . . . . *Diadumene lineata*
— Column (and usually tentacles) yellow, orange, reddish, or pink 12
12. Column and tentacles pink- to salmon-colored, although upper parts of column may show tints of green; long and slender when extended (plate 68) . . . . *Diadumene leucolena*
— Column and tentacles yellow, orange, or reddish; to 20 mm diameter but commonly half that or less 13
13. Extended column about as tall as wide or slightly taller than wide; sometimes reddish; to 10 mm diameter . . . . *Metridium exilis*
— Extended column at least twice as tall as wide; transparent light orange or yellow; commonly no more than 5 mm diameter 14
14. Lives on open coast; column commonly with bulges or kinks, and contracts asymmetrically (plate 68). . . . . *Diadumene lighti*
— Lives in bays and estuaries; column without bulges or kinks; rare individuals 20 mm diameter . . . . *Diadumene* sp.
15. Column many times longer than broad (to 200 mm long by 15 mm diameter); burrows in sand or mud, attached to stones, worm tubes, or shells (plate 68) . . . . *Zaolutus actius*
— Column no more than about five times taller than broad 16
16. Column with verrucae to which debris (bits of gravel, shell, etc.) may adhere 17
— Column smooth, but may nonetheless be capable of holding debris 24
17. Without marginal spherules at top of column just outside and below tentacles. 18
— With white to yellow marginal spherules; column green, gray, yellow, or white 21
18. Column cream, dull green, orangish, or brick red; diameter to 35 mm; oral disc with striking white radial lines, of which those on the directive axis reach the mouth (plate 66) . . . . *Aulactinia incubans*
— Column bright red, in some animals with green or brown patches; commonly more than 100 mm diameter. 19
19. Column densely covered with verrucae to which gravel, shells, etc. strongly adhere; anemone usually buried in gravel or shell debris . . . . *Urticina coriacea*
— Column verrucae sparse, weakly adhesive 20
20. Column scarlet; white verrucae in longitudinal rows make contracted animal appear striped (plate 65). . . . . *Urticina lofotensis*
— Red column may have patches of green or brownish green, or column may be predominantly green; verrucae that are color of column weak, sparse, or even absent (plate 65) . . . . *Urticina crassicornis*
21. Column capable of great elongation—animal lives buried in sand or gravel, with base attached to rock, and extends so tentacles are at surface; verrucae on upper two-thirds of column only; upper one-third of column black or gray, lower two-thirds white or pink; tentacles or oral disc commonly bright pink or orange . . . . . . *Anthopleura artemisia*
— Column generally green, entirely covered with verrucae 22
22. Column to 200 mm diameter, typically deep green; verrucae irregular, compound, not in clearly longitudinal rows; tentacles uniform in color, disc uniform or with faint radial stripes (plate 65) . . . . *Anthopleura xanthogrammica*
— Column green to yellow or white; verrucae circular, in longitudinal rows; tentacles may be tipped with pink or variously marked; oral disc commonly with conspicuous dark radial lines 23
23. Column typically no more than 50 mm diameter; densely massed on rocks of the medium to high intertidal (plate 65) . . . . *Anthopleura elegantissima*
— Column typically >50 mm diameter; solitary; lives in medium to low intertidal (plate 65). . . . . *Anthopleura sola*



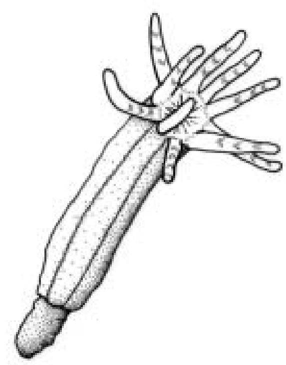
Diadumene spp.



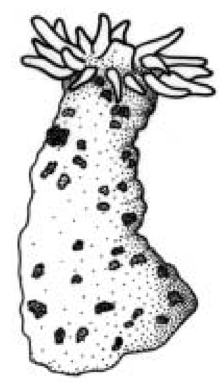
Metridium senile



Zaolutus actius



Halcampa decemtentaculata



Cactosoma arenaria

PLATE 68 More small sea anemones. Looking very similar, an individual of *Diadumene* sp., *D. leucolena,* and *D. lighti* can resemble the anemone in this drawing. In California and Oregon, a specimen of *Metridium senile* is typically no longer than 50 mm. The name was also previously used also for specimens of *M. farcimen,* which can grow to more than 10 times that length. *Halcampa decemtentaculata* has, as its name indicates, 10 tentacles; it has been erroneously identified as the 12-tentacled *H. duodecimcirrata,* which occurs in Europe. *Zaolutus actius* burrows in soft sediments, its pedal disc attached to buried objects. Unlike most anemones lacking a true pedal disc, *Cactosoma arenaria* does not burrow; rather, it adheres to a firm substratum as in an anemone with a true pedal disc (drawings by Tracy R. White).

24. Column 100 mm or more diameter, rich red with velvety appearance; tentacles white or pink (plate 65) . . . . *Urticina piscivora*
— Column no more than 60 mm diameter, commonly reddish, brown, or greenish in color; white radial stripes around pedal disc and on oral disc 25
25. Column dull red to brown, very flat when contracted; sand may adhere to lower column; young brooded internally . . . . *Epiactis ritteri*
— Column dull red, brown, or greenish, domed when contracted, without adherent sand; young anemones may be attached to parent column 26
26. Young anemones on one parent differ in size; parent no more than 25 mm diameter (plate 66). . . . . *Epiactis prolifera*
— Young anemones on one parent of similar size; parent typically >50 mm diameter; bold striping around pedal disc may extend up column (plate 66) . . . . . . *Epiactis lisbethae*

List of Species

ORDER ACTINIARIA

ACTINIIDAE

Anthopleura artemisia (Pickering in Dana, 1846). On open coasts, solitary individuals live in pholad holes; in estuaries, groups of individuals attach to stones below surface of muddy sand, giving the appearance of being burrowers. See Smith and Potts 1987, Mar. Biol. 94: 537–546 (population genetics).

Anthopleura elegantissima (Brandt, 1835). Produces clonal aggregations by longitudinal fission; in bays or on rocks of sandy shores, may be buried by substratum, especially during winter. See Ford 1964, Pac. Sci. 18: 138-145 (reproduction); Francis 1973, Biol. Bull. 144: 64–72 (clone-specific segregation), 1973, Biol. Bull. 144: 73–92 (aggression), 1976, Biol. Bull. 150: 361–376 (social organization); Pearse 1974, Biol. Bull. 147: 641–651, and 1974, Biol. Bull. 147: 630–640 (influence of symbiotic algae on behavior); Hart and Crowe 1977, Trans. Amer. Micros. Soc. 96: 28–41 (role of attached gravel in reducing desiccation); Jennison 1979, Can. J. Zool. 57: 403–411 (reproduction); Smith and Potts 1987, Mar. Biol. 94: 537–546 (population genetics), Tsuchida and Potts 1994, J. Exp. Mar. Biol. Ecol. 183: 227–242 (growth); Yoshiyama et al. 1996, J. Exp. Mar. Biol. Ecol. 204: 23–42 (predation by the sculpin *Clinocottus*); Augustine and Muller-Parker 1998, Limnol. Oceanogr. 43: 711–715 (predation by *Clinocottus*); Seavy and Muller-Parker 2002, Invert. Biol. 121: 115–125 (predation by the nudibranch *Aeolidia*); Geller et al. 2005, Integr. Comp. Biol. 45: 615–622 (evolution of fission).

Anthopleura sola Pearse and Francis, 2000. Common on open coasts south of San Francisco, reported as far north as Coos Bay; formerly known as the solitary ecotype of *A. elegantissima;* can grow nearly as large as *A. xanthogrammica.*

Anthopleura xanthogrammica (Brandt, 1835). The "giant green anemone" of tide pools; differs from *A. sola* in having solid green tentacles and either a solid green oral disc or one on which radial stripes are faint. See Smith and Potts 1987, Mar. Biol. 94: 537–546 (population genetics); Hand 1996, Wasmann J. Biol. 51: 9–23 (predation by the sculpin *Clinocottus* and the nudibranch *Aeolidia*).

Aulactinia incubans Dunn, Chia, and Levine, 1980. Described from San Juan Island, Washington; occasionally found on the coast north of Santa Cruz in protected low-intertidal areas such as under overhangs; broods its young internally.

Epiactis lisbethae Fautin and Chia, 1986. Described from the San Juan Islands, Washington, where it can be confused with the more common *E. prolifera,* but it attains greater size and its externally brooded young are all the same size; rare in California and Oregon. See Edmands 1995, Mar. Biol. 123: 723–733, 1996, Invert. Repro. Dev. 123: 227–237 (mating system).

Epiactis prolifera Verrill, 1869. Ubiquitous in bays and on open coast on rocks, algae, and seagrass; externally broods young of various sizes simultaneously. See Dunn 1975, Nature 253: 528–529 (sexuality), 1975, Biol. Bull. 148: 199–218 (reproduction), 1977, Mar. Biol. 39: 41–49 (brooding), 1977, Mar. Biol. 39: 67–70 (locomotion), 1977, J. Nat. Hist. 11: 457–463 (variability); Edmands, 1995, Mar. Biol. 123: 723–733, 1996, Invert. Repro. Dev. 123: 227–237 (mating system).

Epiactis ritteri Torrey, 1902 (=*Cnidopus ritteri;* see Fautin and Chia, 1986, Can. J. Zool. 64: 1665–1674). Under and on rocks in protected places of outer coast; resembles *E. prolifera,* but young are brooded internally. See Hand and Dunn 1974, Wasmann J. Biol. 32: 187–194 (redescription); Edmands 1995, Mar. Biol. 123: 723–733, 1996, Invert. Repro. Dev. 123: 227–237 (mating system).

Urticina coriacea (Cuvier, 1798) (=*Tealia coriacea*). Middle to low intertidal and deeper, in bays and on outer coast; buried in sand or gravel, which adheres to column. See Hand 1955, Wasmann J. Biol. 12: 345–375 (redescription).

Urticina crassicornis (Müller, 1776) (=*Tealia crassicornis*). Middle to low intertidal and deeper, on outer coast; on undersides of large rocks and in protected pools. See Hand 1955, Wasmann J. Biol. 12: 345–375 (redescription).

Urticina lofotensis (Danielssen, 1890) (=*Tealia lofotensis*). Low intertidal and deeper, on outer coast; on rocks and in protected pools. See Hand 1955, Wasmann J. Biol. 12: 345–375 (redescription); Wedi and Dunn 1983, Biol. Bull. 165: 458–472 (reproduction); Sebens and Laakso 1978, Wasmann J. Biol. 35: 152–168 (redescription).

Urticina piscivora (Sebens and Laakso, 1978) (=*Tealia piscivora*). Strictly subtidal; on rock promontories.

DIADUMENIDAE

Diadumene sp. In embayments such as the Oakland Estuary.

Diadumene franciscana Hand, 1956. Southern and central California; in San Francisco Bay, sporadically abundant in Aquatic Park, Berkeley, on pilings in Lake Merritt in summer, etc. Considered an introduced species by Cohen and Carlton 1895 (see references in "Introduced Species," at the beginning of this book).

Diadumene leucolena (Verrill, 1866). On floats, pilings, stone, oyster shells, etc. in bays; introduced from the Atlantic Ocean.

Diadumene lighti Hand, 1956. In sand among algal holdfasts along edges of rocky shore tide channels.

Diadumene lineata (Verrill, 1871) (=*Haliplanella luciae* Verrill, 1898, and the combinations of the two generic and specific names). High intertidal of bays and estuaries, commonly in barnacle tests and crevices of rotting wood, and common in fouling communities. Transported by humans, it is the most widely distributed sea anemone in the world; it is probably a native of northeast Asia. See Hand 1956 (for 1955), Wasmann

J. Biol. 13: 189–251 (redescription). There is an extensive literature on this species.

EDWARDSIIDAE

Edwardsia sp. A small undescribed or unidentified species occurs in Bodega Harbor among *Phoronopsis* on muddy sand flats. May be the same species as has been called *Edwardsiella* from Tomales Bay.

Nematostella vectensis Stephenson, 1935. Widely distributed in salt marshes of both Atlantic and Pacific coasts of the United States (including San Francisco, Tomales, and Coos Bays), and the Atlantic coast of Europe (it is considered an endangered species in Britain, where its habitat is diminishing); reproduces asexually by transverse fission. See Hand 1955 (for 1954), Wasmann J. Biol. 12: 345–375 (redescription); Hand and Uhlinger 1994, Estuaries 17: 501–508 (biology and ecology); Hand and Uhlinger 1995, Invert. Biol. 114: 9–18 (asexual reproduction).

HALCAMPIDAE

Cactosoma arenaria Carlgren, 1931. On open coasts; frequents kelp holdfasts.

Halcampa crypta Siebert and Hand, 1974. In muddy shale gravel of inshore pools of Duxbury Reef, Bolinas; also found at Friday Harbor.

Halcampa decemtentaculata Hand, 1955. Found among roots of surfgrass *Phyllospadix*, holdfasts of laminarians, and gravelly pools of the low rocky intertidal; also found at Friday Harbor.

ISANTHIDAE

Zaolutus actius Hand, 1955. Specimens from Elkhorn Slough referred to as *Harenactis attenuata* by MacGinitie (1935); rare in central California, more common subtidally to the south; burrows in muddy sand.

ISOPHELLIIDAE

Flosmaris grandis Hand and Bushnell, 1967. Burrows in sand and sandy mud; known only from San Francisco Bay.

METRIDIIDAE

Metridium exilis Hand, 1956. Under rocks and ledges on open coast. See Bucklin 1987, J. Exp. Mar. Biol. Ecol. 110: 41–52 (growth and asexual reproduction).

Metridium farcimen (Brandt, 1835) (=*M. giganteum* Fautin, Bucklin, and Hand 1990, Wasmann Jour. Biol. (for 1989) 47: 77–85). This distinctive large, solitary, subtidal species that lives on pilings in bays and on rocks and shells off the coast was once considered an ecotype of *M. senile*. See Bucklin 1987, J. Exp. Mar. Biol. Ecol. 110: 41–52 (growth and asexual reproduction); Kramer and Francis 2004, Biol. Bull. 207: 130–140 (predation resistance and nematocyst scaling).

Metridium senile (Linnaeus, 1767). Common on pilings, rock jetties, and floats of bays and harbors; reproduces asexually by pedal laceration to form dense clonal groups. See Purcell and Kitting 1982, Biol. Bull. 162: 345–359 (population biology and intraspecific aggression); Bucklin 1987, J. Exp. Mar. Biol. Ecol. 110: 41–52 (growth and asexual reproduction); Kramer and Francis 2004, Biol. Bull. 207: 130–140 (predation resistance and nematocyst scaling). There is an extensive literature on this species.

ORDER CERIANTHARIA

CERIANTHIDAE

Pachycerianthus fimbriatus McMurrich, 1910 (=*P. torreyi* Arai, 1965, and *P. plicatulus* Carlgren, 1924). Rare intertidally in very soft mud; the thick, tough, soft, black, slimy tube extends to a depth of one meter or more. See Arai 1971, J. Fish. Res. Bd. Canada 28: 1677–1680 (taxonomy).

ORDER CORALLIMORPHARIA

CORALLIMORPHIDAE

Corynactis californica Carlgren, 1936. Low intertidal on rocky open coasts; reproduces asexually by longitudinal fission to form dense clusters. See Hand 1955 (for 1954), Wasmann J. Biol. 12: 345–375 (redescription); Chadwick 1987, Biol. Bull. 173: 110–125 (interspecific aggression); Chadwick and Adams 1991, Hydrobiologia 216–217: 263–269 (locomotion, reproduction, ecology); Holts and Beauchamp 1993, Mar. Biol. 116: 129–136 (sexual reproduction).

ORDER SCLERACTINIA

DENDROPHYLLIIDAE

Balanophyllia elegans Verrill, 1864. Low intertidal on rocky open coasts, typically in surge channels, often under overhangs; easily distinguished from *C. californica*, which it may resemble, by its hard skeleton. See Fadlallah and Pearse 1982, Mar. Biol. 71: 223–231 (sexual reproduction); Fadlallah 1983, Oecologia 58: 200–207 (population dynamics, life history, central California); Hellberg 1995, Mar. Biol. 123: 573–581 (gene flow); Hellberg and Taylor 2002, Mar. Biol. 141: 629–637 (sexual reproduction, genetics).

ORDER ZOANTHIDEA (=ZOANTHINIARIA)

EPIZOANTHIDAE

Epizoanthus scotinus Wood, 1958. Strictly subtidal in California, but intertidal in the San Juan Islands.

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Anthozoa: Octocorallia

GARY C. WILLIAMS

(Plates 69–71)

The octocorals are a morphologically diverse group easily distinguished from other cnidarians by having eight pinnate tentacles surrounding the mouth of each polyp. Most West Coast species are strictly subtidal, and several shallow water species of gorgonians (sea fans) occur from Monterey Bay to Baja, California. However, at least seven species of inconspicuous soft corals are occasionally encountered under rocky overhangs in the low intertidal from Southern California to Oregon. The sea pens are subtidal for the most part, but they may be encountered in protected bays at extreme low tide or washed ashore following storms. See the websites "Octocoral Research Center" or "Octocoral Home Page" for details about the group. The "Research Techniques" portion of this website describes a method to isolate sclerites (also known as spicules, the free calcitic skeletal elements of octocorals) from the surrounding tissue for examination.

KEY TO OCTOCORALLIA

1. Colonies attached by a common basal stolon or holdfast to hard substrata in the low rocky intertidal 2
— Colonies partly imbedded in soft sediments of bays or sloughs by a basal peduncle, in extreme low intertidal to shallow subtidal, or occasionally washed ashore. 8
2. Polyps arise from ribbonlike or spreading basal stolons 3
— Colonies arise from a basal holdfast; colony has a membranous shape or is disc-shaped or lobate; polyps contained in globular bodies of tissue (>5 mm high) to form coherent colonies; color cream or white to rose or red 5
3. Polyps are cylindrical and tall (5–12 mm) 4
— Individual polyps appear as densely set rounded mounds (<5 mm high) that arise from a common and broad basal stolon; color cream or tan to gray (plate 69A). . . . . *Cryptophyton goddardi*
4. Whitish polyps are coated with rust-orange sponge; some polyps with one or two daughter polyps emanating from the lateral walls of the parent polyp (plate 70C, 70D) . . . . *Telesto* sp.
— Daughter polyps absent, not coated with sponge (plate 70E) . . . . *Clavularia* spp.
5. Colonies globular, with projecting lobes, grey or rose to red in color (plate 69B) . . . . *Alcyonium* sp.
— Colonies not lobate. 6
6. Colonies membranous, usually somewhat flattened and disc-shaped or globular without lobes, round to oval, polyps fully retractile, pale salmon pink to white in color (plate 69C) . . . . *Discophyton rudyi*
— Colonies membranous, irregularly shaped; polyps retractile and clustered atop moundlike or calyxlike protuberances

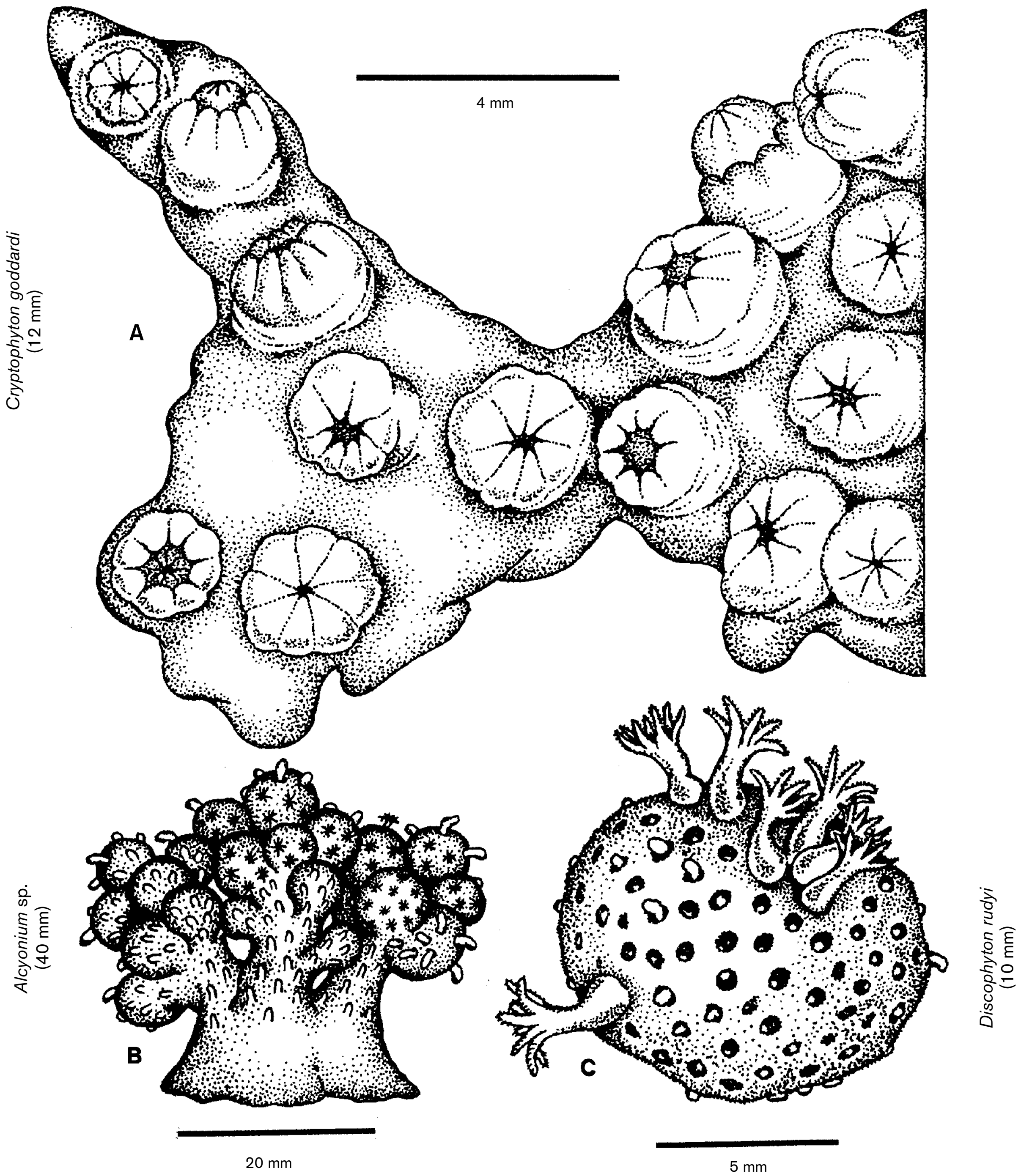

PLATE 69 A, *Cryptophyton goddardi,* scale bar = 4 mm; B, *Alcyonium* sp., scale bar = 20 mm; C, *Discophyton rudyi*, scale bar = 5 mm (all by G. C. Williams).

that are separated from one another by thin membranous regions devoid of polyps 7

7. Sclerites are mostly coarsely tuberculated spindles; polyps heavily armored (plate 70F, 70G) . . . . *Thrombophyton coronatum*

— Sclerites are coarsely tuberculated and robust spindles to ovoid or elliptical forms that give the surface of the colony a rough texture; sparsely tuberculated rods in the colony interior; polyps weakly armored (plate 70A, 70B) . . . . *Thrombophyton trachydermum*

8. Polyp-bearing rachis is heart-shaped and flattened without lateral polyp leaves, lying upon the surface of sand with a wormlike peduncle buried in the sand below; color usually violet to brownish-purple (plate 71A) . . . . *Renilla amethystina*

— Polyp-bearing rachis is erect and stem- or featherlike with lateral polyp leaves; color usually orange, cream, or white and red-purple 9

9. Stout and fleshy with dense, overlapping, large, and thickened polyp leaves; color often bright orange (plate 71E) . . . . *Ptilosarcus gurneyi*

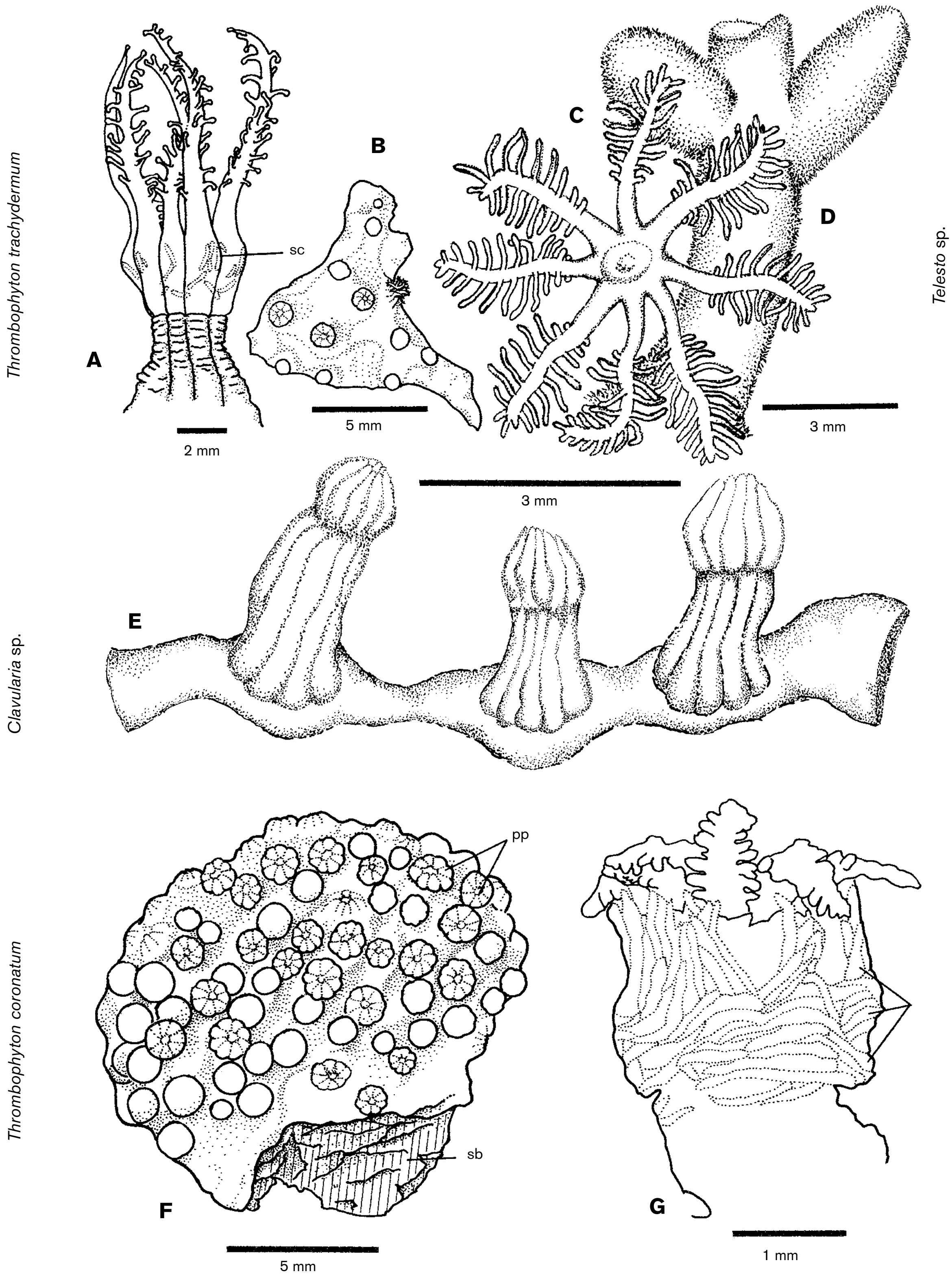

PLATE 70 A, *Thrombophyton trachydermum,* single polyp, scale bar = 2 mm; B, *Thrombophyton trachydermum,* whole colony, scale bar = 5 mm; C, *Telesto* sp., expanded tentacles from a single polyp, scale bar = 3 mm; D, *Telesto* sp., single polyp with two daughter polyps, scale bar = 3 mm; E, *Clavularia* sp., part of a colony, scale bar = 3 mm; F, *Thrombophyton coronatum,* whole colony, scale bar = 5 mm; G, *Thrombophyton coronatum,* single polyp, scale bar = 1 mm (A, B, F, G after McFadden and Hochberg 2003, drawn by Linda D. Nelson; C, D, E by G. C. Williams).

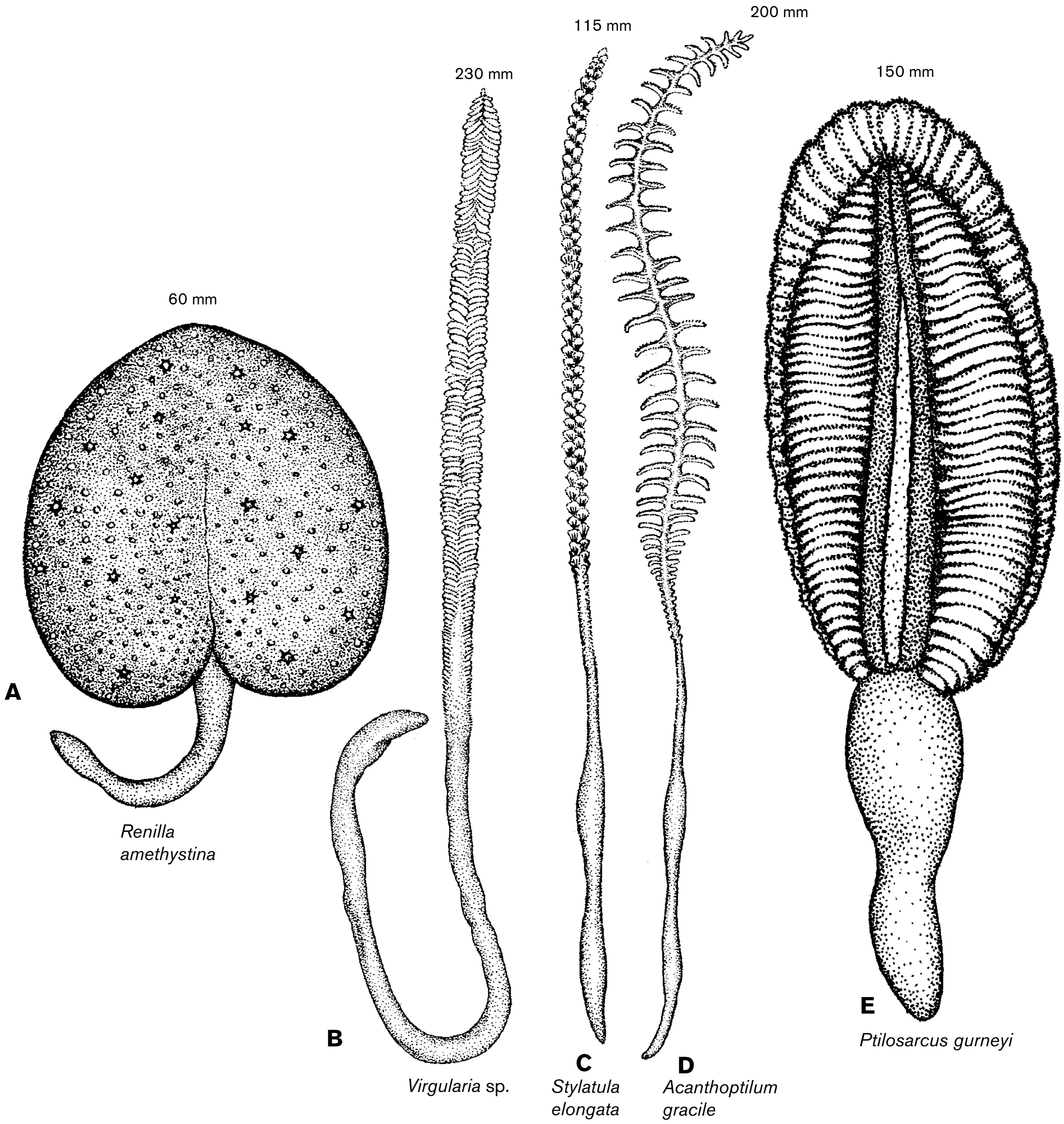

PLATE 71 Measurements are lengths. A, *Renilla amethystina*, 60 mm; B, *Virgularia* sp., 230 mm; C, *Stylatula elongata*, 115 mm; D, *Acanthoptilum gracile*, 200 mm; E, *Ptilosarcus gurneyi*, 150 mm (all by G. C. Williams).

— Slender and elongate with short delicate polyp leaves; often colorless, milky white, or translucent gray to rose or light pink 10

10. Spindlelike sclerites present in polyps or at the bases of polyp leaves 11

— Sclerites absent except for minute oval bodies present mostly in the peduncle (plate 71B) . . . . *Virgularia* spp.

11. Needlelike sclerites form a fan-shaped armature at the base of each polyp leaf; colonies firm and scabrous (plate 71C) . . . . *Stylatula elongata*

— Short, three-flanged sclerites may form a weak cluster at the base of polyp leaf or at least are present elsewhere in the colony; colonies soft and flexible (plate 71D) . . . . *Acanthoptilum gracile*

LIST OF SPECIES

ORDER ALCYONACEA

CLAVULARIIDAE

Cryptophyton goddardi Williams, 1999. This stoloniferous taxon inhabits the underside of rocks and overhangs in low intertidal areas; known from the Oregon coast, but to be expected further south into California; possibly referred to as *"Clavularia"* sp. in some publications. More than one species of stoloniferous octocoral may inhabit the West Coast intertidal (see *Clavularia* spp., below). The genus is characterized by having polyps without sclerites and irregularly shaped sclerites in other parts of the colony. Preyed upon by the nudibranch *Tritonia festiva*.

Clavularia spp. Williams (2000), McFadden and Hochberg (2003) and J. Goddard (pers. comm.) report that members of this genus may inhabit intertidal and nearshore habitats along the California coast. This genus differs from *Cryptophyton* by the presence cylindrical polyps armed with crown and points and sclerites that are primarily spindles.

Telesto sp. An unidentified species has been found intertidally in exposed open coast situations of Santa Barbara County (J. Goddard, pers. comm.). The polyps form relatively dense clusters. Each polyp is usually 8–10 mm tall, and the polyp walls are thinly coated with a pale orange sponge. A few of the polyps have daughter polyps.

ALCYONIIDAE

Alcyonium sp. Sea strawberry. An undescribed lobate soft coral; Alaska to Sonoma County, California. The name *"Gersemia rubiformis"* (Ehrenberg 1834) has been applied by many authors to this taxon, but this application is erroneous because the genus *Gersemia* belongs to the related soft coral family Nephtheidae, and the species *G. rubiformis* (which also may belong to the genus *Alcyonium*) is native to the northern Atlantic. More than one species of *Alcyonium* may inhabit the Pacific coast intertidal area. This soft coral is preyed upon by the nudibranch *Tritonia festiva* (J. Goddard, pers. comm.).

**Alcyonium pacificum* Yamada, 1950. McFadden and Hochberg (2003) report this northern Pacific species to the north and west of the California coast from the Alaskan Aleutian Islands to Japan; rocky substrata of kelp beds, 5–20 m.

Discophyton rudyi (Verseveldt and Ofwegen, 1992). An inconspicuous, disc-shaped soft coral found in the lower intertidal area, usually 8–15 mm in diameter; Vancouver Island to Point Lobos, Central California. The nudibranch *Tritonia festiva* is a reported predator.

Thrombophyton coronatum McFadden and Hochberg, 2003. Southern California (Palos Verdes to San Diego) and Catalina Island.

Thrombophyton trachydermum McFadden and Hochberg, 2003. Vancouver Island to Ano Nuevo Point, California.

ORDER PENNATULACEA

See Williams (1995) for a key and synopses of the sea pen genera. All sea pens in our area are fed upon by the nudibranch *Tritonia diomedea* (Behrens 2004. Proc. Calif. Acad. Sci. 55[2]: 43).

* = Not in key.

RENILLIDAE

Renilla amethystina Verrill, 1864 (=*Renilla koellikeri* Pfeffer, 1886). Sea pansy; common on low intertidal or shallow subtidal sandflats; Santa Barbara County to Baja California. The nudibranch *Armina californica* feeds on this species as well as some other sea pens.

VIRGULARIIDAE

Acanthoptilum gracile (Gabb, 1864). Occasionally encountered subtidally in bays; common in Tomales Bay; known from Central California (Sonoma to Monterey Counties). The genus is in need of revision, and other species are likely present, particularly in Southern California.

Stylatula elongata (Gabb, 1862). Often common in low intertidal areas of sandy mud; more than one species may inhabit the West Coast. The related genus *Virgularia* and this genus are easily confused: *Stylatula* differs from *Virgularia* by having each polyp leaf subtended by a fanlike armature of spindle-shaped or needlelike sclerites (Williams 1995).

Virgularia spp. Several species whose identification has not been verified occur from Monterey Bay and south, forming subtidal beds in the northern part of their range on gentle slopes or flats of sand or silt, but may be encountered on mud flats at low tide in the south.

PENNATULIDAE

Ptilosarcus gurneyi (Gray, 1860). Shallow subtidal; sometimes washed ashore. See Batie 1972, Northwest Sci. 46: 290–300 (taxonomy); Birkeland 1974, Eco. Mono. 44: 211–232 (predator/prey interactions). Preyed upon by the nudibranchs *Tritonia festiva, T. diomedea,* and *Toquina tetraquetra*. The more southern species of *Ptilosarcus*, *P. undulatus,* is found from Baja California to Peru.

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