Ctenophora

(Plates 72-76)

CLAUDIA E. MILLS AND STEVEN H. D. HADDOCK

The ctenophores, or comb jellies, are transparent animals belonging to a small and entirely marine phylum of about 100–150 species, many (perhaps 50) of which are still undescribed. Although ctenophores are like medusae in being more or less transparent carnivores that often use tentacles to capture their prey, these similarities reflect a convergence in life styles rather than close evolutionary ties. Ctenophores are biradially symmetrical (discussion in Hyman 1940: 665), and nearly all West Coast species except *Pleurobrachia bachei* and some look-alikes are bioluminescent (Haddock and Case 1995). All ctenophores have a distinctive, complex, ciliated statocyst organ at the aboral pole that is used for orientation.

Ctenophores are so-named in recognition of the eight rows of ciliary comb plates, or ctenes, used for locomotion. All ctenophores bear these comb plates at some point in their life cycle, although some species can also move by flapping or waving other structures (the lobes and/or auricles). Most ctenophores use paired tentacles to capture prey, and these tentacles usually carry colloblasts—special, very sticky adhesive cells. Some ctenophore species capture prey on large mucousladen, muscular surfaces known as lobes with the assistance of greatly reduced tentacles within the lobes. *Beroe*, lacking both lobes and tentacles, swallow their gelatinous prey whole.

The most commonly seen West Coast ctenophore is *Pleurobrachia bachei*, which is often cast up on beaches looking like a clear, watery marble and called a sea gooseberry or cat's eye. Most other species of ctenophores are not so robust and have little to no recognizable form out of water. Because no ctenophores are strictly intertidal invertebrates (although some may be found, on occasion, stranded in pools at low tide), we have taken some liberties in selecting the species to be keyed out here. The common coastal species and those species often encountered by blue-water divers offshore are included, as well as a small number of distinctive and robust deeper species likely to be recovered in midwater trawls not far from the coast.

Benthic ctenophores, known as platyctenes, account for nearly one-third of the known species. The body is highly flattened and modified, so they creep on a "foot" and can look much like flatworms, often living epizoically on other organisms such as sponges or seaweed (although their planktonic larvae are ciliated like other ctenophores). Although found in many locations worldwide, platyctenid ctenophores occur in warm water and are unlikely to be found within the geographic range of this book. The platyctene *Vallicula multiformis* was present briefly in shallow water in San Diego in 1997, being perhaps a short-lived introduction from the Caribbean.

Preservation of ctenophores is a difficult and frustration-filled endeavor. Some species, including *Pleurobrachia bachei* and some *Beroe*, preserve well, at least some of the time, in a weak (\leq 5%) formalin solution. Some species that leave only bits of debris in the bottle when preserved this way can be better preserved using glutaraldehyde instead of formaldehyde, and storage in a refrigerator after preservation seems to help maintain some specimens. Many fragile ctenophores, however, are simply unpreservable, in which case video, a good set of photographs, and drawings will have to suffice. For further techniques, see the introductory section here on preservation by Williams and Van Syoc.

Families used in the species list are from Cairns et al. (2002). However, a molecular phylogeny (Podar et al. 2001) supports the assertion that the phylum needs to be reorganized (Harbison 1985).

Glossary

(Plate 72)

ABORAL the end opposite the mouth, bearing a ciliated sense organ known as the "statocyst."

AURICLES four slender gelatinous appendages or processes at the base of the lobes and near the mouth (of a lobate ctenophore), with a ciliated edge; these may be short or long, straight or coiled, and may beat in such a way as to help move water past the lobes.

COMB PLATES transverse rows of thousands of fused macrocilia, shaped roughly like a flat paint brush and comprising subunits that are stacked together to form comb rows (also known as "ctenes"); the effector organs of swimming in a ctenophore (see Tamm 1973).

COMB ROWS eight longitudinal rows or costae of comb plates (ctenes), tightly spaced and overlying the meridional canals, which beat in metachronal waves that pass from the aboral end

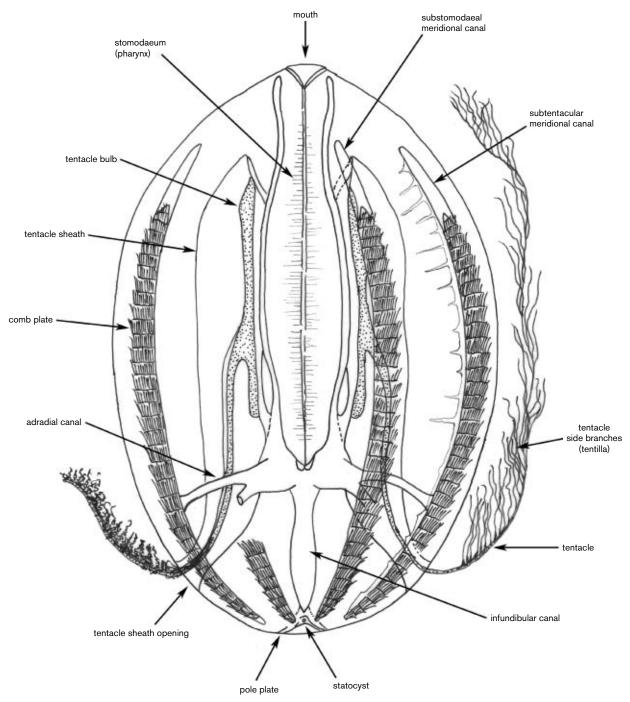


PLATE 72 Hormiphora sp., example of a cyclippid ctenophore with labeled features (undescribed species, redrawn from Stanford, 1931, pp. 32 and 33, figs. 3 and 4).

toward the mouth, and thereby move the animal through the water by ciliary action.

CTENES see "comb plates."

DIVERTICULA (singular diverticulum) side branches or outpocketings emerging from any of the canals; if these meet and join, it is said that they "anastomose."

GASTRIC CAVITY see "stomodaeum."

INFUNDIBULAR CANAL broad, often funnel-shaped, canal running between the base of the stomodaeum and the aboral pole (also known as the "aboral canal").

LOBES a pair of thin, muscular, cuplike oral extensions of the body; they may be as large or larger than the body itself, on both sides of the mouth.

MEDUSIFORM shaped like a jellyfish (a medusa).

MERIDIONAL CANALS usually eight, but in a few species only four, circulatory canals that run under the comb rows, which are connected by smaller internal canals running through the jelly to the stomodaeum.

MOUTH opening into the stomodaeum at the oral end. **ORAL** the end of a ctenophore bearing the mouth.

PARAGASTRIC CANALS pair of canals originating at the base of the stomodaeum, running upward along each flattened surface of the stomodaeum toward the mouth (also known as the pharyngeal canals).

STATOCYST ciliated orientation organ at the aboral pole, which may be flush with the surface or sunken to some extent, and which is connected to the eight comb rows by ciliated grooves (also known as the aboral sense organ).

STOMODAEUM the gastric cavity that opens from the mouth; it is highly expandable (also known as the pharynx).

SUBSTOMODAEAL CANALS the four meridional canals closest to the plane of the stomodaeum.

SUBTENTACULAR CANALS the four meridional canals that lie on either side of the openings of the tentacle sheaths, closest to the plane that runs longitudinally through the two tentacle bulbs

TENTACLE elongate, highly extensile, (paired) filamentous, feeding appendage, emerging from a swollen tentacle bulb at its base, often with side branches (also known as "tentilla") that are finer than the main, lateral tentacular filament. Tentacles are equipped with thousands of microscopic adhesive structures called colloblasts, with which they capture prey. The tentacles are often fragile and may be partially or entirely broken off during collection.

TENTACLE SIDE BRANCHES fine side filaments on the tentacles of many (but not all) tentaculate species, which may be closely spaced or set rather far apart (also known as "tentilla").

TENTACLE BULBS the (two) swellings at the base of the tentacles, often very elongate, up to half of the body length in some species, from which the tentacular filaments emerge; attached to the inner wall of the tentacle sheaths.

TENTACLE SHEATHS the (two) tubelike, or funnel-shaped, openings from the base of the tentacle filaments at their juncture with the tentacle bulbs, through which the tentacles emerge to the outside.

TENTILLA (singular tentillum) see "tentacle side branches." **VESTIBULE** large preoral cavity inside the "mouth" of *Dryodora*, which may hold prey but is separate from the much smaller stomodaeum beneath it.

Key to Ctenophora

1. Body like a sac, mouth opens wide, gastric cavity occupies nearly entire interior; without tentacles or lobes (see plate 76) Order Beroida 23 Body otherwise and usually with some sort of tentacles Body long and flat, like an airplane wing, with fine tentacles along the entire leading edge that sweep back over the body surface Order Cestida 22 3. Body medusiform, open like a shower cap, with eight short comb rows on the upper surface and two small branched tentacles hanging into the open cavity (Order Thalassoca-Body not like a shower cap......4 Body solid, basically rounded at both ends, with a pair of tentacles arising in sheaths on opposite sides of the body; Order Cydippida 5 Body with a pair of muscular, bowl-like lobes at the oral end; usually with small, inconspicuous tentacles between

the lobes (see plates 74, 75) Order Lobata 16

- 8. Tentacle bulbs short, with tentacle sheaths angling out at nearly 45°; stomodaeum less than half the body length; to about 15 mm diameter (plate 73B).....
- Tentacle bulbs one-quarter to one half body length; tentacle sheaths parallel the stomodaeum for some distance; stomodaeum greater than one half body length......9
- Body with tentacle bulbs parallel to, but somewhat removed from, the walls of the stomodaeum; tentacles either nearly colorless and with a small number of side branches that are kept tightly coiled most of the time, or tentacles deeply colored with many disorganized, fine side branches

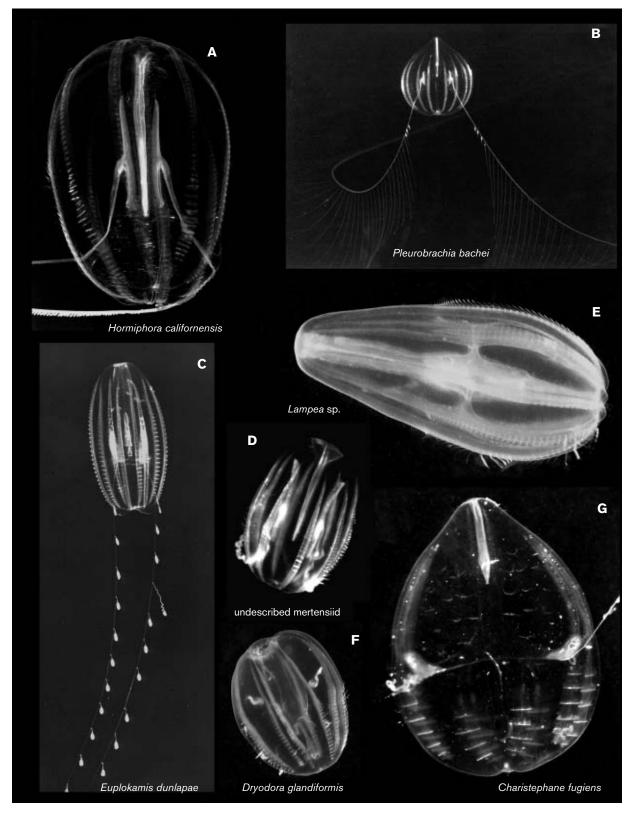


PLATE 73 A, Hormiphora californensis; B, Pleurobrachia bachei; C, Euplokamis dunlapae; D, undescribed mertensiid; E, Lampea sp.; F, Dryodora glandiformis; G, Charistephane fugiens (photographs A–B, D–G by Steven H. D. Haddock; photograph C by Claudia E. Mills).

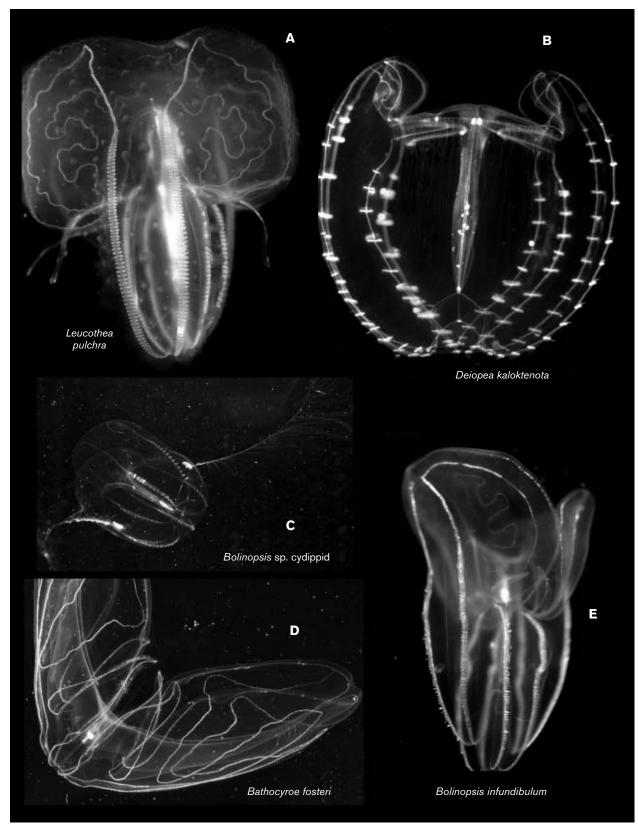


PLATE 74 A, *Leucothea pulchra*; B, *Deiopea kaloktenota*; C, cydippid larva of *Bolinopsis infundibulum*; D, *Bathocyroe fosteri*; E, *Bolinopsis infundibulum*. (all photographs A–E by Steven H. D. Haddock).

Body to 20 mm tall, highly flattened in cross-section; ten-With large, muscular lobes that are used for feeding but can also be clapped together for escape swimming in a movetacle sheaths short, angled, and near outer body wall; comb rows limited to aboral end of body, but subtentacument reminiscent of the swimmer's "frog kick" 21 19. Body oblong and rounded at both ends, not highly flatlar meridional canals extending three-quarters of the way to the oral end; highly transparent and unpigmented, or tened; may have rows of dark spots on the lobes in line with light tan tentacles; deep water (plate 73G)..... with the canals, which in larger specimens may coalesce into dark pigmented lines; total length to 15 cm (this is 13. Tentacle bulbs small, round, and very near the surface, with the common Pacific coast lobate) (plate 74E) sheaths so short that the tentacles are unable to withdraw Bolinopsis infundibulum Body highly flattened (rare coastal visitors from deep wacompletely inside: stomodaeum deep inside a large "vestibule" at the oral end of the animal; body transparent, without a greenish tint; a boreal species seen only rarely as 20. Body rounded to oval in outline, highly flattened; with a pair of relatively small oral lobes; with only a few ctenes, spaced Dryodora glandiformis far apart on each comb row; total length not exceeding 5 cm; Tentacle bulbs very long, typically more than one half rare (plate 74B) Deiopea kaloktenota the body length and with long, orally exiting tentacle Body semi-circular to V-shaped, highly flattened; unpigmented, with a pair of large oral lobes; total length to 30 sheaths; stomodaeum extends all the way to oral end of animal (this feature is true of nearly all ctenophores except Dryodora, above); body usually with a slight green-21. Body flattened and reduced; may have a pair of diffuse ish tint......14 dark spots on the inner surface of each lobe; gut colorless; near-surface species (plate 75B) Ocyropsis maculata 14. Meridional canals unequal in length, maximum are threequarters of body length; comb rows one half to three-fifths Body rounded, much shorter than lobes; with small, darkof body length; without stomodeal canals; body ellipsoid red stomodaeum; deep water species (plate 74D) in cross-section, usually transparent, though may have a Bathocyroe fosteri 22. Length to 1.5 m, but usually <80 cm, the set of canals that Meridional canals all equal in length and nearly as long run out the midline of the body originate near the base of as the body; comb rows less than one half body length; the stomodaeum, rapidly curving up to the midline; gowith stomodeal canals; body nearly circular in cross-secnads continuous; escapes by graceful rapid undulating of tion; usually <10 mm long, with long tentacle sheaths exthe body (plate 75D) Cestum veneris iting the body near the mouth; without distinctive orange Usually <20 cm long, the set of canals that run out the pigment spots, but usually slightly opaque body may midline of the body originate near the center of the stohave red pigment diffusely distributed along canals (plate modaeum, without curves; gonads visible as dashed white line; escape swimming very rapid wriggling (plate 75C, 76G) Haeckelia beehleri 15. Very small, usually <3 mm, with rounded oral end; with 75E) Velamen parallelum long tentacle sheaths exiting about one-quarter of the body length below the mouth; with large orange-red pig-Body cylindrical to moderately compressed25 ment spots on the canals around the base of the sto-24. Body to 15 cm, shaped like a compressed cone, with modaeum and tentacles, and with small red spots along pointed aboral end and broad oral end with very large the comb rows (plate 76J) Haeckelia bimaculata mouth; comb rows all the same length and extend threequarters to five-sixths of body length; with highly Small, usually under 7 mm long, with pointed oral end; with long tentacle sheaths exiting the body near the branched meridional canals forming a network whose mouth; with two pairs of orange-red pigment spots-on branches anastomose (merge) with one another; usually the tentacle bases and about two-thirds to three-quarters tinged rose pink, with darker red along the comb rows down the tentacle sheaths (plate 76H, 76I)..... Body to about 6 cm, soft and flaccid, with aboral end round 16. Body with two rounded, lobe-like extensions used to catch to slightly tapered and oral end very broad with nearly prey and with four elongate, ciliated auricles that help semicircular mouth; comb rows of two lengths, extending about one half and two-thirds to three-quarters body length; meridional canals with many branches that all Body with two rounded, lobe-like extensions used to catch prey, but without auricles; body to 20 cm, rounded with bend toward the mouth and do not merge with one anvery large lobes, colorless but not very transparent, comb other; overall color white or pale pink, with a diffuse orrows end on stubby protrusions near mouth, in the place ange or red spot or pair of stripes on either side of the body of auricles (usually in deep water) (plate 75A)..... overlying the stomodaeum (plate 76E, 76F) undescribed "giant lobate" Beroe mitrata 17. Body surface smooth, mostly colorless; lobes either as large 25. Body slender and elongate, rarely longer than 3 cm and as the rest of the body or considerably smaller; with static usually much less; meridional canals with very few branches, and those present extending inward toward the Body surface covered with brownish orange papillae; stomodaeum rather than in the plane of the body surface with very large lobes that can extend perpendicularly as

Body substantial and thick-walled, typically reaching sev-

eral centimeters in length, meridional canals branched and

running in the plane of the body surface, but few if any of

much as a full body length; with long slender auricles

that beat rhythmically (plate 74A).... Leucothea pulchra

18. Lobes usually shorter than stomodaeum, not capable of

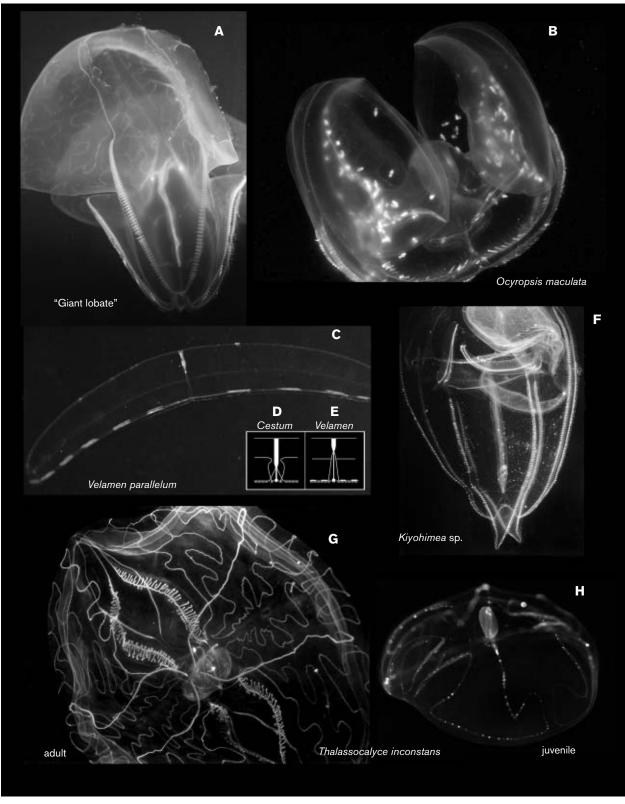


PLATE 75 A, Undescribed "giant lobate"; B, *Ocyropsis maculata* (white spots are symbiotic amphipods); C, *Velamen parallelum*; D, *Cestum veneris*; E, *Velamen parallelum*; F, *Kiyohimea* sp.; G, adult *Thalassocalyce inconstans*; H, juvenile *Thalassocalyce inconstans* (photographs A, B, C, F, G, H by Steven H. D. Haddock).

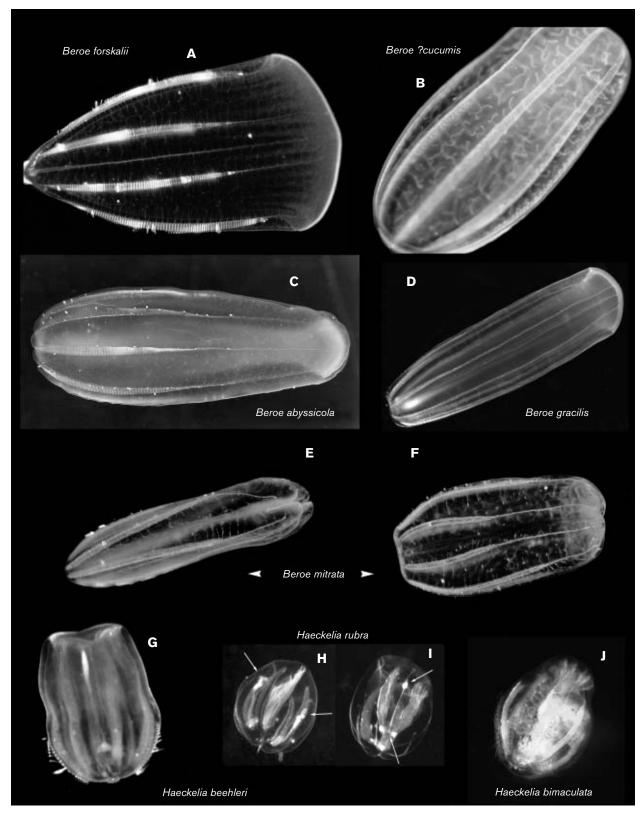


PLATE 76 A, Beroe forskalii; B, Beroe ?cucumis; C, Beroe abyssicola; D, Beroe gracilis; E and F, Beroe mitrata; G, Haeckelia beehleri, H and I, Haeckelia rubra (arrows indicate distinctive spots of red-orange pigment); J, Haeckelia bimaculata (photographs A, B, D, G, H, I, J by Steven H. D. Haddock; photographs C, E, F by Claudia E. Mills).

modaeum; paragastric canals branched—with diverticula;

deep water (plate 76D) Beroe abyssicola

List of Species

Order Cydippida

DRYODORIDAE

Dryodora glandiformis (Mertens, 1833). A boreal species known from both northern and southern oceans; found near Friday Harbor most years in the late winter and spring and rarely seen off central California; usually <1 cm long in our waters, but two or three times that size in the Arctic. Feeds, perhaps exclusively, on appendicularians. Color photograph in Wrobel and Mills 1998 and 2003, p. 63.

EUPLOKAMIDIDAE

Euplokamis dunlapae Mills, 1987. This species (to 2 cm long) is well-known from fjords in Washington and British Columbia. An unidentified Euplokamis, which may prove to be E. dunlapae, has been seen occasionally on video in Monterey Bay. See Mills 1987, Can. J. Zool. 65: 2661–2668 (description, behavior, larvae, depth distribution in British Columbian fjords); Mackie, Mills, and Singla 1988, Zoomorphology 107: 319–337 (prey capture and morphology of prehensile side branches on tentacles); Mackie, Mills, and Singla 1992, Biol. Bull. 182: 248–256 (giant axons and escape swimming). Color photograph in Wrobel and Mills 1998 and 2003, p. 62.

HAECKELIIDAE

Haeckelia beehleri (Mayer, 1912). Usually <1 cm, occasionally seen near the surface by divers, sometimes together with *H. bimaculata* and/or *H. rubra*. Body wall has a distinct green tint. Color photograph in Wrobel and Mills 1998 and 2003, p. 59.

Haeckelia bimaculata Carré and Carré, 1989. A tiny (<3 mm long) species, sometimes seen near the surface by very observant divers. See Carré and Carré 1989, Comptes Rendus de l'Académie des Sciences, Paris, 308 (série III): 321–327. Like *H. rubra*, this species uses cnidocysts from narcomedusan prey in its tentacles instead of colloblasts. Color photograph in Wrobel and Mills 1998 and 2003, p. 59.

Haeckelia rubra (Kölliker, 1853) (=Euchlora rubra). Usually <1 cm and has cnidocysts instead of colloblasts on its tentacles; the cnidocysts are obtained from narcomedusan prey, much in the way some nudibranchs obtain them from hydroids or sea anemones. See Mills and Miller 1984, Mar. Biol. 78: 215–221 (feeding behavior); Carré and Carré 1980, Cah. Biol. Mar. 21:

221–226 (cnidocysts and feeding); Carré, Carré, and Mills 1989, Tissue and Cell 21: 723–734 (cnidocysts in *H. rubra* and narcomedusan prey). Color photograph in Wrobel and Mills 1998 and 2003, p. 59.

LAMPEIDAE

Lampea pancerina (Chun, 1879). A rare visitor to central and southern California. Several species of Lampea could be found in our region, all reaching several centimeters in length. All feed, perhaps exclusively, on salps, to which they may attach and flatten out, looking like parasites, as they feed; large Lampea can ingest whole salp chains. Color photograph in Wrobel and Mills 1998 and 2003, p. 60.

MERTENSIIDAE

Charistephane fugiens Chun, 1879. The refractive index of this highly flattened species is so similar to that of water that it is easily missed among other animals in midwater trawl samples; up to about 2 cm in length. Front and side-view photographs in Wrobel and Mills 1998 and 2003, p. 62.

Undescribed mertensiid. A cydippid to about 2 cm in length, with pink tentacles having high numbers of side branches (tentilla) that look like a fuzzy cloud when extended underwater, is collected occasionally at least from central California and the Puget Sound/Strait of Georgia region. This may be the species erroneously called "Mertensia ovum" in the previous edition; M. ovum is an Atlantic boreal and arctic species not known from the Pacific (alternately, Torrey [1904] mistakenly labeled his drawing of Hormiphora californensis (see below) as M. ovum, which may be the origin of this name in the California fauna in previous editions of this book). Color photograph in Wrobel and Mills 1998 and 2003, p. 63.

PLEUROBRACHIIDAE

Hormiphora californensis (Torrey, 1904). The original description, as Euplokamis californensis, is incomplete, and the figure accompanying it is unfortunately mislabeled as "Mertensia ovum"; occurs at least off San Diego and Santa Barbara and in Friday Harbor with Pleurobrachia bachei and may be substantially larger—to about 3 cm long—but most casual observers will not notice this second species as different. Color photograph in Wrobel and Mills 1998 and 2003, p. 60.

Hormiphora sp. (undescribed). This approximately 3-cm-long Monterey Bay species was treated in the unpublished master's thesis of Stanford (1931) under the nomen nudum Hormiphora coeca. It is possible that it is the same as *H. californensis*, but the branched or diverticulate meridional canals described by Stanford appear to differentiate the two species. Hormiphora spp. on our coast are rarely recognized by the casual observer to be different from *Pleurobrachia bachei*.

Pleurobrachia bachei A. Agassiz, 1860. Probably the most common ctenophore in northeast Pacific coastal waters, to about 1.5 cm long, frequently occurring in great numbers and sometimes left by outgoing tides on the beaches, looking like glassy marbles. See Hirota 1974, Fish. Bull. 72: 295–335 (natural history); Tamm and Moss 1985, J. Exp. Biol. 114: 443–461 (spin feeding in the related *P. pileus*). Color photograph in Wrobel and Mills 1998 and 2003, p. 62.

Order Platyctenida

COELOPLANIDAE

*Vallicula multiformis Rankin, 1956. This small warm-water benthic ctenophore, apparently native to the Caribbean, was seen briefly in shallow water in San Diego late in the El Niño summer of 1997, but disappeared when the water cooled down to normal temperatures (Constance Gramlich and George Matsumoto, personal communication). It can occur on a variety of substrates including algae, eelgrass, rock, and floats. It has also been collected in Hawaii on floats.

Order Thalassocalycida

THALASSOCALYCIDAE

Thalassocalyce sp. Probably *T. inconstans* Madin and Harbison, 1978, described from the Sargasso Sea and Northwest Atlantic slope water, which can reach at least 15 cm in diameter, but specimens seen near shore in our waters are usually much smaller juveniles (plate 75H). As it has become evident that this fragile species is not so uncommon, one wonders if more than one species of *Thalassocalyce* exist under a single name; specific differences have not yet been established. See Madin and Harbison 1978, Bull. Mar. Sci. 28: 680–687. Color photograph in Wrobel and Mills 1998 and 2003, p. 63.

Order Lobata

BATHOCYROIDAE

Bathocyroe fosteri Madin and Harbison, 1978. This not-uncommon species, reaching 4 cm across the lobes, was described from the northwest Atlantic, and it is possible that more than one species of *Bathocyroe* exists under this single name; it is common in deep water off California and easily distinguished by its flap-swimming (but see also *Ocyropsis*). See Madin and Harbison 1978, Bull. Mar. Sci. 58: 559–564. Color photograph in Wrobel and Mills 1998 and 2003, p. 64.

BOLINOPSIDAE

Bolinopsis infundibulum (O. F. Müller, 1776). This common arctic and boreal lobate species occurs from the Bering Sea to California, from the surface to about 400 m, reaching lengths of up to 15 cm, but near-shore specimens along our coast are usually much smaller. (Bolinopsis off central Mexico are apparently B. vitrea [L. Agassiz, 1860], a subtropical species). Feeding behavior described by Matsumoto and Harbison (1993). Color photograph in Wrobel and Mills 1998 and 2003, p. 64.

EURHAMPHAEIDAE

Deiopea kaloktenota Chun, 1879. Known from several sites worldwide, this distinctive smaller lobate (to 4.5 cm) may be a younger (and usually shallower) stage of *Kiyohimea*, the only other known ctenophore with widely spaced ctenes, but the morphology of young stages of *Kiyohimea* is not yet known. Color photograph in Wrobel and Mills 1998 and 2003, p. 65.

*Eurhamphaea vexilligera Gegenbauer, 1856. A warm water species to several centimeters in length that, in some years, is encountered in the southern end of our area. This distinctive lobate has a pair of long filamentous "tails" trailing from the aboral end and releases luminescent ink from sacs near the comb rows when disturbed. Feeding behavior described by Matsumoto and Harbison (1993).

Kiyohimea aurita Komai and Tokioka, 1940. Described from a specimen found near the Seto Marine Biological Laboratory in Japan that had found its way inshore and was possibly damaged, having tentacle bulbs but no tentacles; body semicircular at the aboral end. Entire, undamaged specimens of this extremely fragile species are rarely collected, but may reach 30 cm or more in length.

Kiyohimea usagi Matsumoto and Robison, 1992. A large, very fragile, deep water species described from Monterey Bay, differentiated from *K. aurita* by having tentacles and being more V-shaped. See Matsumoto and Robison 1992, Bull. Mar. Sci. 51: 19–29; color photograph in Wrobel and Mills 1998 and 2003, p. 65. The two species of *Kiyohimea* could very likely be the same, in which case the name *K. aurita* has precedence.

LEUCOTHEIDAE

Leucothea pulchra Matsumoto, 1988. Described from Monterey Bay and near Catalina Island, this species, which may be 25 cm or more in length, is similar to the more cosmopolitan L. multicornis (Quoy and Gaimard, 1824). See Hamner, Strand, Matsumoto, and Hamner 1987, Limnol. Oceanogr. 32: 645–652 (foraging behavior); Matsumoto 1988, J. Plankton Res. 10: 301–311 (description and feeding); Matsumoto and Hamner 1988, Mar. Biol. 97: 551–558 (swimming and feeding behavior). Color photograph in Wrobel and Mills 1998 and 2003, p. 65.

OCYROPSIDAE

Ocyropsis maculata (Rang, 1828). This flap-swimming, surface-dwelling species to several centimeters long is occasionally seen off Catalina Island and other southern California sites, where its occurrence probably best corresponds with strong El Niños, including that of 1997. The species name recalls the pair of large, dark, diffuse spots on the lobes—other species of Ocyropsis do not have these spots. Feeding behavior described by Matsumoto and Harbison (1993). Although most ctenophores are hermaphrodites, this genus usually has separate sexes (see Harbison and Miller 1986, Mar. Biol. 90: 413–424). Color photograph in Wrobel and Mills 1998 and 2003, p. 66.

FAMILY UNKNOWN

Undescribed "giant lobate." Distinctive species only seen as an adult in deep water. Its younger stages have not been described, but should be readily distinguished by the lack of auricles.

Order Cestida

CESTIDAE

Cestum veneris Lesueur, 1813. Venus' girdle. Uncommon from central California south; cosmopolitan in warmer waters where

* = Not in key.

it may reach over 1 m in length. Feeding behavior described by Matsumoto and Harbison (1993). Color photograph in Wrobel and Mills 1998 and 2003, p. 66.

Velamen parallelum (Fol, 1869). This very fast (often described as "darting"), small (to 20 cm) "Venus' girdle" occurs fairly often from central California south. Feeding behavior described by Matsumoto and Harbison (1993). Color photograph in Wrobel and Mills 1998 and 2003, p. 67.

Order Beroida

BEROIDAE

Feeding behavior described by Matsumoto and Harbison (1993). Diversity of oral macrocilia and possible concomitant diet differences are described by Tamm and Tamm (1993).

Beroe abyssicola Mortensen, 1927. A usually deep water species reaching several centimeters in length, but sometimes also found at the surface, distinguished by its darkly pigmented gut; Vancouver Island to central California. See Arai 1988, Contrib. Nat. Sci. Roy. British Columbia Mus. 9: 1–7 (redescription); Mills and McLean 1991, Dis. Aquat. Org. 10: 211–216 (parasitic dinoflagellates on comb rows). Color photograph in Wrobel and Mills 1998 and 2003, p. 67.

Beroe ?cucumis Fabricius, 1780. A several-centimeter-long surface species in central California that may also be taken as deep as several hundred meters off southern California; corresponds fairly well to the description of *B. cucumis*, a bipolar arctic species, but it has not been demonstrated that the California specimens are really the same as those known from the Arctic. Color photograph in Wrobel and Mills 1998 and 2003, p. 68.

Beroe forskalii Milne Edwards, 1841. Probably an oceanic species, but seen fairly often along the California coast, where it reaches several cm in length. See Tamm and Tamm 1991, Biol. Bull. 181: 463–473 (how *Beroe* keeps its mouth shut using epithelial adhesion while swimming in a forward direction). Color photograph in Wrobel and Mills 1998 and 2003, p. 68.

Beroe gracilis Künne, 1939. A small species, often <1 cm long, described from near Helgoland in the northeast Atlantic, seen occasionally in swarms off central California and also collected individually in Friday Harbor. Probably more widely distributed, but not often specifically identified. Color photograph in Wrobel and Mills 1998 and 2003, p. 68.

Beroe mitrata (Moser, 1907). An infrequent visitor, to several centimeters cm in length. This highly mobile ctenophore (which can turn itself inside out), known also from Japan and the Mediterranean, may be an oceanic resident that sometimes is transported inshore. Color photograph in Wrobel and Mills 1998 and 2003, p. 69.

References

- Bigelow, H. B. 1912. Reports on the scientific results of the expedition to the eastern tropical Pacific 1904–05. XXVI. The ctenophores. Bull. Mus. Comp. Zool. Harvard 54: 369–404.
- Cairns, S. D., D. R. Calder, A. Brinckmann-Voss, C. B. Castro, D. G. Fautin, P. R. Pugh, C. E. Mills, W. C. Jaap, M. N. Arai, S. H. D. Haddock, and D. M. Opresko 2002. Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora, 2nd edition. American Fisheries Society Special Publication No. 28, Bethesda, MD, 115 pp.
- Chun, C. 1880. Die Ctenophoren des Golfes von Neapel. Fauna und Flora des Golfes von Neapel 1: 313 pp.
- Esterly, C. O. 1914. A study of the occurrence and manner of distribution of the Ctenophora of the San Diego region. Univ. Cal. Publ. Zool. 13: 21–38
- Haddock, S. H. D. and J. F. Case 1995. Not all ctenophores are bioluminescent: *Pleurobrachia*. Biol. Bull. 189: 356–362.
- Harbison, G.R. 1985. On the classification and evolution of the Ctenophora. In The origins and relationships of lower invertebrates.
 S. Conway Morris, J. D. George, R. Gibson, H. M. Platt, eds. London: Systematics Assoc. Spec. Vol. 28, London, pp. 78–100.
- Hyman, L. H. 1940. The Invertebrates: Protozoa through Ctenophora, Vol. I. McGraw-Hill (Ctenophora, pp. 662–696; also Vol. V, 1959, Retrospect, pp. 730–731).
- Komai, T. 1918. On ctenophores of the neighborhood of Misaki. Annot. Zool. Jap. 9: 452–474.
- Matsumoto, G. I. and G. R. Harbison 1993. In situ observations of foraging, feeding, and escape behavior in three orders of oceanic ctenophores; Lobata, Cestida and Beroida. Mar. Biol. 117: 279–287.
- Mayer, A. G. 1911. Ctenophores of the Atlantic coast of North America. Carnegie Institution of Washington Publication 162, 58 pp.
- Mills, C. E. 1987. Phylum Ctenophora. In Marine invertebrates of the Pacific Northwest, pp. 79–81. E. N. Kozloff, ed. Seattle: University of Washington Press.
- Mills, C. E. 1996. Additions and corrections to the keys to Hydromedusae, Hydroid polyps, Siphonophora, Stauromedusan Scyphozoa, Actiniaria, and Ctenophora, pp. 487–491. In Marine invertebrates of the Pacific Northwest, with Revisions and Corrections. E. N. Kozloff, ed. Seattle: University of Washington Press.
- Mills, C. E. Internet since 1998. Phylum Ctenophora: list of all valid species names. Electronic internet document available at http://fac-ulty.washington.edu/cemills/Ctenolist.html. Published by the author, Web page established March 1998, frequently updated (see date at end of Web page).
- Podar, M., S. H. D. Haddock, M. L. Sogin, and G. R. Harbison 2001. A molecular phylogenetic framework for the phylum Ctenophora using 18S rRNA genes. Molecular Phylogenetics and Evolution 21: 218–230.
- Stanford, L. O. 1931. Studies on the ctenophores of Monterey Bay. Master's of arts thesis, Department of Biology, Stanford University, 67 pp.
- Tamm, S. 1973. Mechanisms of ciliary co-ordination in ctenophores. J. Exp. Biol. 59: 231–245.
- Tamm, S. L. and S. Tamm 1993. Diversity of macrociliary size, tooth patterns, and distribution in *Beroe* (Ctenophora). Zoomorphology 113: 79–89.
- Torrey, H. B. 1904. The ctenophores of the San Diego Region. Univ. Cal. Publ. Zool. 2: 45–51.
- Wrobel, D. and C. Mills 1998 and 2003. Pacific Coast Pelagic Invertebrates: a Guide to the Common Gelatinous Animals. Sea Challengers and the Monterey Bay Aquarium, Monterey, California, 108 pp.