Intertidal Invertebrates of California

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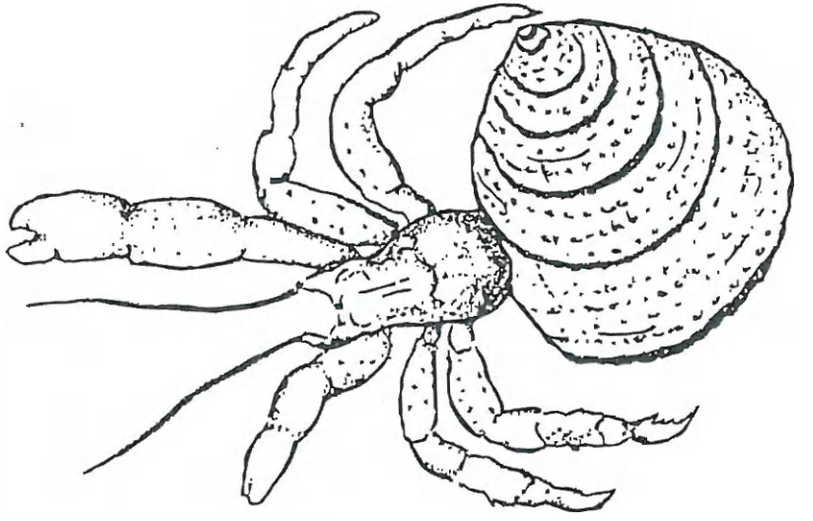
WITH 31 TEXT CONTRIBUTORS



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Chapter 6

Bryozoa and Entoprocta: *The Moss Animals*

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The groups Ectoprocta and Entoprocta, formerly united in the phylum Bryozoa (=Polyzoa), differ in many respects and are now generally treated as separate phyla. The modern tendency is to retain the term Bryozoa for the Ectoprocta only (e.g., Mayr, 1968; J. Soule & D. Soule, 1968; Ryland, 1970; Larwood, 1973), and this treatment is followed here. The phyla Bryozoa and Entoprocta are treated separately below.

The Bryozoa, or Ectoprocta, are virtually all colonial forms, with each colony (zoarium) composed of many small attached individuals (zooids). A colony originates from a single, sexually produced individual (the ancestrula) and increases by asexual budding of new individuals. Bryozoans are widely distributed in the sea, and many are found on rocky shores that are exposed at only the lowest tides, or on harbor pilings or ships' hulls. At first glance some colonies may be mistaken for bushy types of hydroids, branching corals, or marine algae.

The individual zooids in a bryozoan colony are usually less than 1 mm long, and each is encased in a secreted outer cuticle or exoskeleton, which stiffens the colony and provides support and protection for the enclosed soft parts. The exoskeleton surrounding a single individual is termed the zooecium. It is provided with an opening (the aperture) through which the zooid may extend its tentacles to feed, and into which it can withdraw rapidly when disturbed. In some groups the aperture is covered by a hinged lid (the operculum).

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The individual zooids are composed of two main structural parts, the cystid and the polypide. The cystid consists of the boxlike zooecium and the living layers of the body wall that line the zooecium and surround the body cavity or perivisceral coelom. The polypide includes the lophophore, which bears the circlet of tentacles that surround the mouth, the tentacle sheath that encases the lophophore when retracted, and the viscera and associated muscles. The polypide moves conspicuously when the individual extends to feed or withdraws inside the zooecium.

Bryozoans feed on bacteria, phytoplankton, other small organisms, and tiny particles of organic detritus, which are swept to the mouth in water currents created by the ciliated tentacles. The mouth lies in the center of the circle formed by the bases of the tentacles. The gut is U-shaped, and the anus empties on the wall of the membranous tentacle sheath, outside the circlet of tentacles, hence the name "ecto-procta."

Feeding individuals (autozooids) usually form the major portion of a bryozoan colony. However, many bryozoan colonies contain additional zooids (collectively called heterozooids) that are markedly modified in connection with particular functions, such as protection, reproduction, brooding of embryos, anchorage to the substratum, or provision of joints in the colony (see Silén, 1977). Among the specialized heterozooids, the protective avicularia are usually smaller than the autozooids, but some are large and conspicuous. They may replace entire autozooids, or may originate directly from

the individual zooecia. The avicularian polypide is greatly reduced or absent, and the avicularium consists mainly of a small cystid equipped with an oversized operculum and the muscles to operate it. Stalked avicularia resemble the heads of birds, the operculum operating as a lower jaw that can be opened wide or snapped shut on small intruding animals. Sessile avicularia look like small boxes or knobs, each bearing on its free surface an enlarged operculum that can be opened or closed like a movable jaw. The avicularia can handle small crustaceans (see *Bugula californica*, 6.4) but are of little use against such bryozoan predators as browsing nudibranchs and fishes.

Living ectoprocts are most commonly subdivided into two classes: the Gymnolaemata, a large group of species nearly all marine in habitat, and the Phylactolaemata, a smaller group of freshwater species not considered here, although they are widespread. The Gymnolaemata in this chapter fall into three orders, two of which (orders Ctenostomata and Cyclostomata) are relatively small, whereas the third (order Cheilostomata) is large and includes more than half the species considered.

A variety of reproductive modes is found in bryozoans. Sexual reproduction usually results in the production of new colonies, whereas asexual reproduction, by budding, increases the number of zooids within an existing colony. Most bryozoans of the order Cheilostomata are considered to be hermaphroditic, but cross-fertilization between autozooids or colonies occurs. In some species the male or female gonads mature at different times (sequentially), preventing self-fertilization. Reproduction in most bryozoan species has not been studied live or histologically, but a few cheilostomes are known to have morphologically different individual male and female zooecia (e.g., *Hippothoa*) in the same colony (Silén, 1977). Sperm release through tentacle tips has been observed in some species (Silén, 1966; Bullivant, 1967).

The Ctenostomata and some cheilostomes, like the members of the freshwater class Phylactolaemata, have only a membranous sac for the maturation of ova, but most cheilostomes produce external structures called ovicells within which ova are brooded (Ström, 1977). The ovicell is a very specialized structure that lacks ovaries, testes, and polypide. It may originate from a single zooecium or may have a complex origin. In cases that have been studied, the ovicell chamber is formed by contributions from (1) the maternal zooecium that furnishes the egg, (2) the transverse walls of the maternal and next distal (anterior) zooecium, and (3) in some instances the frontal (ventral) surfaces of adjacent zooecia (Ryland, 1968; D. Soule, 1973; Woollacott & Zimmer, 1972b). Ovicells may be hidden (immersed) in some species, but in many species they form a distinctive bulge or hood anterior to the aperture, which may or may not be closed by the operculum. Ovicells, when present, offer good characters for the identification of species.

Female reproductive structures in the order Cyclostomata are quite different from the ovicells of cheilostomes. In the family Crisiidae they are single whole individuals (gonozooids) modified for egg production and brooding. However, in most cyclostomes the gonozooid expands and merges with adjacent autozooids or extrazooidal spaces to form a composite structure better termed an oecium. Cyclostomes may be sequentially hermaphroditic, or the individuals in the colony may be of separate sexes (Borg, 1926; Silén, 1977).

There are several types of larvae among the bryozoans. In some species eggs and sperm are shed into the sea, where fertilization and development of a planktonic larval stage occur. In most species, however, the eggs are retained in ovicells, gonozooids, or oecia, and the embryos are brooded for a time. In some ctenostomes and some cheilostomes (e.g., *Membranipora tuberculata*, 6.1), the planktonic larvae are known as cyphonautes, tiny, free-swimming forms with a bivalve shell. Although the cyphonautes in some species feed on plankton (planktotrophic), others lack a complete digestive tract and are nourished by stored yolk (lecithotrophic). Other non-feeding cheilostome larvae, called coronate larvae, lack shells and have ciliary girdles of various types for swimming. Some coronate larvae are non-feeding spheroids, covered with cilia, that do not move about extensively.

In the order Cyclostomata the early embryonic stages undergo an asexual multiplication (polyembryony) within the gonozooid or oecium. A single fertilized egg undergoes cleavage to form a primary embryo. This divides into secondary and sometimes tertiary embryos, each of which goes on to form a larva. The larvae known are highly modified lecithotrophic spheroids (Borg, 1926; Ström, 1977).

In any case, the bryozoan larva typically swims or moves about for a time, after which it becomes negatively phototactic, tests the substratum, and settles. The larva attaches temporarily by sticky secretions; subsequent eversion of the metasomal sac accomplishes

permanent attachment. Metamorphosis follows rapidly and the adult ancestrula of the colony results (see Zimmer & Woollacott (1977) on metamorphosis; J. Soule (1973) and J. Soule & D. Soule (1977) on bioadhesives).

The bryozoans are an ancient group, with a fossil record extending from the early Paleozoic. Between 3,000 and 4,000 living species of bryozoans are known in the world's oceans. Nearly 250 are recorded from California, and though many are known only from deeper water, the shore collector will still find a bewildering variety much greater than that portrayed in this chapter. Identification of some forms is difficult, but the non-specialist can learn to recognize the more distinctive common species.

Colony growth form is a good starting point in identification. In general, colonies tend to be either (1) recumbent (adnate), with the whole colony closely adhering to the substratum, or (2) erect, with the colony attached over a smaller area and sending branches or processes composed of many individuals into the water above. Some caution must be exercised, for certain species may form erect growths in quiet waters and produce flattened encrustations in turbulent areas. Recumbent bryozoans include (1) soft-bodied species, which either form fleshy, gelatinous clumps or send creeping stolons along the substratum, (2) encrusting species with a mineralized exoskeleton that may be lightly calcified (flexible) or heavily calcified (rigid), and (3) tubular species. Erect bryozoans include those that are (1) branching, and often quite bushy, (2) foliaceous or flustraform (with flattened leaflike or bladelike processes), (3) fenestrate or reteporid (with upright stiffened blades fused into a latticelike or lacelike structure), and (4) tubular.

Other characters used in bryozoan taxonomy relate to the size, shape, ornamentation (spines, pits, ridges, and pores), and degree of calcification of individual zooecia, as well as the form, number, and placement of heterozooids such as avicularia. A hand lens (10× to 15×) is essential for field recognition of most common genera, and it is folly to attempt more serious study of the bryozoans without a good stereoscopic dissecting microscope providing magnifications to at least 70×.

Excellent general accounts of the Bryozoa are found in Brien (1960a), Hyman (1959), and Ryland (1970). An outstanding recent volume (Woollacott & Zimmer, 1977) contains reviews of numerous aspects of bryozoan biology, including sexual reproduction and development (Franzén, 1977; Ström, 1977; Zimmer & Woollacott, 1977a,b), polymorphism (Silén, 1977), feeding (Winston, 1977), life history strategies (Farmer, 1977; J. Soule & D. Soule, 1977), aging (Gordon, 1977), detailed structure of various parts and systems (Bobin, 1977; Lutaud, 1977; Sandberg, 1977), behavior (Ryland, 1977), and population genetics (Schopf, 1977). Reviews of recent research are presented in Annoscia (1968), Boardman, Cheetham & Oliver (1973), Larwood (1973), McCammon & Reynolds (1977), Pouyet (1975), and Ryland (1967, 1974, 1976). Relationships of Bryozoa with other phyla are considered by Brien (1960a,b), Farmer (1977), Hyman (1959), Nielsen (1971, 1977a,b), and Zimmer (1973). The best comprehensive systematic study for the Pacific coast of the Americas is the three-volume work of Osburn (1950, 1952, 1953). Keys useful for identification of California shore species appear in J. Soule, D. Soule & Pinter (1975) and Ross (1970). Bryozoans of the Gulf of California and Baja California are covered in J. Soule (1959, 1961, 1963) and D. Soule & J. Soule (1964).

The phylum Entoprocta includes small animals in which the body consists of a slender stalk topped by an expanded flowerlike calyx. The calyx contains most of the viscera and bears distally a ring of ciliated tentacles used to capture microscopic, particulate food. Superficially, entoproct individuals resemble hydroids, from which they are easily distinguished by their behavior. When disturbed, the zooids roll their tentacles inward and the stalk bends, bringing the calyx down against the substratum, hence the common name "nodding heads," often applied to the group. The entoprocts most commonly seen form colonies.

About 120 species of entoprocts are known for the world. In California, entoprocts are relatively common on the undersurfaces of intertidal rocks, in the fouling community on floats and pilings in bays, and as commensals on the bodies of other animals, but their small size makes them inconspicuous. For more detailed accounts see Brien (1959), Hyman (1951), Nielsen (1971), Mariscal (1975a), and D. Soule & J. Soule (1965); Mariscal (1975b) provides a key to the California species.

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Anasca / Family Membraniporidae

6.1 Membranipora tuberculata (Bosc, 1802)

Commonly encrusted on floating brown algae, especially the kelps *Macrocystis* and *Cystoseira*, also on smaller plants inshore, especially the red alga *Gelidium*, occasionally on shells or wood, low intertidal zone to shallow subtidal depths; prevalent in warm temperate and tropical waters of Atlantic, Pacific, and Indian Oceans, wherever floating *Sargassum* or *Fucus* is found; Pleistocene fossils known from Santa Monica (Los Angeles Co.) and Newport Beach (Orange Co.).

Colony forming a white crust to several centimeters in diameter, consisting of a single layer of zooids and having a fine reticulate honeycomb appearance; individuals 0.5–0.8 mm long, rectangular, covered by a lightly calcified membrane, and with a heavily calcified rim, the rim bearing calcified tubercles at the distal corners, as well as tiny spines projecting inward from side of rim toward center of individual.

The membraniporids are the only members of the order *Cheilostomata* known to have a planktotrophic cyphonautes larva, a free-swimming, plankton-feeding stage with a triangular bivalve shell. This settles and metamorphoses to an ancestrula (often double or twinned), which buds to form a flat, encrusting colony. The relatively transparent living colonies are excellent for observation under the microscope.

Membranipora tuberculata is one of three species in the genus commonly encrusting the kelp *Macrocystis*; under favorable conditions colonies grow rapidly and may coalesce to cover whole kelp blades in 3–4 weeks. Overgrown blades often bear 0.5–1 kg of bryozoans per m^2 of blade surface, and occasionally perhaps ten times as much.

Although *Membranipora* species are among the best-known marine bryozoans, the species have often been confused. **Membranipora membranacea** (Linnaeus) is primarily an Atlantic species; many Pacific identifications of that species may actually be **M. villosa** Hincks, which, in turn, may be a synonym of *M. isabelleana* (d'Orbigny). Usually *M. tuberculata* is much more heavily calcified than the other species; however, young colonies may be difficult to differentiate.

For details of systematics, structure, reproduction, and ecology, see Atkins (1955a,b), Banta (1969), Bobin (1977), Franzén (1956), Haderlie (1968a), Lutaud (1959, 1961, 1977), O'Donoghue (1927), Osburn (1950), Pinter (1969), Robertson (1908, as *M. tehuelca*), Rucker (1968), Ryland (1977), Silén (1944a,b,c, 1966), D. Soule & J. Soule (1967), J. Soule & Duff (1957), J. Soule, D. Soule & Pinter (1975, keys and figures of species), Strathmann (1973), Turner & Strachan (1969), Winston (1977, 1978), Woollacott & North (1971), and Woollacott & Zimmer (1977, index).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Anasca / Family Thalamoporellidae

6.2 Thalamoporella californica (Levinsen, 1909)

An abundant fouling organism on pilings, wharves, ship hulls, rocks, and some algae in shallow warm waters, low intertidal zone to 145 m; northern Channel Islands and Point Conception (Santa Barbara Co.) to Colombia and Galápagos Islands; fossils in Pleistocene deposits at Newport Beach (Orange Co.).

Colony consisting of a basal crust with numerous, coarse, upright projections; projections dichotomously branched and consisting of many zooids; individuals 0.5–0.6 mm long and about 0.3 mm wide, arched distally above the aperture; cryptocyst (calcareous plate underlying transparent front wall of zooecium) porous, and with a large hole on either side, near operculum, through which muscles pass to the membranous frontal wall; overall, individual resembling a flask with two handles at the neck.

Many ovicells, in the form of bilobed calcareous hoods that rise above the individuals, are easily seen when the colony is fertile. Up to four large pink ova can be seen through the translucent centers of the ovicells. Members of the genus *Thalamoporella* possess unique internal spicules, which can be seen only under high magnification by crushing a portion of a dried specimen in a drop of water on a microscope slide. The spicules of *T. californica* are all shaped like curved calipers.

This species is one of the most important bryozoans en-

crusting the giant kelp *Macrocystis*; where best developed, under dense kelp canopies, it averages 284 gm per m² of blade surface and constitutes nearly half the total animal biomass present. Inshore plants most commonly bearing colonies in southern California are the red algae *Gelidium*, *Lithothrix*, *Pterocladia*, and *Gigartina*, and the brown alga *Egregia*.

The anatomy and embryology of a related species (*T. evelinae*), which has separate male and female zooids borne on the same colony, are beautifully shown in Marcus (1941). See also Osburn (1950), Pinter (1969), Powell & Cook (1966), Robertson (1908, as *T. razieri*), Rucker (1968), Silén (1938, 1977), D. Soule & J. Soule (1964), J. Soule & Duff (1957), J. Soule & D. Soule (1970), J. Soule, D. Soule & Pinter (1975), Turner & Strachan (1969), Winston (1978), and Woollacott & North (1971).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Anasca / Family Scrupocellariidae

6.3 Tricellaria occidentalis (Trask, 1857)

On rocks and algae, low intertidal zone to 30 m or more; also on offshore kelp; Queen Charlotte Islands (British Columbia) to Isla Cedros (Baja California); Japan; abundant in San Francisco Bay area.

Colony forming white bushy tuft not over 2 cm high; branches arising alternately, the node joints yellow-brown, the internodes usually formed by three zooecia; individual zooecia about 0.4 mm long, with a frontal membranous covering bordered by five to seven long spines; a specialized spine (scutum) projecting from border out over frontal membrane below midline area; avicularia present; ovicells large, globose, and perforate.

A nominal subspecies, T. occidentalis catalinensis (Robertson), generally having a more elaborate scutum, is abundant in warmer waters off southern California.

See Mawatari (1951b), Osburn (1950), Pinter (1969), Robertson (1905, as *Menipea occidentalis*), J. Soule, D. Soule & Pinter (1975), and Woollacott & North (1971).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Anasca / Family Bicellariellidae

6.4 Bugula californica (Robertson, 1905)

Commonly found on rocks and mollusk shells in shallow waters to 60 m depth; British Columbia to Galápagos Islands, especially Channel Islands.

Colony composed of one to several fronds, each frond to 5 cm or more in height, formed by spiral whorls of branches, giving the colony the appearance of having been trimmed evenly at several levels; color usually whitish, but sometimes tan, or (during sexual reproduction) somewhat orange; branches formed of two rows of individuals, widening to four or five zooids at bifurcation points; individuals about 0.5–0.6 mm long and 0.2–0.25 mm wide; examination with hand lens showing three spines at end of each zooid, globular ovicells that sit straight across end of zooid, and large "bird's head" avicularia attached at middle of side walls.

The *Bugula californica* reported as a fouling organism from ports such as San Francisco Bay and Los Angeles harbor has recently been recognized as B. stolonifera Ryland. Although very similar to *B. californica*, *B. stolonifera* is grayish and lacks the distinctive, whorled colony pattern; it is found on both sides of the Atlantic Ocean.

Under a dissecting microscope the activities of the *B. californica* avicularia are readily seen; the ability of avicularia to catch and hold small objects can be demonstrated easily by probing them with a hair, or by introducing copepods, or the nauplius larvae of barnacles or brine shrimp, into the dish. Soule and Soule have seen this species use avicularia of several zooecia to pull apart small crustaceans (caprellid amphipods); the tentacles then directed the fragments into the polypide mouths. Experiments with other species suggest that the avicularia play a role in defending the colony against small disruptive invaders.

The coronate larvae of *B. californica* settle in Los Angeles harbor year around, in warm years. In Monterey Bay they settle in all but the winter months; colonies growing on shallow suspended panels reached a height of 30 mm in 4 months.

See Calvet (1900), Haderlie (1968b, 1969, 1974), Kaufman (1968), Maturo (1959), Mawatari (1946), Osburn (1950), Reish (1963), Robertson (1905), Rucker (1968), Schneider (1963), S. Smith & Haderlie (1969), D. Soule, J. Soule & Henry (1979), J. Soule, D. Soule & Pinter (1975), Thompson & Chow (1955), and Woollacott & North (1971).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Anasca / Family Bicellariellidae

6.5 Bugula neritina (Linnaeus, 1758)

A common fouling organism on harbor installations and boat hulls, low intertidal zone to 80 m depth; Monterey Bay to Canal Zone (Panama) and Galápagos Islands; Gulf of California as far north as Isla Ángel de la Guarda; in warm waters around the world.

Colony bushy, 3–10 cm in height, easily distinguished from similar species by its reddish-brown or purplish-brown color; individuals 0.6–0.8 mm long, 0.2–0.3 mm wide; spines and avicularia absent; ovicell set diagonally at tip of zooecium.

This cosmopolitan species has been studied extensively in many areas because of its abundance and general importance as a fouling organism. The animals may be cultured in the laboratory on a diet of the flagellate *Monochrysis lutheri*.

Individual zooids are hermaphroditic, and sperm are probably released through pores at the tips of the tentacles. Developing coronate larvae are brooded one at a time in large ovicells, each of which consists of a small heterozooid that lacks a differentiated polypide and that combines with parts of both the maternal zooid and the zooid just distal to it. The embryo, surrounded by maternal tissues, is nourished by yolk and other materials from the mother. A placenta-like system aids in the transport of extraembryonic nutrients.

Released larvae swim rapidly by means of cilia; at first they swim toward light, but later some become photonegative. Two pigmented spots, one on each side, appear to be eyespots of a unique type; each contains one cell, probably a photoreceptor, provided with a cluster of unmodified cilia held at right angles to the incoming light. The larvae, still laden with yolk, lack mouths and indeed any trace of a gut. They usually swim for less than 10 hours, then settle, and attach by inversion of an internal sac that, in metamorphosis, gives rise to the ancestrula epidermis. The body, still nearly solid, elongates and forms a cuticle. Larval organs degenerate almost completely, and tissues of the first zooids derive largely or wholly from larval ectoderm. Many environmental factors, such as temperature, light, materials in the water, and character of the substratum, affect attachment and metamorphosis. At Monterey the release and settlement of larvae occur through most of the year; they virtually cease in midwinter (December to February) and reach a peak in June and July. At Los Angeles and San Diego, settlement is most abundant from April through October, but larvae can be obtained in all months.

Growth is rapid. At La Jolla (San Diego Co.), 3-week-old colonies were 8 mm high, with 8 branches and over 50 zooids; at 6 weeks they were 12 mm high, with 32–64 branches and about 300 zooids. Colonies in Monterey harbor on shallow submerged panels reached a height of 120 mm in 4–6 months, and some colonies persisted for at least 14 months. Since sexual reproduction begins 6–8 weeks after settlement (La Jolla), three or four generations a year are possible.

Bugula neritina rarely settles on plants other than the giant kelp *Macrocystis*, and it is not abundant there. It provides a favorite perch for the skeleton shrimp *Caprella californica* (228).

See especially Woollacott & Zimmer (1971, 1977, 1978); see also Bullivant (1967, 1968b), Calvet (1900), Coe (1932), Gooch & Schopf (1970), Grave (1930), Haderlie (1968b, 1969, 1974), Hammen & Osborne (1959), Keith (1971), Loeb & Walker (1977), Lynch (1947, 1961), Maturo (1959), Mawatari (1951a), Miller (1946), Osburn (1950), Pinter (1969), Reish (1963), Rucker (1968), Ryland (1960, 1976, 1977), S. Smith & Haderlie (1969), J. Soule, D. Soule & Pinter (1975), Ström (1977), Winston (1978), Woollacott & North (197.), Woollacott & Zimmer (1972a,b,c, 1975), and Zimmer & Woollacott (1977a,b).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Anasca / Family Bicellariellidae

6.6 Dendrobeania laxa (Robertson, 1905)

In shaded areas protected from strong surf, low intertidal zone on rocky coasts; subtidal to 90 m; British Columbia to San Pedro (Los Angeles Co.).

Colony extensive, recumbent, the fronds numerous, curved, petal-like, of variable size and shape; rootlike attachment processes (radicles) intertwining with fronds to form a tangled mass; individuals about 0.7–0.9 mm long, with an uncalcified frontal membrane surrounded by heavy spines; avicularia lacking; ovicell round, prominent, and faintly striated.

See Calvet (1900), Osburn (1950), and J. Soule, D. Soule & Pinter (1975).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Ascophora / Family Schizoporellidae

6.7 Schizoporella unicornis (Johnston, 1847)

Common on rocks and shells along open coast and on wharf pilings in bays and harbors, low intertidal zone to 60 m depth; Strait of Georgia (British Columbia) to southern California; Hawaii, Japan; western Europe, Mediterranean Sea.

Colony encrusting, the overall color brown, golden yellow, or reddish orange; zooids hexagonal in shape, each 0.5–0.6 mm long, 0.3–0.4 mm wide, in district longitudinal rows separated by definite grooves; aperture wider than long, with a shallow, U-shaped proximal sinus, and with a tiny tooth inside the aperture at each corner of proximal lip; umbonate frontal wall with many small pores; avicularia, when present, single or paired; ovicell globose, finely perforate, with radiating flutings on surface.

This species is often confused with S. *errata* (Waters) on both Atlantic and Pacific coasts. Ross & McCain (1976) provides evidence of the presence of *S. unicornis* in Spanish Bay (Washington) in 1927. Powell (1970) suggests that *S. unicornis* was introduced to California from Japan in 1932 with Pacific oysters planted at Morro Bay (San Luis Obispo Co.), and that *S. errata* was introduced from the Atlantic coast along with the oyster *Crassostrea virginica*.

Atlantic coast "*S. unicornis*" (=*S. errata*) has been the subject of recent studies on population genetics and calcification of the shell. The exoskeleton contains calcium carbonate in the forms of both calcite and aragonite.

Studies of *S. unicornis* in southern California have shown (1) that sperm are released through pores at the tentacle tips, (2) that the population suffered a high mortality during a "red tide," and (3) that the larvae tend to settle on substrata other than algae.

See Bullivant (1967), Gooch & Schopf (1970), Haderlie (1974), Maturo (1959), Pelluet & Hayes (1936), Pinter (1969), Powell (1970), Reish (1963), Ross & McCain (1976), Rucker (1968), Sandberg (1977), Schopf (1977), Schopf & Allen (1970), Schopf & Gooch (1971), D. Soule & J. Soule (1968), J. Soule, D. Soule & Pinter (1975), Strathmann (1977), Sutherland (1977, 1978), and Winston (1977, 1978).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Ascophora / Family Schizoporellidae

6.8 Hippodiplosia insculpta (Hincks, 1882)

Abundant in lower middle and low intertidal zones on rocky shores, encrusting stones, mollusk shells, hydroids, algae, and other bryozoans; common on *Phyllochaetopterus prolifica* tubes (18.22) on piles in Monterey harbor; subtidal to 234 m; Alaska to Gulf of California and Isla del Coco (Costa Rica); Pleistocene fossils at San Pedro (Los Angeles Co.).

Colony encrusting, to 5 cm or more in diameter, but also rising in double-layered frills or faulike folds; color light yellow or pale tan, light orange when ova are present; individuals 0.5–0.7 mm long, 0.3–0.4 mm wide, rectangular to hexagonal in shape; distinguishable from other species of the genus on this coast by the presence of large globular ovicells that are imperforate but bear radiating striations and by the absence of avicularia.

This species is excellent for observation under the dissecting microscope. Individuals readily extend the lophophore in

freshly collected colonies, and the embryos or larvae can be liberated by rupturing the ovicells carefully with a sharp needle. A comparison of colonies collected at different latitudes shows that individual zooid size may decrease as water temperature increases.

See Calvet (1900), Osburn (1952), J. Soule & Duff (1957), J. Soule, D. Soule & Pinter (1975), Thompson & Chow (1955), and Woollacott & North (1971).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Ascophora / Family Eurystomellidae

6.9 **Eurystomella bilabiata** (Hincks, 1884)

On stones and mollusk shells, low intertidal zone on rocky shores; subtidal to 64 m; Alaska to Bahía de Tenacatita (Mexico); common in central California (Monterey area), but most abundant in waters north of California; Pleistocene fossils from San Pedro (Los Angeles Co.) and Japan.

Colony flat, encrusting in a single-layered sheet to 5 cm or more in diameter; color rose-red, red-orange, or brown; individuals averaging 0.6–0.7 mm long and 0.5 mm wide, smooth and shiny, arranged in a distinct regular pattern in the colony; apertures of zooids large and bell-shaped; frontal wall calcified, imperforate, with a raised umbo in the center; spines and avicularia absent (see also Fig. 12.31).

The species name *bilabiata* of this beautiful and conspicuous form calls attention to the unusual pair of lips or folds that operate with the operculum to close the aperture when the tentacles are withdrawn.

Colonies from central California often bear on their surfaces numerous, small, black folliculinid protozoans. These sessile ciliates inhabit tubular shells from which they extend two ciliated lobes to feed.

Eurystomella bilabiata is preyed upon by the nudibranch *Hopkinsia rosacea* (14.37). The color of the nudibranch closely matches that of rose-red colonies of *E. bilabiata*, and the pigment responsible (hopkinsiaxanthin) appears to be identical in the two species.

See McDonald & Nybakken (1978), Osburn (1952), Robertson (1908, as *Lepralia bilabiata*), J. Soule & Duff (1957), and J. Soule, D. Soule & Pinter (1975).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Ascophora / Family Reteporidae

6.10 **Phidolopora pacifica** (Robertson, 1908)

On rocks in deep, sheltered tidepools and subtidal to 200 m along open coast and in bays; British Columbia to Peru; most abundant in shallow subtidal waters from Oregon to southern California, and common on breakwaters of Los Angeles harbor and at scuba depths around the Channel Islands.

Colony fenestrate, forming an erect, lacy, convoluted mass to 110 mm across and 65 mm high, orange to orange-pink; zooecia to about 0.6 mm long, 0.3 mm wide, frontal avicularia and ovicells often prominent.

The zooids all open on one side of the stiff, lacelike sheets that make up the colony. Water emerging from between the tentacles of feeding zooids passes through the holes in the lace without disruption of incoming feeding currents. The fenestrated form not only provides for more efficient feeding, but it renders the colony more resistant to currents than if it were a solid sheet of zooids.

In Puget Sound (Washington) the sea star *Dermasterias imbricata* (8.3) occasionally feeds on *Phidolopora*.

See Haderlie (1969), Mauzey, Birkeland & Dayton (1968), Osburn (1952), Robertson (1908, as *Retepora pacifica*), J. Soule & Duff (1957), J. Soule, D. Soule & Pinter (1975), Thompson & Chow (1955), Turner, Ebert & Given (1969).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Ascophora / Family Celliporidae

6.11 **Costazia robertsoniae** Canu & Bassler, 1923
(= Celliporina robertsoniae)

Common on rocks and algae, low intertidal zone to 100 m depth along rocky shores; British Columbia to northern Mexico, but most common from Dillon Beach (Marin Co.) to La

Jolla (San Diego Co.); Pleistocene fossils at Santa Monica and San Pedro (both Los Angeles Co.).

Colony rough in appearance, encrusting and forming small nodules or rising in irregularly forked branches to 50 mm or more in height; individuals about 0.6–0.7 mm long and 0.4 mm wide, heavily calcified, with few pores on frontal wall but many pores at edges between adjacent zooids, aperture rounded but with a V-shaped notch; raised avicularia small, lying on each side of the aperture and often above it where an ovicell is lacking; ovicells exposed or embedded, each with a frontal area bearing triangular pores around the edge.

This is one of the bryozoans that most commonly encrust blades of the giant kelp *Macrocystis* from Monterey Bay to Baja California.

See Osburn (1952), Rucker (1968), J. Soule & Duff (1957), J. Soule, D. Soule & Pinter (1975), and Woollacott & North (1971).

Phylum Ectoprocta / Class Gymnolaemata / Order Cheilostomata
Suborder Ascophora / Family Celliporidae

6.12 **Celleporaria brunnea** (Hincks, 1884)
(=Holoporella brunnea)

Common on rocks, shells, worm tubes, or algae, on rocky shores from low intertidal zone to depths of 185 m; on wharf piles in harbors; British Columbia to Colombia and Galápagos Islands; extremely common in Gulf of California; Pleistocene fossils at San Pedro (Los Angeles Co.).

Colony encrusting, to several centimeters in diameter, building a heavy multilayered crust to 10 mm or more in thickness, composed of more or less randomly arranged individuals heaped on one another, often produced into coarse folds and branches; color gray or brown; individuals about 0.6–0.8 mm long, 0.4 mm wide, each with a suboral spike giving the colony a bristly appearance; avicularian mandibles large, distinctive, black or brown; extended tentacles conspicuously blood-red in color.

This is the most common encrusting bryozoan in Monterey harbor. *C. brunnea* larvae settled on submerged panels there in all months of the year; the rate was highest from March through September, lowest in December and January. (In Los Angeles–Long Beach harbor results were similar; larvae did not settle during the winter months on panels at 3 m depth.) At Monterey very little settlement was noted at 15 m depths on panels 215 m from shore. Growth was fastest in colonies just below the level of the lowest tides—one colony here reached a diameter of 6 cm in 7 months. The growth rate declined with increasing depth. Old colonies on pilings become thickened and form globular crustose masses up to 6 cm in diameter.

Living specimens are excellent for study under a dissecting microscope, for the zooids extend readily. Many of the zooids in larger colonies have asymmetrical lophophores, the tentacles on one side being longer than those on the other. In this species, and in *C. albirostris*, localized clusters of zooids appear to behave in a coordinated manner in feeding and in retracting. Retracting zooids often show a curious response involving a writhing of the tentacles against the surface of the colony. These features of asymmetry and behavior are not unique, but appear in some other genera and species as well.

In Monterey harbor, *C. brunnea* is preyed upon by the flatworm *Hoploplana californica* (4.6), which mimics the bryozoan in color and texture. The flatworm eats mainly the older zooids at the centers of the colonies, and thus has little effect on marginal growth. (Both species are shown in Fig. 4.6.)

See especially Haderlie (1968a,b, 1969, 1974); see also Bullivant (1967), Marcus (1938), Osburn (1952), Pinter (1969), Reish (1963), S. Smith & Haderlie (1969), D. Soule, J. Soule & Henry (1979), J. Soule & Duff (1957), J. Soule, D. Soule & Pinter (1975), and Winston (1978).

Phylum Ectoprocta / Class Gymnolaemata / Order Cyclostomata
Suborder Tubuliporina / Family Diastoporidae

6.13 **Diaperoecia californica** (d'Orbigny, 1852)
(=Idmonea californica)

On rocks, mollusk shells, and other hard substrata, from just below the level of the lowest tides to depths over 185 m along rocky shores; British Columbia to Costa Rica; common in

Gulf of California and along Pacific coast of Mexico, and dredged in quantity off Los Angeles harbor and Santa Catalina Island (Channel Islands); Pleistocene fossils from Santa Barbara, and from Santa Monica and San Pedro (both Los Angeles Co.).

Colony coral-like in appearance, the branches erect or spreading, 25 mm or more in height, often anastomosing to form large reticular masses 20–25 cm in diameter and 10 cm high, the branches formed by successive rows of four or five zooids fused together for all or part of their length; individuals tubular, larger than most cyclostomes, averaging 0.22 mm in diameter, curved, bearing circular terminal apertures; reproductive chamber a large individual (gonozooid) usually occurring below bifurcating branches and appearing as a perforate swollen area surrounding the bases of a number of tubules.

One of the most common ectoprocts at scuba-diving depths in southern California, particularly near the tops of natural reefs. The interstices of the branches provide a habitat reminiscent of the crevices between branches on a coral head. Branches of a colony that touch become fused, and growing branches that reach rock surfaces become secondarily attached. Colonies taken in calm, deep water have thin, more erect branches; in those from more-exposed locations the branches are thicker and more flattened. Small colonies are widely distributed, but usually not abundant, on the giant kelp *Macrocystis*.

Anatomy and biology of related forms are covered in Borg (1926), Harmelin (1975), and Nielsen (1970). See also Osburn (1953), Robertson (1910, as *Idmonea californica*), J. Soule & Duff (1957), J. Soule, D. Soule & Pinter (1975), Turner, Ebert & Given (1969), and Woollacott & North (1971).

Phylum Ectoprocta / Class Gymnolaemata / Order Cyclostomata
Suborder Articulata / Family Crisiidae

6.14 **Crisulipora occidentalis** Robertson, 1910

On rocks along open shores, on dock pilings, in clusters of the mollusk *Mytilus* (15.9, 15.10) in sheltered waters, low intertidal zone to 86 m depth; Monterey Bay to Peru; Japan; Brazil; common from San Pedro (Los Angeles Co.) to San Diego, Channel Islands, and Gulf of California.

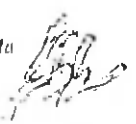
Colony to 30 mm high, white to pale tan, fragile, erect, branching, bushy, with jointed rootlets; autozooids tubular, variable in length, fused at their bases but flaring out separately along branches, averaging 0.12 mm in diameter at tips; apertures located at free tips of zooids and lacking opercula; avicularia absent; female reproductive structures consisting of separate individuals (gonozooids) with inflated bodies much larger than those of autozooids; surface of both autozooids and gonozooids bearing minute perforations.

In gross appearance this species resembles *Bugula* (i.e., 6.4, 6.5) and other related erect bryozoans. However, examination with a hand lens clearly reveals the characteristic features of cyclostome ("round mouth") bryozoans: the tubular shape of the zooids, the round terminal apertures, and the absence of opercula.

The sexes are separate in *C. occidentalis*; only the female colonies possess gonozooids. As often happens in cyclostomes, the embryo subdivides to give rise to numerous larvae; gonozooids may bear many offspring in various stages of development. In Monterey Bay, swimming larvae have been observed to settle and start colonies in all months of the year, but the main settlement is from May through September. Faster-growing colonies reach 50 mm in height in 6–7 months.

For general cyclostome biology, see Borg (1926), Harmelin (1975), Nielsen (1970), Ross (1977), Winston (1977, 1978), and Zimmer & Woollacott (1977a). For *C. occidentalis*, see Coe (1932), Haderlie (1968a,b, 1969, 1974), Nielsen (1970), Osburn (1953), Robertson (1903, 1910), S. Smith & Haderlie (1969), and J. Soule, D. Soule & Pinter (1975).

Phylum Ectoprocta / Class Gymnolaemata / Order Cyclostomata
Suborder Articulata / Family Crisiidae



6.15 **Filicrisia franciscana** (Robertson, 1910)

On rocks and algae on outer coast, on pilings and floats in harbors, upper middle to low intertidal zone and subtidal to 100 m depth; Orca (Alaska) to southern California; Japan.

Colony bushy, 15–25 mm high; branches straight; zooecia

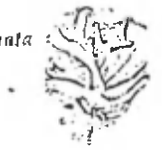
tubular, 0.6–0.9 mm long, three to five per internode; gonozooids swollen and recumbent; colony white, with joints on branches often black and conspicuous.

This small and delicate form occurs higher in the intertidal zone than any other California ectoproct; it attaches to the bases of such red algae as *Endocladia*, *Gelidium*, and *Gastroclonium*, and in higher pools is associated with strands of the green algae *Enteromorpha* and *Chaetomorpha*. Colonies often grow on blades of giant kelp, as well.

Colonies are probably either male or female. Origin of the germ cells and embryonic development have been followed in some detail. At about the 20–24-cell stage, the primary embryo develops multicellular projections from which secondary embryos arise. These, in turn, may develop tertiary embryos. Eventually all embryos, including the primary, develop into larvae that are liberated to swim and settle. In Monterey harbor, settlement occurs from May to October.

See Borg (1926), Coe (1932), Glynn (1965), Haderlie (1968a, 1969), Nielsen (1970), Osburn (1953), Pinter (1969), Robertson (1903, as *Crisia occidentalis*; 1910, as *C. francistana*), J. Soule, D. Soule & Pinter (1975), Woollacott & North (1971), and Zimmer & Woollacott (1977a).

Phylum Ectoprocta / Class Gymnolaemata / Order Ctenostomata / Suborder Carnosa / Family Flustrellidridae



6.16 **Flustrellidra corniculata** (Smitt, 1871)
(=Flustrella corniculata)

A cold-water species characteristic of rocky shores, often growing on calcareous algae and stipes of the large brown alga *Laminaria*, low intertidal zone; subtidal to 75 m or more; Alaska to Point Buchon (San Luis Obispo Co.); northern Europe.

Colony pale tan to dark brown, often 4–6 cm long, forming cylindrical sheath on algal stipes or branching into small cylinders or leafy shapes depending on nature and shape of substratum; feeding individuals about 0.7–0.8 mm long and about 0.4–0.6 mm wide; spines, produced by numerous special zooids, tall, chitinous, branched, giving colony a coarse fuzzy appearance.

This species takes its specific name *corniculata* ("provided with little horns") from the conspicuous spines borne on special zooids. Post-larval development of the polypide and muscles has been followed. A related Atlantic species, *F. hispida*, produces a shell-bearing larva that is nourished by stored yolk and does not feed on plankton. Its attachment and metamorphosis have been studied.

See especially J. Soule (1954, as *Flustrella corniculata*); see also Barrois (1877), Loeb & Walker (1977), Osburn (1953, as *Flustrella corniculata*), Pace (1906), Prouho (1890), Ryland (1960), L. Smith (1973), J. Soule, D. Soule & Pinter (1975), Ström (1977), Winston (1977), and Zimmer & Woollacott (1977a,b).

Phylum Ectoprocta / Class Gymnolaemata / Order Ctenostomata / Suborder Stolonifera / Family Vesiculariidae

6.17 **Zoobotryon verticillatum** (Delle Chiaje, 1828)

A common fouling organism in warmer harbors and at lowered salinities, often seen floating in tangled spaghetti-like masses from docks, floats, and ship hulls; San Diego to Gulf of California and Central America, and, in recent years, in harbors as far north as Long Beach (Los Angeles Co.) and Corona del Mar (Orange Co.); circumtropical, extending into warm Mediterranean waters.

Colony stringy, to 1–2 m long, consisting of tangles of soft flaccid stolons 0.4–0.7 mm in diameter; individuals barrel-like, ovoid, 0.36–0.5 mm long, arising in groups from the stolons.

The biology of this species has been studied at Newport harbor (Orange Co.). The zooids have small mouths and feed only on particles 45 μm or less in diameter. Small flagellates are readily taken as food. Newly budded zooids are sexually precocious, and mature sperm develop in the body cavity before the immature animal first extends its tentacles. The sperm emerge from pores on the tentacle tips, and most are emitted during the first 6 hours of active life. Fertilization is internal, and single white larvae are found in zooids undergoing regression. Larval release occurs mainly in the morning in the laboratory; larvae are attracted to light, and attach to the walls of tanks just below the water surface. At metamorpho-

sis a tubular ancestrula is produced, with a polypide that is fully functional (unusual in ctenostome ancestrulae). A stolon arises from the base of the ancestrula, branches repeatedly, and produces buds that become autozooids. These function for about 6 days, then degenerate. Colonies fed and kept at 25–26°C grew and produced larvae; those fed and held at 20°C did not.

See especially Bullivant (1967, 1968a,b,c); see also Osburn (1953), Ries (1936), D. Soule & J. Soule (1967), J. Soule (1954), Winston (1977, 1978), and Zimmer & Woollacott (1977a,b).

Phylum Ectoprocta / Class Gymnolaemata / Order Ctenostomata
Suborder Stolonifera / Family Vesiculariidae

6.18 Bowerbankia gracilis (O'Donoghue, 1926)

Common on low intertidal rocks and pilings in quieter waters; Puget Sound (Washington) to Isla del Espíritu Santo (Baja California); Atlantic coast from Greenland to Brazil; cosmopolitan, if all identifications are correct.

Colony consisting of stolons from which arise clusters of erect, tubular zooecia about 1–1.5 mm long, usually densely packed to form a brown encrusting fuzz.

Bowerbankia, like many ctenostomes, possesses, at the base of its esophagus, a gizzard, equipped with a set of chitinous teeth, each tooth secreted by a single cell. It takes approximately 1 hour for ingested particles to traverse the gut from mouth to anus.

In sexual reproduction, the zooids produce only one egg at a time. Enlargement of an egg is accompanied by regression of the polypide. The egg is retained after fertilization and is brooded in the vestibule of the parent. A non-feeding coronate larva develops there, escapes by the aperture, swims, settles, metamorphoses, and buds to form a colony. Development of the polypide and muscles has been followed, for both the zooid structure and the order of development of the muscle sets are important in separating bryozoans of the order Ctenostomata into two major subgroups.

Bowerbankia gracilis is abundant in Los Angeles and Monterey harbors. At Monterey, larvae settle from January or February to October, with the greatest settlement from April to September. Colonies then grow rapidly and often cover settled barnacles and ascidians (e.g., *Ascidia ceratodes*, 12.25).

See Bobin (1977), Eiben (1976), Franzén (1956), Haderlie (1968a,b, 1969, 1974), Osburn (1953), Ryland (1960, 1970), J. Soule (1954), J. Soule, D. Soule & Pinter (1975), Ström (1977), Winston (1977, 1978), and Zimmer & Woollacott (1977a,b).

Phylum Ectoprocta / Class Gymnolaemata / Order Ctenostomata
Suborder Stolonifera / Family Triticellidae

6.19 Triticella elongata (Osburn, 1912)

On carapace and appendages and inside gill chamber of the pea crab *Scleroplax granulata* (25.41), in tunnels made by burrowing organisms in mud flats of protected bays; Elkhorn Slough (Monterey Bay); Atlantic coast from Massachusetts to North Carolina.

Colony consisting of creeping stolons; individual zooids 0.9–1.8 mm long and 0.18–0.24 mm wide, arising erect, in pairs or clusters, from stolonial internodes, each zooid with an elongated narrow stalk (pedicel), the stalk expanding into an inflated ovoid area containing tentacles and alimentary system; aperture terminal.

This species is excellent for observations of bryozoan behavior. Living on the body of a tunnel-dwelling crab, the zooids are accustomed to being knocked about; when disturbed, they contract, only to reemerge and commence feeding almost immediately.

Reproduction has been observed in a related European species, *T. koreni*, which lives on the burrowing crustacean *Calocaris*. The eggs are released, but having sticky external membranes, they adhere for a day to the exterior of the bryozoan. A ciliated gastrula hatches and swims away, to complete its development in the plankton. Rudiments of a larval gut develop, but feeding probably does not occur. Larval development takes only a week, but the larvae may spend months in the pelagic realm before settling.

See Franzén (1956, 1977), Osburn (1953), J. Soule (1954), J. Soule, D. Soule & Pinter (1975), Ström (1977), and Zimmer & Woollacott (1977).

6.20 Barentsia benedeni (Foettinger, 1887)

On pilings, floats, worm tubes, barnacle and bivalve shells, and other hard substrata in harbor and estuarine areas, low intertidal and adjacent subtidal zones; San Francisco Bay; Europe.

Colony to several centimeters in diameter, consisting of prostrate stolons bearing upright individuals often 1–4 mm long, each with an enlarged muscular base, a stalk, and a distal calyx; calyces bowl-shaped, 0.1–0.3 mm deep, carrying a fringe of tentacles; stalk in young zooids often plain and unjointed, in older zooids usually with 1–12 (average 4) joints marked by muscular swellings.

This is one of several *Barentsia* species reported from California. It is often confused with B. gracilis (M. Sars), a cosmopolitan species that differs from *B. benedeni* in lacking joints marked by muscular enlargements along the stalk.

Barentsia benedeni colonies in San Francisco Bay (Palo Alto) reproduce sexually and brood larvae from February to July or August. Autumn colonies lack larger zooids, and many stalks lack calyces. Regeneration of calyces increases in January. The brooded developing larvae are attached to the upper surface of the parental calyx, where they feed by diverting food from the adjacent parental food grooves with their ciliary tracts.

For adult and larval structure and behavior of *B. benedeni*, see Mariscal (1965, as *B. gracilis*). For other California species of *Barentsia*, see Mariscal (1975b) and Osburn (1953). For extensive reviews and bibliographies on entoprocts, see Hyman (1951), Mariscal (1975a), and Nielsen (1971). See also Atkins (1932), Brien (1956–57, 1959, 1960a), Brien & Papyn (1954), Franzén (1956), Haderlie (1968b, 1969), Nielsen (1977a,b), Prenant & Bobin (1956), D. Soule & J. Soule (1965), and Woollacott & Eakin (1973).

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