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BRYOZOANS

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freshwater group which is the main focus of this chapter; Gymnolaemata, a vastly larger, polyphyletic collection of species, mostly marine except for a few species in the subclass Ctenostomata which occur in fresh or brackish water. In this chapter ctenostomes are included in the general discussion. Entoproct bryozoans, phylogenetically distant from ectoprocts, are treated in a separate section, but still included in this chapter more for reasons of tradition than systematics.

II. MORPHOLOGY AND PHYSIOLOGY

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A. External Morphology

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1. Zooids and Lophophores

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The phylactolaemate bryozoan colony is composed of identical zooids fused seamlessly into a single structure (Fig. 13.1). Major anatomical features of a zooid are

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I. INTRODUCTION

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Bryozoans are among the most commonly encountered animals that attach to submerged surfaces in freshwater. During warm months, they are found in almost any lake or stream where there are suitable attachment sites. The variety of forms ranges from wisps of stringy material to massive growths weighing several kilograms. In the days before sand filtration, bryozoans were notorious for clogging the distribution pipelines of public water systems. Today they still foul industrial water-cooling systems, irrigation lines, water-treatment plants, and decorative fountains.

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In general, bryozoans are sessile, modular invertebrates with ciliated tentacles that capture suspended food particles. Historically they have included what are now recognized as two very distinct and unrelated phyla: Ectoprocta and Entoprocta. Within the ectoproct bryozoans are two major classes: Phylactolaemata, an exclusively

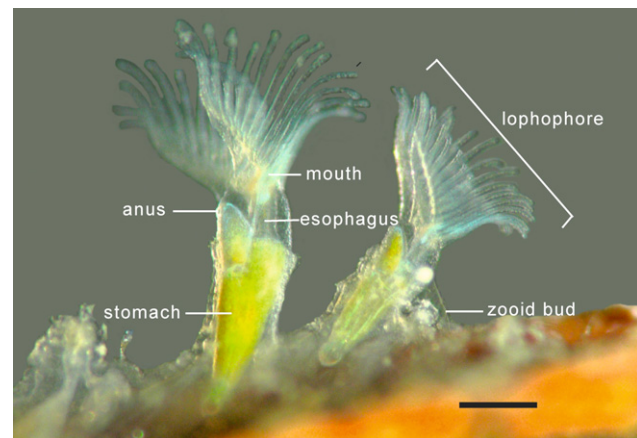
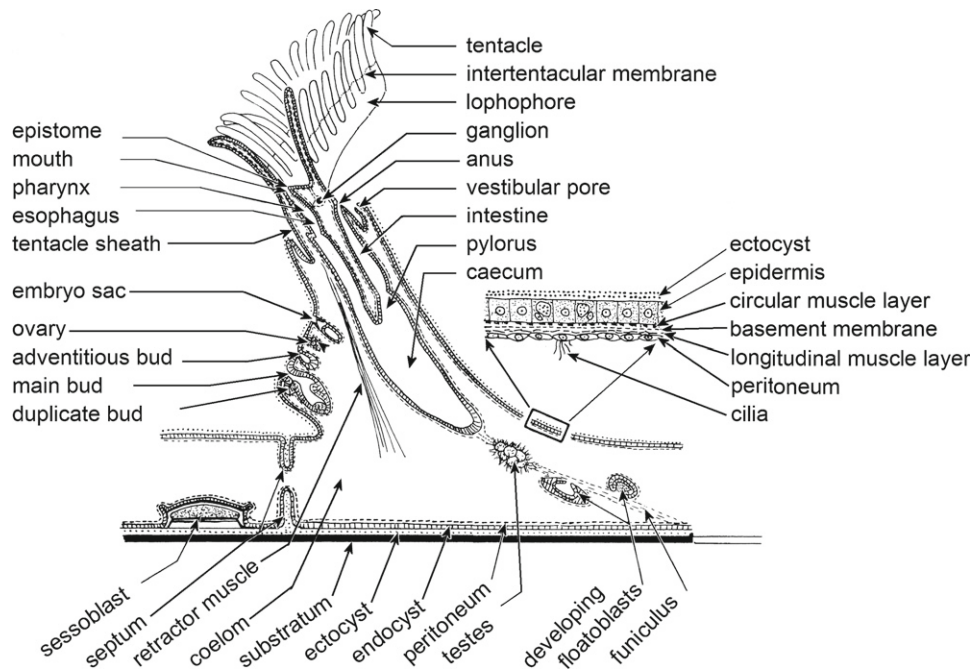


FIGURE 13.1 Two zooids of a hyalinellid bryozoan colony. Scale bar = 0.25 mm.

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f0020 **FIGURE 13.2** Schematic longitudinal section of a generalized zooid (based on Mukai^[62]).

shown in Fig. 13.2. Each zooid in the colony has two basic parts: an organ system, or polypide, which can be partially protruded as a unit and a body wall which can enclose the entire polypide and which separates the colony's interior from the surrounding water. These parts are joined in different places by three structures: a tentacular sheath, prominent retractor muscles, and a slender funiculus loosely running from the gut caecum to a point on the interior of the body wall.

p0040 The polypide bears a prominent lophophore composed of ciliated tentacles arranged around a central mouth. In *Fredericella* species, the tentacles simply encircle the mouth (Fig. 13.3). In all other phylactolaemates, the lophophore extends dorsally in a bilateral pair of arms, forming a U-shaped structure with an outer row of long tentacles and an inner row of shorter ones (Fig. 13.4). In most species, each tentacle bears one medial and two lateral tracts of cilia which beat in metachronal waves. Tentacles are loosely joined near their base by an intertentacular membrane, effectively forming a groove between the rows of tentacles. Two such grooves converge from the lophophore arms towards the mouth. Adjacent to the mouth is the epistome, a small, heavily ciliated lobe which may function in food selection.

p0060 In gymnolaemate (ctenostome) bryozoans the zooids are tubular and rather delicate looking, with small, conical lophophores (Fig. 13.15a–d). The body wall is thin and transparent. Colonies are diffuse, consisting of creeping chains of zooids sometimes separated by narrow pseudostolons.

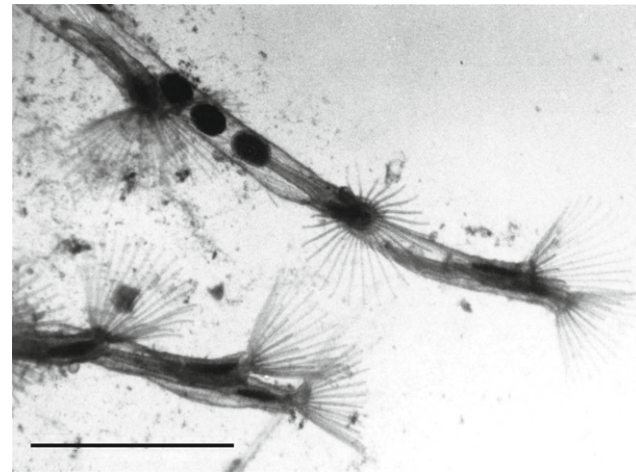


FIGURE 13.3 Portion of a *Fredericella* colony showing characteristic circular outline of the lophophore and three dark statoblasts. Scale bar = 2mm.

2. Statoblasts

A conspicuous feature of phylactolaemate bryozoans is the asexual production of encapsulated dormant buds, called *statoblasts*. The various distinctive types are widely used for species identification. Most species produce free statoblasts that can be released from the colony as disseminules, each bearing a peripheral band of sclerotized chambers normally filled with a gas for buoyancy. Typically, the free statoblasts (often called floatoblasts) acquire their buoyant gas in a late developmental stage within the colony,

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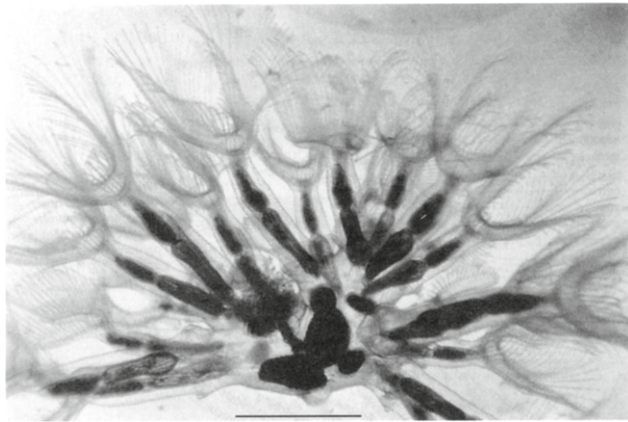


FIGURE 13.4 Portion of a *Lophopodella* colony showing the typical horseshoe-shaped lophophore. Scale bar = 2 mm.

while in a few other species the floatoblast must be dried or frozen before becoming buoyant. Many species with self-inflating floatoblasts also produce specialized sessile statoblasts (sessoblasts) cemented to the substratum upon which colonies grow, and bearing a distinctive annulus around the rim. A third type of statoblast, the ptioblast, is a simple, bean-like structure known only in *Fredericella* species, lacking specialized external structures and held firmly within the tubular branches of the colony. Mukai^[62] provides an excellent overview of statoblast development.

All statoblasts are composed of paired valves joined at an equatorial suture. In most floatoblasts the valves have two structural layers (Fig. 13.5a). An inner capsule contains germinal tissue and food reserves; the outer periblast covers the capsule completely and includes the peripheral annulus and a central fenestra. In most species, the so-called dorsal (or cystigenic) valve generally has a smaller fenestra and correspondingly wider annulus than the ventral (deutoplasmic) valve. At least one species forms leptoblasts in which the capsule is lacking and a fully formed zooid is enclosed by the periblast only (Fig. 13.6). The reverse occurs in fredericellid ptioblasts, which are composed of the capsule only without a periblast (Fig. 13.16a, b).

Sessoblasts have a similar arrangement of inner capsule and outer periblast (Fig. 13.5b). The thin peripheral annulus is considered homologous with the floatoblast annulus, although it is never inflated. The basal valve provides a large, irregular ring which adheres tightly to the substratum.

Gymnolaemate bryozoans do not produce statoblasts. Instead, many of the species restricted to fresh or brackish water form special thick-walled hibernacula. These irregularly shaped bodies are integrated into the colony structure and attached firmly to the substratum, remaining long after the colony disintegrates. Like statoblasts, hibernacula survive desiccation, changes of salinity, and other suboptimal conditions, although the limits of their resistance have not been documented.

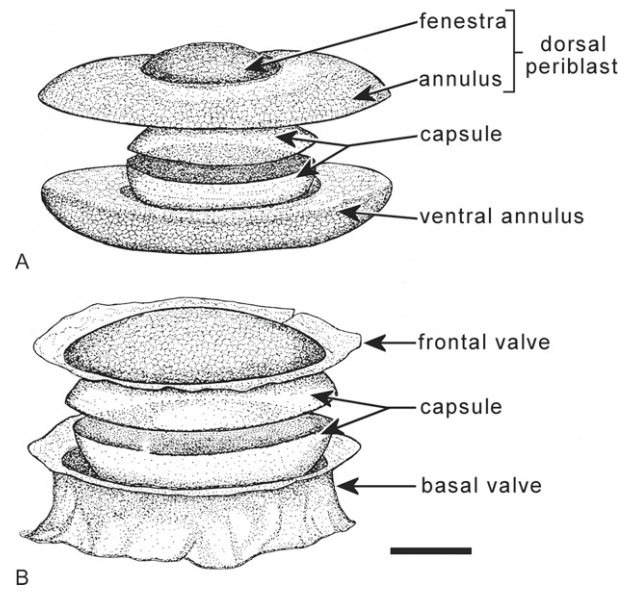


FIGURE 13.5 Sclerotized components of generalized phylactolaemate statoblasts in exploded view: (A) floatoblast; (B) sessoblast. Scale bar = 0.1 mm.

B. Organ System Function

1. Coelom, Neural System, and Body Wall

Most ectoproct colonies have a spacious coelom shared by all zooids. A clear coelomic fluid is circulated by cilia on the peritoneum. The main gastric coelom communicates through an incomplete diaphragm with the coelom of the lophophore, which extends fully into every tentacle.

A small nerve ganglion is located on the diaphragm at the base of the epistome between the mouth and the anus. A single nerve tract extends to each of the paired arms of the lophophore, with nerves branching off to each tentacle. Other nerves from the ganglion innervate the epistome, the tentacle sheath, and the digestive tract. There is no nervous communication between zooids.

The body wall is composed of living tissues, collectively called the endocyst, together with a nonliving outer ectocyst (Fig. 13.2). Lining the main coelom is a peritoneum bearing scattered tracts of cilia. Behind the peritoneum lies a thin, longitudinal muscle layer followed by a basement membrane. Overlying this is a thin layer of circular muscles and a single layer of epidermis. Near the apex of the zooid, the endocyst folds inward to form a flat pocket, the vestibule, and then joins the lophophore as an eversible tentacle sheath. When the polypide is fully retracted, a well-defined opening, or orifice, remains at the zooid tip. A pore in the vestibular body wall of many species is normally closed except to permit the release of floatoblasts from living colonies. In some tubular species, a portion of the body wall grows inwardly to form a kind of sclerotized, reinforcing ring or incomplete septum.

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Those branches of tubular colonies that are attached to a substratum may have a raised line, or keel, running along the outer surface.

The composition of the ectocyst is highly variable among species. In most tubular colonies it is sclerotized and remains intact for a time after the living parts have died. In at least two species, the ectocyst is composed largely of chitinous microfibrils with random orientation. A thin, proximal electron-dense layer is overlain by a thicker stratum of looser fibrils^[34]. Many organic and inorganic particles adhere to this outer coat, including bacteria which also penetrate the interior of the loose layer. The ectocyst in these species varies from thin and flexible to leathery, opaque, and brittle. With age the ectocyst may darken as the chitin is thickened and tanned. Thus, the growing tips of the zooids are often distinctly lighter in color than the rest of the colony. In *Plumatella casmiana* with increasing age a separate sclerotized layer can form in the inner body wall^[77].

In nontubular phylactolaemates, the ectocyst is gelatinous and often restricted to certain parts of the colony. Many vacuolar cells, apparently with a secretory function, reside in the epidermis of these species^[64]. The massive jelly-like substance produced by *Pectinatella magnifica* (Fig. 13.7) is more than 99% water and contains partially

denatured protein along with some chitin, calcium, and sodium chloride^[61].

2. Feeding Mechanics

The lophophore is a complex feeding organ capable of capturing a wide variety of food particles. In contrast with marine bryozoans, the lophophore of most freshwater species is large and powerful, bearing many closely positioned tentacles. Such an organ may be particularly well suited to lentic habitats; certainly those species with the largest lophophores seem to grow best in quiet water. In species where lophophores are tightly crowded (e.g., *Cristatella* or *Pectinatella*), the processed water exits along defined excurrent channels. This results in a significant feeding efficiency, according to one model^[26]. In a study using *Plumatella repens* the ingestion rate per zooid was higher for large colonies than for small ones and also varied directly with ambient water current^[72].

Differential beating of the lateral and frontal cilia sorts particles by density, rejecting heavier, inedible materials before they reach the epistome^[33]. Food gathering involves cilia that bring in nanoplankton (5–10 μm), and tentacles, which orient segments of filamentous algae for ingestion^[48]. Flicking movements of individual tentacles sometimes throw particles towards the mouth; at other times the tips of tentacles are brought together to prevent the escape of an active protozoan or rotifer.

Exactly how the lophophore captures minute particles is not entirely clear. In U-shaped lophophores, the membrane joining the base of all tentacles creates an intertentacular groove of relatively still water. It is possible that particles accelerating towards the lophophore are impelled

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FIGURE 13.6 Germinating leptoblast of *Plumatella casmiana* with thin-walled periblast and no inner capsule, germinating within the hour of its release. Yolk granules are visible on the gut wall. Scale bar = 0.2 mm.



FIGURE 13.7 Gelatinous colonies of *Pectinatella magnifica* growing on a ladder lifted from the water. This conspicuous bryozoan is common in North America and has now spread to northern Asia and Europe. (Photograph by Amee Baily.)

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the final short distance into this groove by their own momentum, while the water is deflected abruptly to the sides^[7]. This would be consistent with the observation that species with the most powerful lophophores can capture the smallest particles^[48].

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Food particles entering the mouth collect momentarily in a short, ciliated pharynx and then are swallowed through a narrow esophagus to the Y-shaped stomach. A short, unciliated cardia leads to the long, cylindrical caecum, where particles are churned by rhythmic peristaltic contractions. In well-fed colonies, waste products collect in brownish, longitudinal bands, giving the caecum a striped appearance. A short proximal part of the caecum, the pylorus, leads through a narrow sphincter to a straight intestine. Here processed particles are consolidated, infused with mucus, and ejected as a fecal pellet through the anus, which lies just outside the whorl of tentacles. The bundle of eliminated material is too large to be reingested by the neighboring zooids, and it falls away from the colony.

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3. Reproductive Systems and Larvae

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In temperate climates, phylactolaemate bryozoans are sexually active during a single brief period of the year. Sperm develop in conspicuous masses on the funiculus of certain zooids, from which they later detach to circulate passively throughout the colony coelom. Egg clusters develop on the peritoneum ventrally within the zooid. There is now direct evidence for outcrossing in populations of *Cristatella mucedo* based on RADP assays^[46], but the mechanism for gamete transfer is unknown. In at least one plumatellid species the body wall breaks down when contact is made between the adhesive pads from germinating statoblasts^[66]. The resulting colonies are confluent, possibly allowing a sort of outcrossing when sperm are circulated within the common coelom. Sperm have been observed emerging from a coelomic pore when polypides are rapidly withdrawn, but how such free sperm might then contact an egg is unknown.

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Assuming that fertilization occurs in the coelom, the zygote somehow migrates to a special sac formed as an ingrowth of the body wall. The embryo develops into a specialized free-swimming structure usually called a “larva,” although technically it is a motile colony. Embryology of the planktonic larva and the steps leading to its metamorphosis are summarized by Hyman^[41], and a fine structure is described by Franzén and Sensenbaugh^[31]. The larva is composed of a heavily ciliated outer mantle and an inner pear-shaped mass (Fig. 13.8a). The inner parts include one-to-four fully formed polypides together with their funiculi and associated musculature. Released from the colony usually after dark, the larva swims with its aboral pole forward, which contains special gland cells and a neural center. Settling normally occurs within an hour (Fig. 13.8b–d).

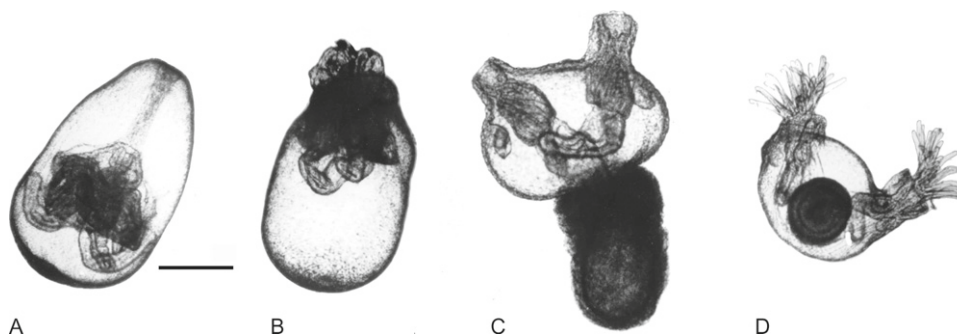
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Among most Gymnolaemata, sexual reproduction leads to the development of small larvae totally unlike those of Phylactolaemata. In egg-brooding species, the larvae have no feeding or digestive organs, so settling and metamorphosis always occur shortly after their release^[112]. However, in *Hislopi*a eggs are released directly into the water where they develop into planktotrophic cyphonautes larvae, similar to those of certain marine species^[98]. The brooding biology of *Pottsiella*^[89] and larval development of *Paludicella*^[4] are described elsewhere. Virtually nothing is known of larval ecology or behavior among freshwater ctenostome bryozoans.

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All bryozoan zooids can bud new zooids. In the Phylactolaemata, buds arise from a specific site on the midventral wall of the parental zooid (Figs. 13.1, 13.2). The development of a new zooid is accompanied by the appearance of new bud primordia, which may or may not develop further. Every zooid bears two bud primordia: a *main bud*, which forms the first daughter zooid, and an *adventitious bud* between the main bud and parental zooid, which becomes the second daughter zooid^[5]. In addition, each main bud itself has a small *duplicate bud* primordium on its ventral side. In the process of budding, duplicate and

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FIGURE 13.8 Settling and transformation of a larva: (A) swimming larva containing two fully developed zooids; the more tapered end is the oral pole; (B) the mantle peels back immediately after the larva attaches to a glass substratum; (C) constricted mantle appears as a dark mass; the two zooids are now clearly visible, each with its own duplicate bud; (D) the mantle is drawn into the body cavity, lophophores are extended, and the two zooids begin feeding. Scale bar for all figures = 0.3 mm. (From Zimmerman^[111].)

adventitious buds become main buds, and new duplicate and adventitious buds are formed^[65].

p0230 In ctenostomes the new zooidal bud originates from an outgrowth of the body wall of a parental zooid. An interior wall then grows across the base of the bud to separate it from the parental body cavity. Most often, a new bud develops at the distal end of a lineal series of zooids; and as it grows, a wall forms at the tip to separate it from the body cavity of the next distal bud in the series.

p0240 In addition to asexual budding, certain phylactolaemate species increase their numbers significantly by active fission of the colony. This is a common occurrence among the globular colonies of *Cristatella*, *Pectinatella*, *Lophopodella*, *Lophopus*, and *Asajirella*. The products of fission glide slowly apart along the substratum, propelled mostly by the combined forces exerted by lophophore cilia.

s0100 C. Environmental Physiology

p0250 Little is known about the digestive physiology of phylactolaemate bryozoans, except that the esophagus environment is alkaline, the stomach is acidic, and the intestinal pH is neutral^[54]. Passage time through the gut varies from 1 to 24 hours depending on the ingestion rate. Zones of basophilic and acidophilic cells line the caecum, but there is no agreement among investigators on their function.

p0260 Statoblasts have been the subject of considerable study. The period of obligate dormancy imposed on most statoblasts serves to maintain populations through periods of unfavorable environmental conditions. Those statoblasts not fixed to immobile substrata may also function in passive dispersal, carried either by water currents or by migrating animals. In separate trials, plumatellid statoblasts have been shown to be viable after passing through the digestive tracts of a salamander, frog, turtle, and duck^[6].

p0270 Like statoblasts, the hibernacula of gymnolaemates maintain the populations during periods of unfavorable conditions. Unlike most statoblasts, however, they are an integral part of the colony, can never be released freely into the water, and thus would not normally function as independent disseminules.

p0280 The resistance of statoblasts to environmental stress was reviewed by Bushnell and Rao^[13]. Most *Plumatella* and *Fredericella* statoblasts survive desiccation or freezing for periods of one-to-two years. Some *Plumatella* floatoblasts can germinate after more than four years in cold water. *Lophopodella carteri* statoblasts have remained viable during cold, wet storage for over eight years. Other less hardy statoblasts include those of *P. magnifica*, which do not withstand prolonged desiccation and survive only brief periods of freezing temperatures.

AUQ5 Statoblasts stored in water at a favorable temperature eventually germinate after a variable dormant period.

p0340 However, when that period is prolonged by continuous

exposure to cold, dry, anaerobic, or other unfavorable conditions, a near simultaneous germination can be achieved when a suitable environment is restored. In some species, light is an important factor for germination^[68,80]. Ultrastructure of the statoblast suture and its possible relation to germination have been studied^[13,76].

The budgeting of energy resources for colony growth and reproduction is poorly understood. In many cases, gametogenesis precedes statoblast production, but the two processes may also operate concurrently. The first zooid to germinate from a statoblast never forms statoblasts itself but may participate in gametogenesis. In laboratory colonies of "*Plumatella emarginata*" (probably *Plumatella mukaii*), sexual activity occurred only in certain colonies, which varied in size from as few as 10 zooids^[63]. Only those colonies with the most vigorous development of testes eventually formed mature larvae.

Regulation of sessoblast development in Plumatellidae has not yet been clarified. Apparently, statoblast primordia can differentiate into either floatoblasts or sessoblasts, and this differentiation becomes evident during the late epidermal-disk stage^[63]. In natural populations, it has been noted that most sessoblasts are formed either early or late in the season, suggesting that this is a response to suboptimal conditions^[55]. However, laboratory-reared *Plumatella* colonies frequently form both floatoblasts and sessoblasts under growing conditions that appear favorable.

III. ECOLOGY AND BEHAVIOR

A. Diversity and Distribution

Freshwater bryozoans are generally restricted to relatively warm water, flourishing at 15–28°C. However, *C. mucedo* has been found at 6°C^[11], and *Lophopus crystallinus* survives at 0°C for brief periods^[99]. *Fredericella indica* lives through the winter in most of North America, budding new zooids at 3°C and producing ptioblasts above 8°C. All these species also grow well at higher temperatures. Only *Stephanella hina* has never been found above 17°C and is probably restricted to cool water^[88]. Temperatures as high as 37°C were recorded for living *Plumatella nitens* and *Plumatella fruticosa*^[11]. *P. emarginata* in India shows only meager growth at 34°C^[84].

Phylactolaemates tolerate a wide range of pH, but they favor slightly alkaline water^[90]. A *Fredericella* species (probably *F. indica*) has been collected in acidic conditions as low as pH 4.9^[30], *P. fruticosa* at pH 5.7^[99], and both *P. repens* and *Hyalinella punctata* at pH 6.3^[90].

Most species occur in both still and running water, but *P. emarginata* and *F. indica* grow especially well in lotic habitats. Among those species associated with still waters are *P. nitens*, *P. repens*, *P. recluse*, *L. crystallinus*, *H. punctata*, and *H. orbisperma*. Many common species

tolerate turbid water, but *P. magnifica* does not, possibly because its large colonies are necessarily more exposed to settling particles^[20].

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The reputation of bryozoans as clean water species is not entirely warranted. In one report, *Fredericella sultana*, *P. emarginata*, and *Plumatella fungosa* thrived in high concentrations of heavy metals and PCB's, although none of these toxic substances had accumulated in the tissues^[37]. These same species also tolerate extreme contamination from sewage and industrial wastes^[12]. More recently, *Plumatella vaihiriaie* has been noted as an important fouling species in secondary clarifiers and tertiary sand filters of wastewater-treatment plants (Fig. 13.9)^[103]. Both *P. repens* and *P. fungosa* survive at only 30% saturation of dissolved oxygen^[86]. Many species, such as *L. carteri* flourish both in the laboratory and the field when supplied with large quantities of suspended organic particles. In Europe, the distribution of *P. fungosa* is correlated with nutrient-enriched water^[44]. *P. magnifica* in the United States, Japan, and Korea become luxuriant in areas that are visibly eutrophic.

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One clearly limiting factor for all species is the availability of suitable surface on which to grow. Almost any solid, biologically inactive material is acceptable, including rocks, glass, plastics, automobile tires, and aged wood. Surfaces that are seldom successfully colonized include newly dead wood, corroded metal, and oily or tarred materials. Aquatic plants are common substrata, and there is no indication of species specificity^[11]. However, among large, floating leafed plants, the lotus lily, *Nelumbo lutea*, often supports heavy growths of bryozoans, while other lilies, such as *Nymphaea* or *Nuphar*, are seldom colonized.

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FIGURE 13.9 *Plumatella vaihiriaie* reared in the laboratory in a 2 inch petridish inverted in a culture tank. This is an unusually prolific and aggressive species, often clogging pipelines and filters in nutrient-rich water.

Free floatoblasts, of course, are passive carriers of living material to new substrata. Swimming larvae, on the other hand, actively select attachment sites. Particle size discrimination has been demonstrated with larvae of *P. magnifica*, which consistently avoid rock particles smaller than 1 mm diameter^[39]. Additional selection criteria are likely. Larvae of *Paludicella articulata* seem to settle selectively on mussel shells^[21].

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In general, freshwater bryozoan species are widely distributed but variable in local abundance. Some species appear to occur as metapopulations with regular cycles of local extinction followed by new immigration^[71]. Two of our most common species, *F. indica* and *Plumatella reticulata*, are rare in Europe^[57–58]. Similarly, the abundant European *P. fungosa* is seldom found on our continent. A near worldwide distribution is enjoyed by *P. casmiana*, *L. carteri*, and *P. articulata*. However, the old notion that many other species have a cosmopolitan distribution was apparently based on faulty identification. In North America, *C. mucedo* is restricted to holarctic regions, while *Fredericella browni* and *Pottsiella erecta* are most common where winters are mild. About 25% of North American species are considered rare, and one, *L. crystallinus*, has not been reported since 1897. Some species are known to be expanding their range. For example, *P. magnifica* jumped from North America to Europe, Japan, and Korea, and probably occurs also in China. *L. carteri* is increasingly common since its introduction to North America in the 1930s, and the once scarce *P. vaihiriaie* is appearing in eutrophic lakes and wastewater-treatment facilities across the continent. Species believed to be endemic to North America now include *P. nitens*, *P. orbisperma*, *P. recluse*, and the tiny ctenostome, *Sineportella forbesi*.

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All known North American species have been reported east of the Mississippi River and north of the 39th parallel. A total of 19 of the 24 species occur in states bordering the Great Lakes, and an additional two species are described only from New England. Only the brackish *Victorella pavida* has not been found farther north than Chesapeake Bay.

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Relatively little is known about freshwater bryozoans west of Ontario and the Mississippi River. Most states and provinces have no published records of bryozoans. However, various reports show Colorado and Utah with natural populations of *P. repens*, *P. casmiana*, *P. emarginata*, *P. fruticosa*, *P. fungosa*, *F. indica*, and *C. mucedo*. Other western sightings show *C. mucedo* in British Columbia^[78] and *P. repens* in Arizona and Nevada^[23,96]. *P. magnifica*, once confined east of the Mississippi River, now appears to be well established across North America and has recently appeared far north into Canada.

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Other recent regional surveys have been published for Massachusetts^[87], Michigan^[8–10], Ohio^[100], and eastern Canada^[79]. Each of these has revealed significant new species records for North America. There are also recent

reviews of freshwater bryozoans in Europe^[104] and Southeast Asia^[107].

In temperate climates, sexual activity in phylactolaelmates has been reported as rare even in thoroughly documented field studies^[107]. Among the Plumatellidae, with a prolific production of asexual statoblasts, sexual reproduction would seem a relatively unimportant means for recruitment. However, in *P. magnifica* and *H. punctata*, with only one statoblast generation per year, sexually produced larvae play a significant role in establishing new colonies^[39,108–109]. Likewise, in *Fredericella* species, because of their fixed statoblasts, larvae are assumed to be instrumental for both population growth and dispersal.

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B. Reproduction and Life History

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In most parts of the United States, bryozoan populations have two or more generations during the growing season. Only *F. indica* typically is found throughout the year, living even under a cover of ice. Populations of other species are normally maintained during unfavorable seasons by dormant statoblasts. An unusual exception to this pattern was reported for a population of a species identified as *P. repens* inhabiting an Arizona cave, where nearly constant conditions permitted uninterrupted active growth^[23].

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Winter dormancy in statoblasts is broken by conditions favorable to colony growth. In temperate climates the principal triggering factor appears to be the temperature. Viable statoblasts often germinate within a few days of each other when the water temperature rises above 8°C. In those regions where winter water temperature never approaches freezing, the time of germination may be more variable.

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The single zooid that emerges from a statoblast is termed the ancestrula. It eventually buds one-to-five new zooids, each similarly capable of multiple zooid budding. Colonies grow rapidly as water temperature rises. Naturally occurring colonies of *P. nitens* (initially identified as *P. repens*) have been recorded which triple and quadruple in size within one week^[11]. Doubling times of five days have been reported for both *P. casmiana* and *F. indica*^[63].

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In species of *Plumatella*, *Fredericella*, and *Lophopodella* statoblasts may appear in colonies having fewer than five zooids; but in most other species, they are not formed until colonies are much larger. Among natural populations, a second generation usually arises either from statoblasts or larvae of early spring colonies, or even from fragments of colonies surviving from the first growth period. Third-generation colonies also are known, but any statoblasts they produce normally remain in diapause until the following spring. *P. casmiana* is unique in releasing thin-walled statoblasts which germinate immediately, so there may be many overlapping generations throughout the growing season.

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Gametogenesis, when it occurs, is normally encountered in the first spring generation of colonies, with larvae released two-to-four weeks after fertilization. Sperm masses develop on the funiculus as ova appear on the peritoneum. The sperm later break free to circulate in the coelom for one-to-two weeks. This is followed by larval development and eventual release. There appears to be little overlap in larval release dates among closely related species living in the same area. In two Ohio lakes, free-swimming larvae of *P. repens* appeared throughout June; *P. casmiana* larvae were released during July; then came *H. punctata* in late July–early August, followed by *P. emarginata* in late August–early September^[111].

C. Ecological Interactions

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The constant flow of water through bryozoan lophophores creates a favorable environment for the microscopic aufwuchs community. Protozoans, rotifers, gastrotrichs, microcrustaceans, and other small animals congregate especially on and around branching tubular colonies of bryozoans. Flatworms, oligochaetes, snails, oribatid mites, crayfish, and such insect larvae as caddisflies and midges occasionally graze on the living zooids. Predation is seldom extensive but can occasionally become a serious limiting factor.

p0480

Larvae of true midges (Chironomidae) enter old tubes of *P. repens*, hastening their disintegration and occasionally damaging living portions of the colony. Some workers consider such damage to be accidental rather than the result of direct feeding, while others regard these midges as important predators. Colonies of *P. casmiana* escape such harm, possibly because the midges cannot fit themselves inside the narrow, branching tubules, but instead build detritus tubes alongside the exterior colony wall where they cause little harm. *P. magnifica* is often a host to midge larvae, which find shelter by burrowing into the gelatinous base close to the substratum and causing no apparent damage. One of these, *Parachironomus longiforceps* Kruseman 1933, is reported to be a frequently commensal on *P. magnifica*^[25].

p0490

Myxozoan and microsporidian parasites are sometimes visible as small particles or sacs circulating within the bryozoan coelomic fluid^[17]. One myxozoan species, *Tetracapsuloides bryozoides*, was described in detail from small sacs found in *C. mucedo*^[16,70]. Part of that life cycle is now known to include the large, enigmatic worm-like parasite originally described as *Buddenbrockia plumatellae*^[56,83]. The complete ecology, development, and pathogenicity of *T. bryozoides* has been reported from several bryozoan species in North America and Europe^[18]. A related myxozoan parasite of bryozoans, *Tetracapsuloides bryozalmonae*, also infects salmonid fish where it triggers a devastating condition known as proliferative kidney disease (PKD)^[15]. This is considered the most serious parasite in the salmon industry, capable of causing losses of up to 90% in infected populations. Evidence suggests that

p0500

bryozoans are the ancestral hosts, and that fish infections are accidental. Although the parasite can transfer between fish and bryozoans, it is the fish that are the most severely affected^[60].

p0510 Extensive predation by fish has not been verified, although there is abundant indirect and anecdotal evidence from stomach contents^[1]. At Bull Shoals Reservoir (Arkansas), fredericellid bryozoans composed as much as 75% by volume of the sunfish diet^[93]. However, in many cases it is likely that more nutrition is derived from insect larvae associated with the colonies^[24]. A homogenate of *L. carteri* tissues is highly toxic to fish^[59], and sustained feeding by fish on this or any other gelatinous species has never been observed. Freshwater prawns will graze on colonies of *P. vaihariae*, but only when no other food is available^[3], suggesting the colonies either lack nutritional value or have repellent toxins. Other invertebrates are documented predators on bryozoans, including crayfish^[14], apple snails^[107], caddisflies, and elmids beetles^[11]. Predation is often suspected when bryozoan populations flourish on floating or dangling substrata, while nearby surfaces accessible to crawling grazers are denuded^[104].

p0520 As sessile suspension feeders, bryozoans handle a wide variety of food. Ingested particles include diatoms, desmids, green algae, cyanobacteria, dinoflagellates, rotifers, small nematodes, protozoa, and even microcrustaceans, along with bits of detritus and inorganic materials. In a comparative study of three species, 95% of ingested particles were under 5 μm in diameter^[48]. *P. repens*, with its wide mouth and strong gut musculature, ingested larger organisms than did either *C. mucedo* or *P. fruticosa*. These included rotifers (*Keratella*), colonial green algae, and cyanobacteria as large as 75 μm. In general, organisms with long body extensions could avoid ingestion by bryozoans, while small, rounded shapes were easily taken.

p0530 Analysis of stomach contents alone does not reveal the important sources of bryozoan nutrition. Rotifers and green algae have been known to pass through the gut completely unharmed^[41], although there are reports that a large portion of ingested organisms are variously damaged^[48,82]. *P. fungosa* can thrive on a strict diet of suspended bacteria^[80]. Bacteria may be assimilated in the gut after being carried there on suspended detrital particles.

p0590 The quantity of seston removed from a 460 ha eutrophic lake by *P. fungosa* is estimated at 15 metric tons per year^[49]. At the same time, 8.8 tons of fecal pellets are deposited in the sediments, about twice the amount contributed by fish or waterfowl, but less than that deposited by molluscs.

IV. EVOLUTION AND PHYLOGENETICS

p0600 Ectoprocta is one of the three animal phyla collectively known as lophophorates. The other two, Brachiopoda and

Phoronida, are represented by a small number of solitary, mostly sessile, marine animals. The main unifying feature of these phyla is a lophophore with hollow tentacles containing an extension of the coelom and with cilia beating in metachronal waves to bring water and suspended food towards the mouth.

As a group, lophophorates show no clear affinity with any other invertebrates. The semblance of radial cleavage, mesoderm formation, and other elements of morphology and development in brachiopods appears distinctly deuterostome^[28,110]. However, analysis of 18S rDNA sequence data suggest that lophophorates are protostomes^[36], a conclusion supported by other biochemical and morphological studies^[35,97].

Structural similarities have been noted between ectoprocts and the worm-like sipunculids. The anterior introvert of a sipunculid is protruded and withdrawn in a manner very similar to that of the ectoproct polypide, using coelomic pressure and retractor muscles. The sipunculid introvert ends in a mouth surrounded by hollow, ciliated, tentacular outgrowths. The gut is U-shaped and the anus is situated near the base of the introvert. However, similarities such as these may simply reflect the independent evolution of sessile lifestyles.

Nucleotide sequence data suggest that lophophorates in general and ectoprocts in particular are not monophyletic assemblages^[19,53]. For example, new evidence supports the hypothesis of an ancestral line leading directly to phoronids and phylactolaemate ectoprocts^[102]. Only these two groups have a crescentic lophophore and an epistome. They also both produce new buds from a region on the oral (ventral) side of the adult, while in other ectoprocts budding is in an anal direction^[42]. In contrast to gymnolaemate bryozoans, phoronids and phylactolaemates share similar body wall musculature and lophophore ontogeny^[67]. Many phoronids produce special fat bodies for energy storage, which are strikingly similar to early developmental stages of phylactolaemate statoblasts. While the larvae in general are quite different, the phoronid, *Phoronis ovalis*, has a unique, ciliated actinotroch^[85] that appears similar to the phylactolaemate “larva.” Significantly, *P. ovalis* also forms colonies which resemble somewhat those of the phylactolaemate family Fredericellidae.

Nucleotide data also show gymnolaemate bryozoans to be more distantly related with phoronids than phylactolaemates, as also reflected in their different embryology and larval metamorphosis^[102]. The phoronid actinotroch larva, for example, has a distinct coelom, the larval gut is retained in the adult, and the lophophore develops from the metatroch ring of cilia. By contrast, the gymnolaemate cyphonautes larvae have no larval coelom, the larval gut is not retained, and tentacles develop from the episphere region.

Within the Class Phylactolaemata, similarities in the mode of colony growth and statoblast morphology have long been regarded as the basis for evolutionary

p0620

relationships. The six major families appear to offer a clear, almost linear sequence (Table 13.1). In this scheme, *Fredericella* species would exhibit primitive features with their simple statoblasts and an open, dendritic pattern of colony branching. The circular outline of the lophophore, associated with a relatively small number of tentacles would also be a primitive character, perhaps linking phylactolaemates with marine cyclostome bryozoans. The evolutionary trends would include a shift towards greater compactness of the colony and the accommodation of increasing numbers of tentacles on the lophophore. Statoblasts serve the two seemingly conflicting roles of dispersal and of retaining a position on proven favorable substratum.

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However, this model is challenged by nucleotide data placing the more gelatinous species close to ancestral phylactolaemates (Fig. 13.10)^[38,74,102]. This would be consistent with a phoronid-like ancestor bearing a large, crescentic lophophore with many tentacles. The compact, gelatinous colony design occurs in the Lophopodidae, Pectinatellidae, and Cristatellidae (Table 13.1). Their relatively large statoblasts incorporate a buoyant ring and radiating marginal hooks (Fig. 13.17). The branching tubular colonies of Plumatellidae would appear later, introducing their separate free and sessile statoblasts for performing the two competing functions of effective dispersal and substratum retention. According to this model, the morphological simplicity of Fredericellidae is a derived state, not a primitive one. Stephanellidae presents a complication in this scheme, since its basal position would be inconsistent with its tubular design and the presence of both free and sessile statoblasts. However, data for this group are

not yet very strong and further work is needed to resolve the issue.

Fossil statoblasts resembling those of recent *Plumatella*, *Hyalinella*, and *Stephanella* species appear in rock strata from the Late Permian^[92]. Even more recognizable plumatellid statoblasts appear in strata from the Lower Cretaceous^[43], and statoblasts similar to *Pectinatella* have been recovered from the Upper Triassic^[51].

The freshwater Gymnolaemata, all ctenostomes, seem to have invaded freshwater habitats in several independent

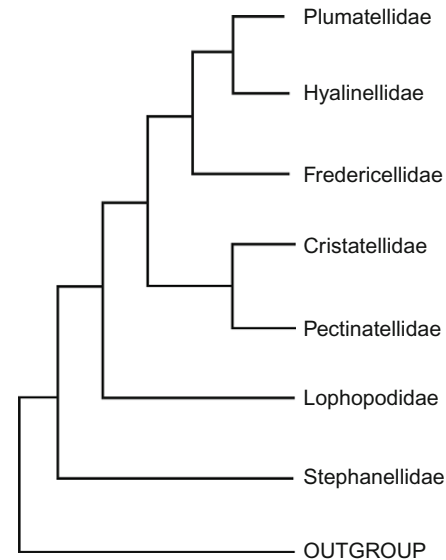


FIGURE 13.10 A generalized phylogenetic tree summarizing the inferred relations among families based on molecular data from three independent studies^[35,42,67].

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TABLE 13.1 Summary of key characteristics among the six recognized species of phylactolaemate bryozoans.

Family	Colony form	Zooid spacing	Lophophore	Statoblasts
Fredericellidae	Branching	Widely spaced	circular	Sessile, simple, unadorned
Stephanellidae	Branching	Widely spaced	U-shaped	Two types: free (self-inflated) and sessile (no spines on either)
Plumatellidae	Branching	Widely spaced to compact	U-shaped	Two types: free (self-inflated) and sessile (no spines on either)
Hyalinellidae	Branching	Compact	U-shaped	Free, self-inflation variable
Lophopodidae	Globular	Compact	U-shaped	Free (not self-inflated, peripheral spines)
Pectinatellidae	Globular	Compact	U-shaped	Free, self-inflated, peripheral spines
Cristatellidae	Globular	Compact	U-shaped	Free, self-inflated, fenestral spines

events. A recent cladistic analysis suggests the appearance of victorellids and paludicellids some time after the rise of marine cheilostomes^[91]. The tropical freshwater hislopiids, on the other hand, most likely evolved well before then. At this time no molecular data are available to address these questions.

zooid is disturbed, the tentacles fold over the vestibule and are covered by a tentacular membrane.

Internal organs include a fully ciliated digestive tract and a large medial ganglion. A number of excretory flame bulbs communicate through short ducts to a common nephridiopore; additional flame bulbs occur in the stalk. The body cavity is a pseudocoel filled with loose mesenchyme and extending into each tentacle.

The head is deciduous, dropping off at the onset of cold temperatures or other unfavorable conditions. The basal segments of stalks, containing food and germinal tissue, can survive winter much like ectoproct statoblasts, forming new heads when the water temperature returns to around 15°C. New zooids develop by budding from the stalk, as illustrated particularly well by Oda^[69]. Young colonies may disperse locally by crawling over the substratum^[75]. Sexual reproduction leads to the development of swimming larvae, presumably similar to those of other Pedicellinidae; details are unknown.

Like other bryozoans, *U. gracilis* is a suspension feeder, consuming organic particles, unicellular algae, and protozoans. Two especially important foods are the diatom *Melosira* and two green algae species, *Pediastrum duplex* and *Pediastrum simplex*^[95]. Feeding mechanics in entoprocts involve compound cilia that swat food particles into a groove on the tentacles leading to the mouth^[81].

U. gracilis is known from every continent but Antarctica and Australia. In North America its reported distribution ranges from the east to the west coast and from Florida, Louisiana, and Texas to as far north as Michigan. Zooids attach to almost any substratum, including rocks, sticks, aquatic plants, bivalve shells, ectoprocts, and such debris as nails, beverage cans, and lead fishing weights^[29]. Individuals occur most frequently in flowing water or in shallow areas of large lakes where there is extensive water movement. The species tolerates a wide range of chemical and physical conditions^[22,40].

In some areas, especially on new substratum, entoprocts may comprise a sizeable fraction of the macroinvertebrate community. Stalk densities of over 225,000/m² and an average biomass of 868 mg/m² (dry weight) were reported from a seven-month old artificial stream in Mississippi^[49].

Entoproct phylogeny is even less clear than that of the ectoprocta. Any similarities to ectoproct bryozoans are clearly the result of convergent evolution rather than common ancestry. A close comparison of entoproct tentacles and the ectoproct lophophore reveals little in common despite their outwardly similar structure and function. Body cavities of the two groups are likewise irreconcilable: a pseudocoel on one hand and a true coelom on the other. Analysis of 18S r-RNA data support a wide separation between entoprocts and ectoprocts, placing the entoprocts instead among the pseudocoelomates^[36]. Nevertheless, puzzles such as this are expected in animals so highly modified by sessile life-

V. ENTOPROCTA

Entoprocta is a small group of about 60 species distinct in almost every way from the Ectoprocta but historically included with them under the name “bryozoan.” Both groups are sessile with ciliated tentacles and an incomplete separation of budded zooids, but the similarities stop there. The only known freshwater species, *Urnatella gracilis*, was discovered in North America in 1851. Two other species have been proposed elsewhere based mainly on number of stalk segments and morphology of the basal plate. All these species are now considered synonymous with *U. gracilis*^[27]. Although normally classified as Urnatellidae, the genus is similar to the marine species *Barentsia* and may be united with it in the family Pedicellinidae.

The zooid is a bulbous head borne on a flexible, segmented stalk measuring up to 5 mm long (Fig. 13.11). Several such stalks, either solitary or sparingly branched, may arise from a basal plate. The head bears a single whorl of 8–16 uniformly short, ciliated tentacles. The area of the head enclosed by the tentacles, called an atrium or vestibule, includes both the mouth and the anus. When the

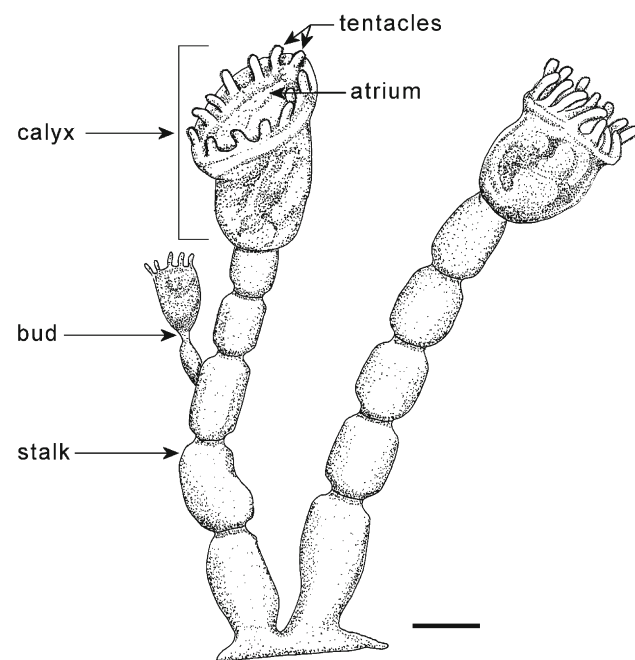


FIGURE 13.11 Small entoproct colony (*Urnatella gracilis*) showing external structures. Scale bar = 0.5 mm.

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style and modular architecture, and for now the question of entoproct origins remains open.

s0170 VI. STUDY METHODS

p0720 Bryozoans are normally found in areas of shallow water where suitable firm substratum exists. Although most species are plainly visible to the unaided eye, a 10× or 14× Coddington magnifier is useful for field identification. Many species can be detected by examining the waterline of floating objects for free statoblasts. Some gelatinous colonies can be nudged gently from the substratum with little damage, but with other species it is better to collect pieces of substratum with colonies attached. Basic equipment for this includes a sturdy knife for organic substrata and a cold chisel and hammer for rocks. In lakes where colonies are elusive, statoblasts can often be retrieved from sediments using a stack of standard sieves with mesh openings of 1.0 mm, 500 μm, and 150 μm^[46].

Swimming larvae are most easily detected by placing large colonies in a shallow tray of water. If larvae are present, they will generally be released with gentle prodding or will emerge spontaneously during the night. They are best seen against a dark background. Before their release from the colony, zooids with larvae appear swollen at the tip.

Bryozoans are not difficult to rear in the laboratory, but the substratum on which they attach must always be inverted so that fecal material and other settling debris will not accumulate around the zooids (Fig. 13.9). Most species can be kept at room temperature. At lower temperatures there are fewer problems with fouling organisms but colony growth is slow. Food appears to be the most important variable for success with laboratory-reared bryozoans. *L. carteri* has been maintained on pure cultures of *Chlamydomonas reinhardtii*^[68]. *P. repens* was maintained for three years using a variety of unicellular green algae in 1:1 Knop's solution and soil extract^[94]. Other works have achieved limited short-term success using mixed protozoan cultures, pet fish food, and fine detritus. One reliable and trouble-free source of food is simply the suspended organic particles circulated through a dark rearing tank from a large, well-lit aquarium in which active fish are maintained^[101].

If specimens are to be preserved, they should be anaesthetized before fixing so that the lophophores will remain extended. The most convenient method is to confine colonies to a small covered dish of water with thin wafers of menthol floating on the surface. The menthol diffuses slowly into the water and relaxes the zooids within an hour or two. Lophophores of anaesthetized zooids can be hardened with drops of full-strength formalin. The colony is then fixed and preserved in 70% ethyl alcohol.

f0130 Confirmed identification of most species requires the presence of statoblasts inside the colony. Statoblast

dimensions and surface topography are species-specific. In specimens stored for an appreciable time, any gas in the floatoblast annulus is replaced by liquid, making the entire capsule clearly visible through the periblast. In this case, it is important not to mistake capsule dimensions for those of the fenestra. Length and width of sessoblasts should be measured from the base of the annulus, not from its outer edge.

Surface features of the floatoblast fenestra can often be seen in isolated valves using ordinary light microscopy (Fig. 13.12). However, features of the annulus require the use of a scanning electron microscope (Fig. 13.13). In various species the floatoblast fenestra may be smooth (Fig. 13.14a), reticulated (Fig. 13.14b), tuberculated, or bearing a reticulum in which each cell contains a single

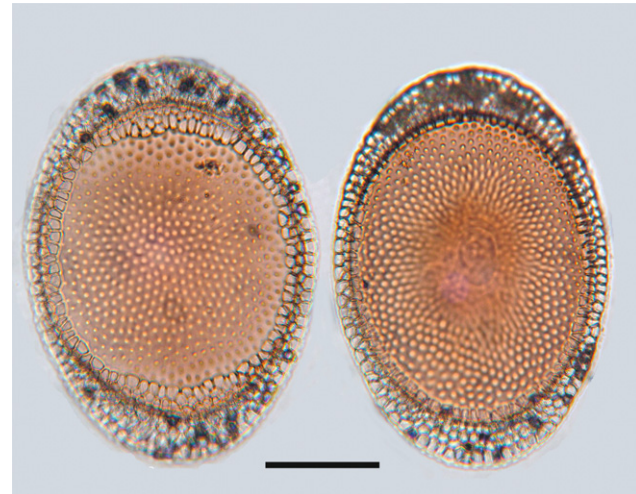


FIGURE 13.12 Separated valves of a plumatellid floatoblast. Tubercles on the fenestra can be focused to become small points of light; net-like reticulation appears similar but never forms points of light. Scale bar = 0.1 mm.

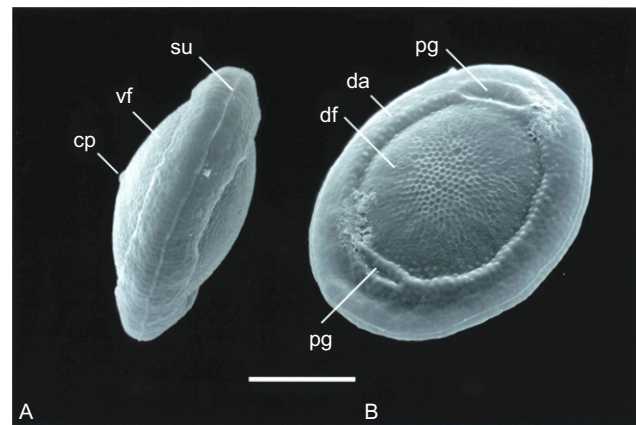


FIGURE 13.13 Scanning electron micrographs showing floatoblast features: (A) lateral view; (B) frontal view of dorsal valve. cp = central prominence, da = dorsal annulus, df = dorsal fenestra, pg = polar groove, su = suture, vf = ventral fenestra. Scale bar = 0.1 mm.

interstitial tubercle (Fig. 13.14d). Other diagnostic features of the floatoblast include polar grooves on the dorsal valve (Fig. 13.13b) and appearance of the intact suture (Fig. 13.14c). All recent species descriptions include statoblast details such as these.

p0780

For detailed examination of a statoblast using light microscopy, it is useful to first separate the component parts by placing it for about one minute in a hot solution of potassium hydroxide. Then transfer it to distilled water where the valves should separate spontaneously. Use fine insect pins (size #000) to assist in this process and to tease away the yolky contents. I find it convenient to arrange these parts under the microscope and photograph them for my working records (Fig. 13.12).

To prepare statoblasts for scanning electron microscopy, it is first necessary to remove manually the thin membrane that often adheres tightly to the surface. If

subsequent cleaning is necessary, ultrasonic treatment is too harsh. Instead, place the statoblasts in a small Eppendorf vial with a 0.05M sodium hexametabisulfite, then hold the vial against the shaft of an electric vibrating blade shaver. Wash the statoblasts in several changes of distilled water. Freeze-drying helps prevent distortion of the fenestra. Sputtering is advisable but not essential.

Well over half the recognized phylactolaemate species are represented by type specimens in major museums, including all species named since the 1940s^[105]. Even long neglected and desiccated material remains valuable for morphological study of statoblasts.

Certain techniques for subcellular study of freshwater bryozoans have proven particularly useful. These include analysis by karyotype^[2], by randomly amplified polymorphic DNA^[73], 18S ribosomal DNA^[36, 102], and identification of polymorphic microsatellite loci^[32].

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VII. TAXONOMIC KEY TO NORTH AMERICAN FRESHWATER BRYOZOANS

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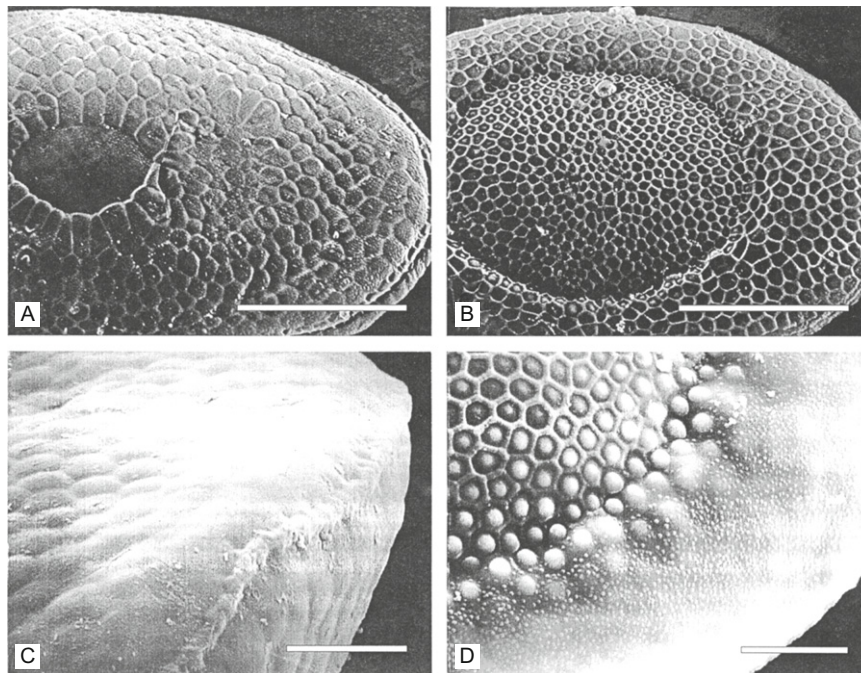
- 1a. Zooid composed of bulbous head on externally segmented stalk; tentacles folding individually toward center when zooid is disturbed; statoblasts absent (Fig. 13.11) phylum Entoprocta . . . *Urmatella gracilis* Leidy
- 1b. Zooid without externally segmented stalk; tentacles withdrawn together when zooid is disturbed; statoblasts may be present phylum Ectoprocta 2
- 2a (1b). Colony composed of branching tubules, sometimes fused; body wall transparent to opaque; statoblasts (if present) with smooth margins; tentacles fewer than 65 3
- 2b. Colony globular and either lobed or entire in outline; body wall transparent; statoblasts with peripheral spines, hooks, or pointed extensions; sessoblasts absent; tentacles more than 65 26

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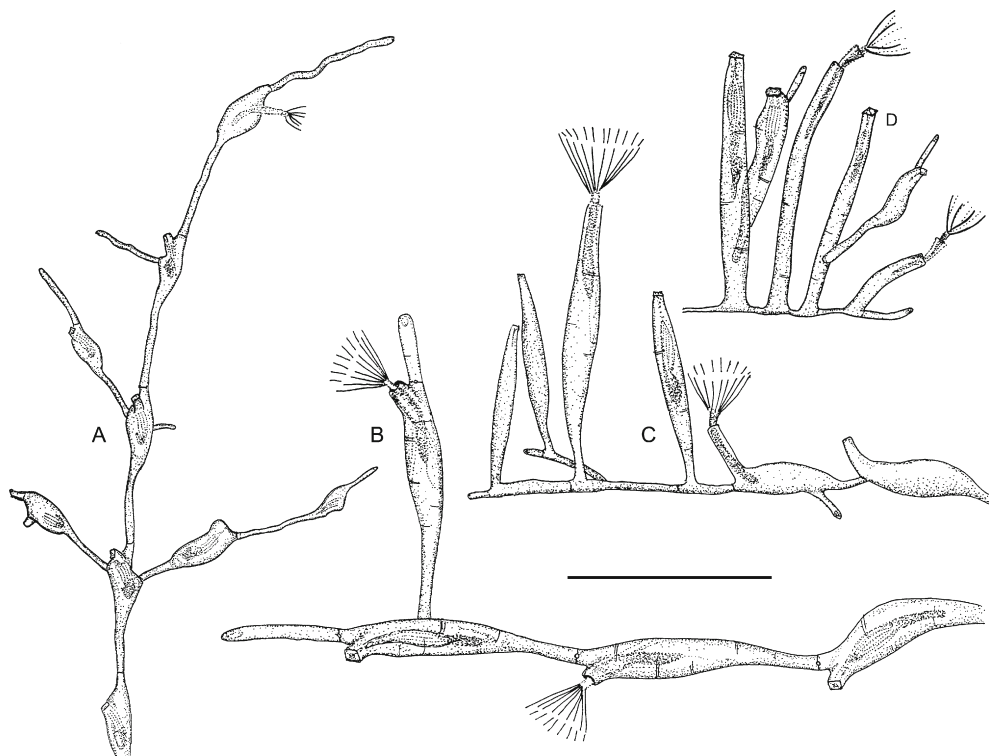


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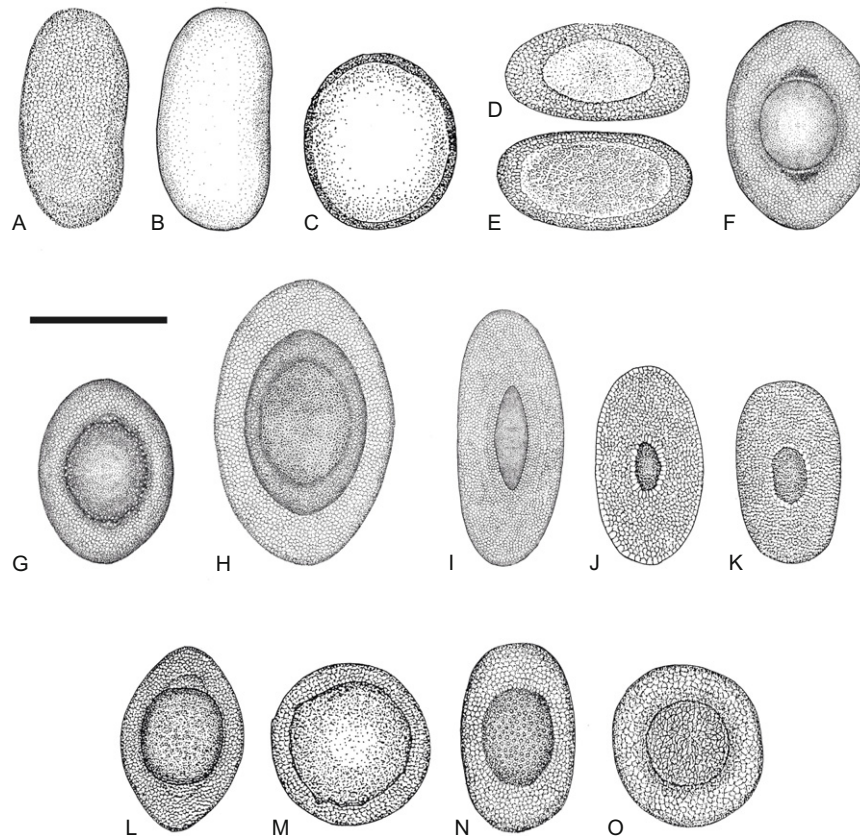
FIGURE 13.14 Scanning electron micrographs showing floatoblast surface morphology: (A) *Plumatella emarginata* dorsal valve with paved annulus and smooth fenestra; (B) *Plumatella vaihiriaae* with reticulated fenestra and annulus; (C) *Hyalinella punctata* with paved annulus and suture as a raised cord; (D) *Plumatella orbisperma* with reticulation and “interstitial” tubercles on the annulus, small nodules on fenestra. Scale bar = mm.

	3a (2a).	Extended lophophore circular in outline; statoblasts (if present) piptoblasts only (Fig. 13.16a, b); tentacles fewer than 254	p0870
	3b.	Extended lophophore U-shaped in outline; statoblasts either floatoblasts or sessoblasts (or both); tentacles more than 2510	p0880
	4a (3a).	Statoblasts never formed; ectocyst stiff, shiny, and transparent; tentacles fewer than 20; individual zooids clearly demarcated by internal septa; orifice appears quadrangular when lophophore is withdrawnclass Gymnolaemata . . . order Ctenostomata . . . 5	p0890
p0900	4b.	Statoblasts formed, especially in zooids attached to substratum, but possibly missing in some specimens; ectocyst not stiff and shiny; tentacles more than 19class Phylactolaemata . . . family Fredericellidae . . . Fredericella . . . 8	
p0910	5a (4a).	Each zooid includes a uniformly narrow, sinuous, stolon-like tubule by which it is joined to a parental zooid6	
p0920	5b.	Stolon-like tubules absent; zooids branch from each other at nearly right angles; widely distributed in North America and worldwide. (Fig. 13.15b)family Paludicellidae <i>Paludicella articulata</i> (Ehrenberg).	
p0930	6a (5a).	Tentacles numbering exactly 8family Victorellidae . . . 7	
p0940	6b.	Tentacles more than 15; zooids ranging from straight and erect to bulbous and recumbent (Fig. 13.15c); known throughout eastern North America, especially south of the 40th parallel family Pottsiellidae <i>Pottsiella erecta</i> (Potts)	
p0950	7a (6a).	Erect portion of zooid 0.6–1.6 mm long and only slightly contractile (Fig. 13.15d); occurring mainly in brackish water; reported south from Chesapeake Bay and in southeastern Louisiana <i>Victorella pavidata</i> (Kent)	
	7b.	Erect portion of zooid never more than 0.3 mm long and highly contractile (Fig. 13.15a); known only from a single site in east central Illinois <i>Sineportella forbesi</i> Wood and Marsh	p0960
	8a (4b).	Piptoblast surface densely pitted or minutely roughened; appearing dull and granular when dry9	p0970
	8b.	Piptoblast surface appearing mirror-smooth and shiny when dry (Fig. 13.6b); common in Europe; known in North America only from the Pacific Northwest <i>Fredericella sultana</i> (Blumenbach)	p0980
	9a (8a).	Piptoblast broadly oval to round (Fig. 13.16c), often more than one per zooid; valves covered by a minutely wrinkled mantle which is easily removed by five minute immersion in concentrated KOH solution to reveal smooth sclerotized surface; reported throughout North, Central, and South America <i>Fredericella browni</i> (Rogick)	p0990



f0150 **FIGURE 13.15** Gymnolaemate colonies occurring in fresh water: (A) *Sineportella forbesi*; (B) *Paludicella articulata*; (C) *Pottsiella erecta*; (D) *Victorella pavidata*. Scale bar for all figures = 1 mm.

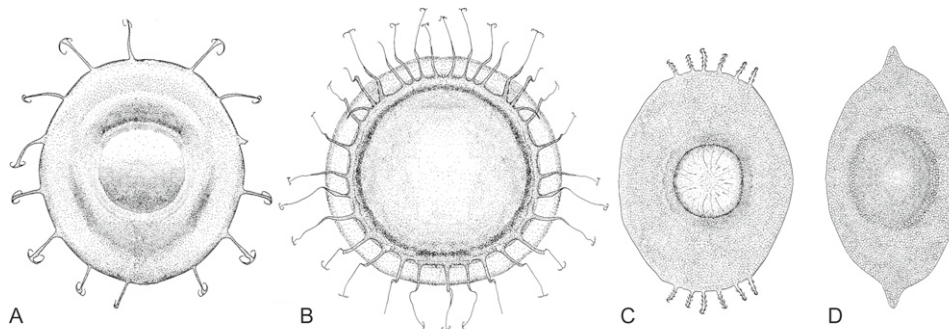
	9b.	Piptoblast oval to elongate (Fig. 13.16a), seldom more than one per zooid; surface uniformly pitted and unaffected by KOH; common throughout North America, also scattered sites in Europe and Asia; probably includes several species not yet distinguished .. <i>Fredericella indica</i>(Annandale)	p1000
	10a (3b).	Floatoblasts circular or nearly so, with little difference in appearance between dorsal and ventral sides; colony wall thick, soft, transparent; uncommon	p1010
p1020	10b.	Floatoblasts oval or oblong; fenestrae of two valves distinctly different in size; colony wall not necessarily thick or transparent; abundant and widespread	
p1030	11a (10a).	Zooids erect, extending up to 4mm. but collapsing when removed from water; polypide and lophophore relatively small; floatoblast fully reticulate and lacking tubercles (Fig. 13.16o); confirmed in North America only from several sites in Massachusetts, although floatoblasts reported from Oregonfamily Stephanellidae <i>Stephanella hina</i>Oka	
p1040	11b.	Zooids not as above, floatoblast surface variable family Plumatellidae . . . 12	
p1050	12a (11b).	Floatoblast fenestra tuberculated, annulus adorned with minute nodules (Figs. 13.16m), sessoblast circular or nearly so; thick walls of large colonies fusing into a firm, transparent matrix; known only from a few sites in Michigan and the northern Great Lakes .. <i>Plumatella orbisperma</i> (Kellcott)	
p1060	12b.	Floatoblast fully reticulated and without tubercles; sessoblast long oval to rectangular; known only from small ponds in forested sites of New England <i>Plumatella recluse</i> Smith	
p1070	13a (10b).	Colony wall thick, soft, and transparent; colony entirely adherent to substratum; sparsely branched; zooids forming low mounds when polypides are retracted (Fig. 13.18d); floatoblast width greater than 300µm, length over 450µm (Fig. 13.16h), floatoblasts dark and seldom buoyant upon release from colony, sessoblasts never formed; widely distributed family Hyalinellidae . . . <i>Hyalinella punctata</i> (Hancock).....	



f0160 **FIGURE 13.16** Free statoblasts from the families Plumatellidae and Fredericellidae: (A) *Fredericella indica*; (B) *Fredericella sultana*; (C) *Fredericella browni*; (D) *Plumatella casmiana* (capsuled floatoblast); (E) *Plumatella casmiana* (leptoblast); (F) *Plumatella fungosa*; (G) *Plumatella repens*; (H) *Hyalinella punctata*; (I) *Plumatella fruticosa*; (J) *Plumatella emarginata*; (K) *Plumatella reticulata*; (L) *Plumatella vaihiriae*; (M) *Plumatella orbisperma*; (N) *Plumatella bushnelli*; (O) *Stephanella hina*. (A, C–E, J–K modified from Wood^[100]; C, F–I modified from Wood and Okamura^[104]; L based on Rogick and Brown^[114]; M–O based on Bushnell^[9]; N based on Wood^[115]). Scale bar for all figures = 0.25 mm.

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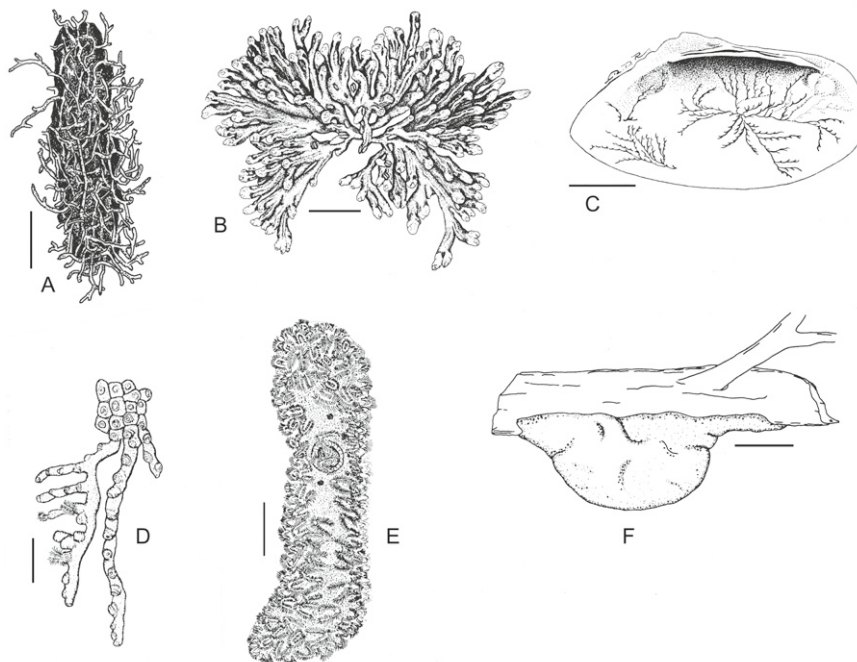
	13b.	Floatoblast and colony not as above, or sessoblasts present family Plumatellidae	14	p1080
	14a (13b).	Floatoblast dorsal fenestra small, its width much less than half the total floatoblast width (Fig. 13.16j, k); internal septa frequent	15	p1090
	14b.	Floatoblast dorsal fenestra larger, its width at least half the total floatoblast width (Fig. 13.16 f, g, l-o); internal septa present or absent	18	p1100
	15a (14a).	Floatoblast length less than 0.55 mm; colony variable; sessoblast length less than twice the width	16	p1110
	15b.	Floatoblast length more than 0.55 mm; colony with long, slender, often free branches; sessoblast length more than twice the width <i>Plumatella fruticosa</i>	Allman	p1120
	16a (15b).	Floatoblast dorsal valve nearly flat, long edge curved; suture between valves visible in dorsal view (Figs. 13.5a, 13.16j); sessoblast surface uniformly tuberculated; internal septa perpendicular to colony wall	17	p1130
	16b.	Floatoblast valves almost equally convex, long edge relatively straight (Fig. 13.16k), sessoblast surface roughened by network of raised lines; internal septa slightly oblique	<i>Plumatella reticulata</i> Wood	p1140
p1150	17a (16b).	Floatoblast surface smooth, including tubercles; common and widely distributed <i>Plumatella emarginata</i> Allman.....		
p1160	17b.	Floatoblast surface, including tubercles, appeared wrinkled, a feature conspicuous with Scanning electron micrography (SEM) and otherwise visible by reflected light; Asian species reported from the Pacific Northwest <i>Plumatella mukaii</i>	Wood	
p1170	18a (14b).	Floatoblast length to width greater than 1.7 (Fig. 13.16d, e); colony composed of short, profusely branched tubes always closely adherent to substratum (Fig. 13.18b), tubes becoming erect and fused when crowded; floatoblast dorsal fenestra lacking prominent tubercles; delicate thin-walled floatoblast sometimes present (Fig. 13.16e); sessoblast annulus relatively narrow; common and widely distributed ... <i>Plumatella casmiana</i>	Oka	
p1180	18b.	Floatoblast length to width less than 1.7 (Fig. 13.16f, g, m); colony branches not particularly short, colony or statoblasts not as above	19	
p1190	19a (18b).	Floatoblast dorsal annulus bulging around inner capsule to form a distinct shoulder; sessoblast surface densely pitted and without tubercles; uncommon but often locally abundant, especially in productive waters	<i>Plumatella vaihiriae</i>	(Hastings)
p1200	19b.	Floatoblast dorsal annulus extending evenly from suture to fenestra without bulging around the inner capsule; sessoblast surface densely tuberculate	20	
p1210	20a (19b).	Floatoblast lateral edges relatively straight (13.16-n) dorsal fenestra with prominent tubercles annulus with dense nodules visible by SEM; sessoblast annulus relatively wide; known from southeastern United States; also occurs in Guam and New Zealand <i>Plumatella bushnelli</i>	(Wood)	
p1220	20b.	Floatoblast lateral edges evenly curved (Fig. 13.16f, g) common and widespread	21	
p1230	21a (20b).	Floatoblast ventral annulus distinctly wider at the poles than along the sides	22	
p1240	21b.	Floatoblast ventral annulus width, uniformly narrow all around; known from Massachusetts to Wisconsin, mostly north of the 41st parallel	<i>Plumatella nitens</i>	Wood
p1250	22a (21a).	Colony tubules seldom fused together; floatoblasts laterally symmetrical or nearly so, internal septa uncommon	23	
p1260	22b.	Colony forming tight masses of fused tubules without free branches, colonies capable of exceeding 1 cm thick; floatoblasts laterally asymmetrical with the dorsal valve almost flat; internal septa present; occurring in highly eutrophic water	<i>Plumatella fungosa</i>	(Pallas)
	23a (22a).	SEM shows floatoblast annulus surface roughened by concave cell walls; common and widespread in North America, especially in lentic habitats	24	p1270
	23b.	SEM shows floatoblast annulus lacking concave cell walls	25	p1280



f0170

FIGURE 13.17 Statoblasts in the families Lophopodidae, Pectinatellidae and Cristatellidae. Scale bar for all figures = 0.5 mm. (A) *Pectinatella magnifica*; (B) *Cristatella magnifica*; (C) *Lophopodella carteri*; (D) *Lophopus crystallinus*. (A–D modified from Wood and Okamura^[104]).

24a (23a).	SEM shows floatoblast annulus lacking rash-like nodules; colony often reddish in color; common and widely distributed(Wood et al.)	p1290
24b.	SEM shows floatoblast surface entirely covered with rash-like nodules <i>Plumatella nodulosa</i> Wood.....	p1300
	[Note: The uncertain taxonomic value of floatoblast nodules places some doubt on the validity of <i>Plumatella nodulosa</i> and <i>Plumatella semilirepens</i> . Known only from a narrow band extending from northeastern Illinois to the New York Finger Lakes region.]	p1310
25a (23b).	Floatoblast suture bordered on each side by a single row of large tubercles; SEM shows floatoblast annulus surface smooth except for tiny, rash-like nodules; common in Europe; confirmed in Ohio and Illinois, but North American range unknown <i>Plumatella repens</i> (L.)	p1320
25b.	Floatoblast suture lacking a border of large tubercles; annulus marked by rounded contours of underlying cell structure; nodules sparse; see caveat from 24b; known from two fish hatcheries in Illinois, also reported from a fish hatchery in Italy <i>Plumatella similirepens</i> Wood	p1330
26a (2b).	Mouth region with red pigmentation; prominent pair of white spots at end of each arm of lophophore; statoblasts round with hooked spines radiating from outer margin of annulus (Fig. 13.17a). Colony gelatinous and slimy, ranging from a flat sheet to football-sized mass. (Figs. 13.7, 13.18f); common and widely distributedfamily Pectinatellidae <i>Pectinatella magnifica</i>(Leidy)	p1340
26b.	Mouth region without red pigmentation, lophophore lacking pair of white spots27	p1350
27a (26b).	Colony linear, often longer than 2 cm (Fig. 13.18e); statoblasts round with wiry, hooked spines radiating beyond periphery from margin of fenestrae of both valves (Fig. 13.17b); occurring mainly in oligotrophic waters family Cristatellidae <i>Cristatella mucedo</i>Cuvier	p1360
27b.	Colony not distinctly linear; statoblasts oblong, not round28	p1370
28a (27b).	Statoblast with series of small hooks localized along the polar margins (Figs. 13.4, 13.17c); uncommon, but can be locally abundant <i>Lophopodella carteri</i>(Hyatt)	p1380
28b.	Statoblast tapering to a single point at each pole (Fig. 13.17d); rare; last reliable North American report in 1897 ... <i>Lophopus crystallinus</i> (Pallas)	p1390



f0180

FIGURE 13.18 Various colony forms in Phylactolaemata: (A) *Fredericella indica* growing on a piece of wood, showing many free branches, scale bar = 5 cm; (B) *Plumatella casmiana*, with zooids attached throughout their length to the substratum or to each other, scale bar = 2 mm; (C) *Plumatella rugosa* growing on the inner surface of a mussel valve, scale bar = 2 cm; (D) *Hyalinella punctata*, showing both densely packed and free-ranging growth, all zooids firmly attached to the substratum, scale bar = 5 mm; (E) *Cristatella mucedo* showing a single statoblast inside, scale bar = 5 mm; (F) *Pectinatella magnifica* growing on the underside of a small log, scale bar = 2 cm.(B from Rogick^[113]; C from Rogick and Brown^[114]; C–F from Wood^[100]).

AUQ3

VIII. SELECTED REFERENCES

08. Bushnell JH. On the taxonomy and distribution of freshwater Ectoprocta in Michigan. I. *Trans Am Microsc Soc.* 1965;84:231–244.
09. Bushnell JH. On the taxonomy and distribution of freshwater Ectoprocta in Michigan. Part II. *Trans Am Microsc Soc.* 1965;84:339–358.
10. Bushnell JH. On the taxonomy and distribution of freshwater Ectoprocta in Michigan. Part III. *Trans Am Microsc Soc.* 1965;84:529–548.
11. Bushnell JH. Environmental relations of Michigan Ectoprocta, and dynamics of natural populations of *Plumatella repens*. *Ecol Monogr.* 1966;36:95–123.
29. Eng LL. The freshwater entoproct, *Urnatella gracilis* Leidy, in the Delta-Mendota Canal, California. *Wassman J Biol.* 1977;35:196–202.
50. King DK, King RH, Miller AC. Morphology and ecology of *Urnatella gracilis* Leidy, (Entoprocta), a freshwater macroinvertebrate from artificial riffles of the Tombigbee River, Mississippi. *J Freshwater Ecol.* 1988;4(3):351–359.
52. Lacourt AW. A monograph of the freshwater Bryozoax—Phylactolaemata. *Zool Verhandelingen.* 1968;93:1–159.
62. Mukai H. Development of freshwater bryozoans (Phylactolaemata). In: Harrison FW, Cowden RR, eds *Developmental Biology of Freshwater Invertebrates*. New York: Alan R. Liss; 1982:535–576.
79. Ricciardi A, Reiswig H. Taxonomy, distribution, and ecology of the freshwater bryozoans (Ectoprocta) of eastern Canada. *Can J Zool.* 1994;72:339–359.
104. Wood TS, Okamura B. A new key to the freshwater bryozoans of Britain, Ireland, and continental Europe. *Freshwater Biological Association, Scientific Publication No. 63*, Ambleside, UK; 2005:113 pp.

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- {AUQ5} Do you mean “statoblasts” in place of “floatoblasts” in the sentence “Some *Plumatella*...in cold water”.
- {AUQ6} Please spell out H. in *H. orbisperma*.
- {AUQ7} Please provide the spelt out form of the acronym PCB.
- {AUQ8} Please check the sentence “One of these..magnifica” for clarity of meaning.