# Bryozoa: an introductory overview

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## Introduction

Bryozoa, sometimes called Ectoprocta, constitute a phylum in which there are probably more than 8,000 extant species (the much quoted figure of 4000, made nearly 50 years ago (HYMAN 1959), is certainly a serious underestimate). Some authorities regard the phylum Entoprocta to be related to Bryozoa, but the evidence is conflicting and opinion divided (see NIELSEN 2000). The bryozoans are a widely distributed, aquatic, invertebrate group of animals whose members form colonies composed of numerous units known as zooids. Until the mid 18th century, and particularly the publication of John ELLIS' "Natural History of the Corallines" (1755), bryozoans, like corals and hydroids, were regarded as plants. This is reflected both in the name of the phylum, which translates as 'moss animals' and in the term 'zoophyte' which was used by LINNAEUS (1758) to embrace both bryozoans and hydroids. Seventy-five years after ELLIS, bryozoan zooids were distinguished from those of cnidarians by possessing both a mouth and an anus (DE BLAINVILLE 1820) and, a decade later, EHRENBERG (1831) formalized the distinction by introducing the names Bryozoa and Anthozoa. Bryozoans are separated into three classes: Phylactolaemata (freshwater dwelling); Stenolaemata (exclusively marine); and Gymnolaemata (mostly marine). The order Cheilostomatida (class Gymnolaemata), containing over 600 genera, is the most successful bryozoan group. General accounts of the phylum have been provided by CORI (1941), HYMAN (1959), BRIEN (1960), RYLAND (1970), and WOOLLACOTT & ZIMMER (1977), though all are now, in certain respects, outdated. More specific but important reviews have been provided by RYLAND (1976a), MCKINNEY & JACKSON (1989), REED (1991) and, comprehensively, by MUKAI et al. (1997), whose survey should be consulted by those seeking information on zooidal soft-part morphology, cells, and ultrastructure in extant bryozoans of all classes. The account also includes much original description based on the phylactolaemate *Asajirella* (formerly *Pectinatella*) *gelatinosa*. This work essentially provides the English language update for HYMAN's (1959) classic text, incorporating a thorough review of 40 years' significant research. The linkage of the Bryozoa with Brachiopoda and Phoronida, as 'lophophorates' (following HYMAN 1959) may no longer be tenable; certainly, the feeding mechanisms may not be as similar as once supposed (NIELSEN & RIISGÅRD 1998, and references therein).

## General features: size range and diversity of structure

Bryozoan colonies vary in size. Among Gymnolaemata, colonies of *Monobryozoon*, which live between particles of marine sand, consist of little more than a single feeding zooid less than one millimetre in height. Colonies of the coralline genus *Pentapora* of European seas, however, can reach 1 m or more in circumference; in the warm-water *Zoobotryon*, which hangs from harbour pilings, and the phylactolaemate *Pectinatella*, massive colonies may exceed 0.5 m in diameter. Colonies that form crusts generally cover only a few square centimetres; erect colonies may rise only 2-5 cm, though the gelatinous *Alcyonidium* (Fig. 1), washed ashore during autumn gales, may exceed 15 cm.

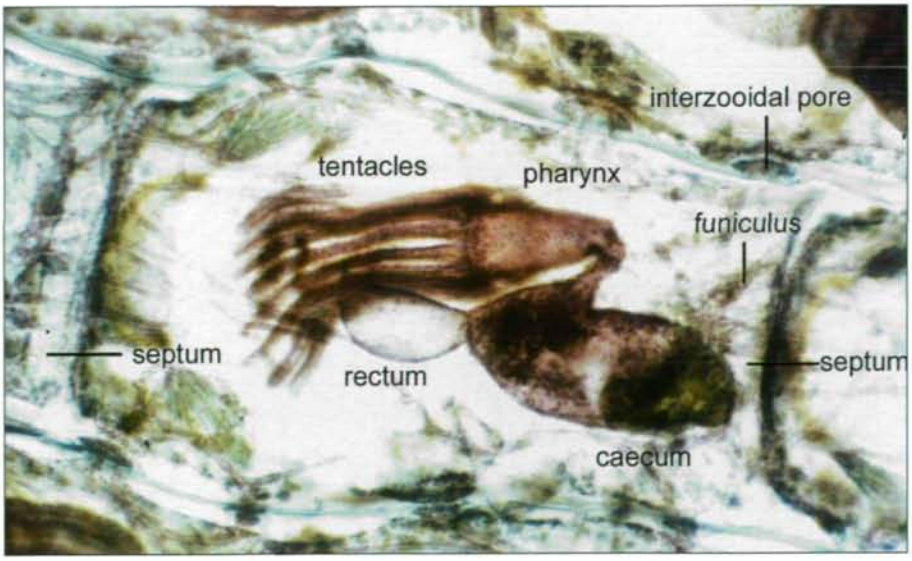
The texture of colonies is variable. Some, especially in fresh water and on seashores, are gelatinous or membranous; others are tufted, with flat, leaf-like fronds or whorls of slender branches, whose horny texture results from

**Fig. 1**: Erect, gelatinous colonies of *Alcyonidium diaphanum* (Ctenostomatida). Many zooids in the colonies contain clusters of developing oocytes and/or larvae in zooidal brood chambers derived from the tentacle sheath. Scale bar 5 x 1 cm. Origin: west coast of Scotland, Junde 1998.

lightly calcified zooid walls. Still other colonies are hard and have strongly calcified skeletons. Such colonies may form rough-surfaced patches or may rise in slender branching twigs (such as those that form a network in the 'lace corals', e.g. *Reteporella*).

The colonies, diverse and complex in structure, are composed of individual modules, or zooids, each of which has considerable individuality. A bryozoan colony usually has many zooids, which may be of one type or of types that differ both functionally and structurally. Neighbouring zooids are usually firmly joined and communicate via tiny pores in the dividing walls. Zooids capable of feeding have a protrusible ring of slender tentacles at their distal end, on which are found cilia that propel tiny particles of food toward the mouth. The mouth opens into a digestive tract that is divided into several regions and terminates at an anus, which is outside (but near) the tentacles (hence the name alternative name Ectoprocta, meaning 'outside anus'). If zooids are disturbed, they withdraw their tentacles inside the body cavity. Only if the zooids have transparent walls, as in the gymnolaemate genera *Bowerbankia* and *Membranipora*, is the digestive tract visible. The internal living parts of each zooid – i.e., the nervous and muscular systems, the tentacles, and the digestive tract – are called the polypide, while the surrounding walls and their associated tissues constitute the cystid (Fig. 2).

**Fig. 2**: A stained zooid of *Membranipora membranacea*, the polypide brown and the cystid walls pale. Mural pore chambers can be seen (Preparation made by Dr. Geneviêve Lutaud).



## Form and function: zooids

Although zooid appearance and structure vary considerably from class to class, and even between orders, all conform to a common basic plan (Fig. 2). The predominant, feeding zooid in a bryozoan colony is the autozooid. Autozooids are rarely longer than one millimetre and the primitive shape appears to have been cylindrical (as e.g. in Fig. 6). The skeleton is external, ranging from a thin cuticle to a thick, calcified layer. The tentacles, collectively termed the lophophore, can be raised above the zooid on a slender extension of the body wall (the introvert or tentacle sheath clearly apparent in Fig. 6) and outspread for feeding. If disturbed, the tentacles can be withdrawn into the body cavity in a movement that involves inrolling the tentacle sheath, with the mouth and tentacles being pulled down within it by the action of paired retractor muscles. Eversion of the withdrawn tentacles is effected by raising the hydrostatic pressure of the body fluid, so compressing the tentacle sheath; but the precise mechanism differs from class to class. Phylactolaemates have a muscular and contractile body wall to achieve this function; in gymnolaemates the wall is non-muscular but in whole or part flexible, so that it can be pulled inward by the body musculature associated with it (parietal muscles). In most extant gymnolaemates the zooids are not cylindrical but flat, with rigid side walls as seen in Fig. 9. The upward facing or frontal wall either remains flexible or has concealed below its calcified surface a membranous cavity, the ascus (sac), which can be inflated with sea water, thereby compressing the body fluid. At the free end of a cylindrical zooid or near the distal end of a flat zooid is an opening known as the orifice, through which the tentacle sheath and tentacles emerge; in cheilostome gymnolaemates the orifice has a closable lid, the operculum. Stenolaemate zooids are different, and the walls form a slender calcareous tube, no part of which can be inflected to evert the tentacles; instead, body fluid is forced from one part of the zooid to another by muscles (NIELSEN & PEDERSEN 1979).

The alimentary canal forms a deep loop (Fig. 2); the pharynx, ciliated distally, descends to the stomach, the anterior part of which is termed the cardia or forms a gizzard in a few genera, such as the gymnolaemate *Bowerbankia* (MARKHAM & RYLAND 1987); the main stomach section is the caecum, and the slender posterior region, which is ciliated, the pylorus; the rectum continues from the pylorus; and the anus is situated just outside the lophophore. A detailed and fully illustrated account of the lophophore and gut has been provided by MUKAI et al. (1997). Respiratory, circulatory, and excretory systems are absent in bryozoans. The reproductive organs (ovary, testes) are situated on the lining of the body wall or on the funiculus, a cord of tissue that links the stomach to the lining of the body wall (and often also links zooids throughout the colony, see below). The polypide degenerates periodically during the lifetime of a zooid, and a compact mass, called a brown body, is either expelled or remains alongside the new polypide which soon differentiates from living cells of the cystid (GORDON 1977).

Zooid polymorphism exists among cheilostomate colonies in particular, having given rise to several types of heterozooid (SILÉN 1977). The operculum seems to have been significant in the evolution of some types of specialized zooids in this order. The avicularium type of zooid has a small body and a rudimentary polypide; the operculum, however, is proportionally larger, has strong adductor muscles, and has become, in effect, a jaw. Avicularia are found among normal zooids, but usually are smaller and attached to the autozooids, as in *Schizoporella*. In *Bugula* the avicularia are movable on short stalks and closely resemble miniature birds' heads; hence the name avicularium (cp. contribution of WÖSS, this volume). Another specialized form of zooid is the vibraculum, in which the operculum has become a whip-like seta. The functions of avicularia and vibracula are not clearly known, but both types of zooids may help to keep the colony free from particles and epizoites (i.e., organisms that attach to the surface of the colony but do not parasitize it). A recent summary may be found in MCKINNEY & JACKSON (1989).

## Form and function: colonies

Despite their ill-defined shape, colonies, at least in extant bryozoans, are not just aggregations of zooids but whole organisms having a physiology and behaviour that appear to be coordinated to some extent. Integration is made possible by a system of interzooidal pores (Fig. 2) and the cells that traverse them (see BOBIN 1977 and MUKAI et al. 1997 for details). Most conspicuous are those of the funiculus, which in gymnolaemates becomes a colonial network capable of distributing nutrients to nonfeeding zooids (such as ovicells or gonozooids) or areas (such as the growing edge). The zooidal nervous system of bryozoans consists of a small ganglion positioned between the mouth and the anus that supplies nerves to the various organs. In some bryozoans a colonial network, that unites the zooids through the interzooidal pores, has been demonstrated. A stimulus that causes the lophophore to withdraw in a zooid of the gymnolaemate *Membranipora* almost instantaneously evokes the same response nearby; and nerve impulses can at that time be recorded. Nevertheless, to a large extent the colony is not individualistic; for example, it usually has no definite shape, can grow in any direction, and can be partially destroyed without harm to the rest. It may live a few months or a couple of years, or it may be theoretically immortal, its life of continual budding terminated only by some catastrophe. The high species diversity of bryozoans and the remarkable adaptive radiation of the Cheilostomatida during the Cretaceous

**Fig. 3**: Erect, foliose colony of *Flustra foliacea* (Cheilostomatida) supporting colonies of *Crisia* (Cyclostomatida: white) and *Scrupocellaria* (Cheilostomatida: brown). No source information; frame size approximately 9 x 6.5 cm.

and Tertiary, have been attributed by RYLAND (1979) to the unique combination of zooidal individuality combined with a sophisticated system for metabolic integration (provided by the funiculus-interzooidal pore system), which have facilitated the evolution of heterozooids and replicated patterns of heterozooids – which may be interzooidal or variously aggregated on a bearer autozooid to form cormidia BEKLEMISHEV (1969) – that make up a colony. The several distinctive basic patterns evolved by colonies of Bryozoa (encrusting crusts, erect fronds, spirals, free-living disks, and so on (Fig. 1, 3) are related to the habitats they occupy, and to the requirements of obtaining food and of reproduction, topics that have been explored by MCKINNEY & JACKSON in their book "Bryozoan Evolution" (1989).

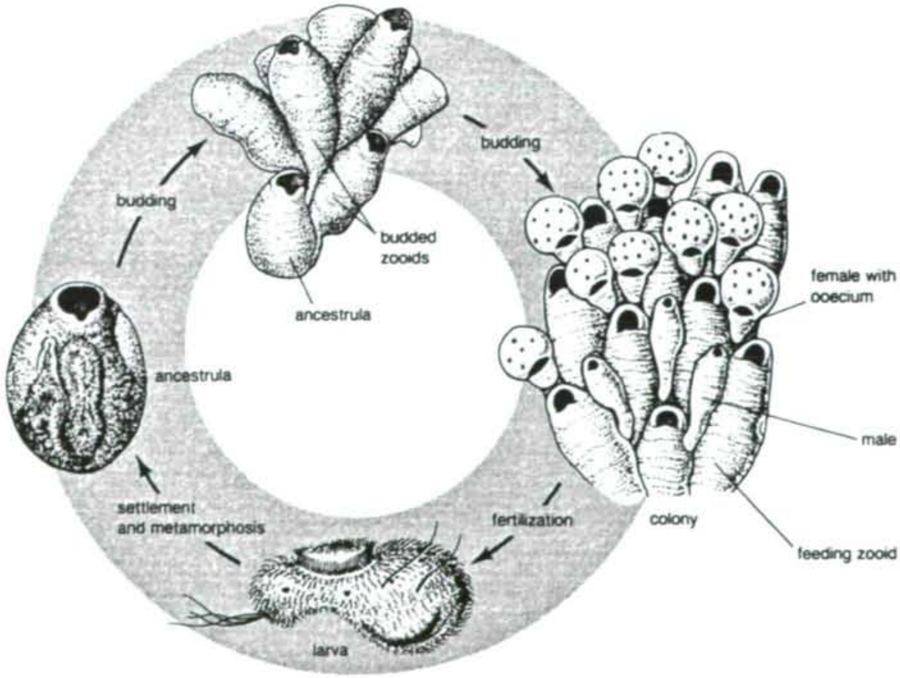


**Fig. 4**: Life cycle in *Celleporella* (a cheilostomate). Reading clockwise from the left, the diagram shows an ancestrula, the pattern of early budding, a selection of fully developed zooids (autozooids, small males, and ovicellate females), and the coronate larva (Various sources, from RYLAND 1989).

## Reproduction and life cycles

Bryozoans, like other modular animals, have a life cycle that incorporates phases of asexual and sexual reproduction (Fig. 4). Asexual reproduction in larger invertebrate animals (e.g., sea anemones) may, by fission, produce genetically identical progeny, which separate to form clones. In bryozoans, as in hydroids and corals, the progeny (the zooids) are produced by asexual budding and almost invariably remain in intimate contact, giving rise to a colony. Some bryozoan species, however, also propagate colonies asexually. The cheilostome *Discoporella* lives as small, non-attached, saucer-like colonies on the sea floor. Groups of zooids at the colony rim detach at special fracture zones and grow into new colonies. The statoblasts (dormant buds) of freshwater bryozoans constitute another means of asexual reproduction, and probably evolved initially as a means of surviving adverse conditions (e.g. winter or drying out) in situ rather than for dispersal. Asexual reproduction typically, whether leading to a clone, a colony, or a clone of colonies, is a means of perpetuating and locally increasing a successful genetic constitution (genotype) rather than one for colonising new territories (WILLIAMS 1975).

**Budding**. A bryozoan colony originates from either a primary zooid (ancestrula) or a statoblast. The ancestrula is formed by the metamorphosis of a sexually produced larva (ZIMMER & WOOLLACOTT 1977). The ancestrula is frequently smaller and/or morphologically different from the budded zooids (Fig. 4). New zooids bud from the ancestrula to produce colonies of definite or indefinite shape and characteristic growth habit (ZIMMER & WOOLLACOTT 1977). The process of colony formation and differentiation is known as astogeny (in contrast to the morphogenesis and ageing of a zooid, which is ontogeny). Early astogeny often progresses through a gradation of metric or morphological changes until the typical (ephebic, see RYLAND 1970) zooid form is achieved (BOARDMAN & CHEETHAM 1969, 1973). In phylactolaemates, the primitive zooids are cylindrical in form, and astogeny results in a branched colony. In more highly evolved phylactolaemates, colonies are more compact, and discrete zooids can be recognized only with difficulty. New polypides, which originate by ingrowth of the superficial cell layer, or epithelium, remain suspended within a common colonial coelom, or body cavity (generally regarded as a coelom). Among living members of the primitive (and mainly fossil) marine stenolaemates, the long and slender zooids have calcified tubular skeletons. A larva metamorphoses into a hemispherical primary disk (pro-ancestrula). A cylindrical extension grows from the pro-ancestrula, and the matrix of the colony then is built up by repeated divisions of the zooidal walls. Internal walls of the colony are called septa. The growth and budding zones of the colony are found at its outer edges. Cells from the surface epithelium push inward to produce the polypide, and the septa create a chamber (cystid) around it. In the gymnolaemates, in which the zooids frequently are flattened, budding occurs as transverse septa form and cut off parts of the primary zooid (or any other parent zooid). As each bud enlarges to become a zooid, a polypide forms inside. In the order Cheilostomatida, budding usually produces rows of identical zooids that radiate from the primary zooid. The rows divide periodically to keep pace with the increasing circumference of the colony and to maintain 'hexagonal close packing' organisation that maximizes the number of feeding lophophores per unit area (THORPE & RYLAND 1987). Successive zooids in a row are separated by transverse septa, but adjoining rows are separated by double walls. Interzooidal pores are present both in the walls and in the septa (Fig. 2).

**Sexual reproduction**. Sexual reproduction, by the production and subsequent fission of gametes, generates the genetic variability necessary for a species to survive in a habitat that varies from place to place and from time to time (WILLIAMS 1975; RYLAND 1981; JACKSON 1986). As the colony continues its growth by budding, some zooids become sexually mature, producing eggs and spermatozoa. Fertilized eggs develop into larvae (Fig. 4), which disperse and found new colonies. Mature gymnolaemate and phylactolaemate zooids are most commonly hermaphroditic (i.e., both male and female reproductive organs occur in the same zooid); small gonads are attached in clusters to the membrane that lines the body wall or the polypide. In a few species the individual zooids are of one sex only. In these circumstances, female zooids are usually larger (e.g., in the cheilostomate *Reptadeonella*), male zooids may be simpler or just have fewer tentacles in the lophophore (e.g., in the ctenostomate *Alcyonidium nodosum* and the cheilostomate *Hippoporidra* (RYLAND 2001), or female and male reproductive zooids each may be distinguishable from ordinary feeding zooids (e.g., in the cheilostomate *Celleporella*, Fig. 4). Sperm are discharged through the terminal pore found in all tentacles, or just through the dorso-medial pair (between and below which the nerve ganglion is situated), and must be dispersed through the enveloping water before entering another zooid (SILÉN 1972). Experimental evidence is accumulating that cross, or between colony, fertilization is the norm for bryozoans, irrespective of the mode of embryonic development (RYLAND & BISHOP 1993; TEMKIN 1996; HUGHES et al. 2002). Among living stenolaemates most zooids contain only testes. The few female zooids enlarge to form spacious brood chambers, which are called gonozooids. During development, a remarkable form of asexual budding (polyembryony) takes place: young embryos squeeze off groups of cells that form secondary embryos; these in turn may form tertiary embryos. In this way, many larvae can develop in a single brood chamber. The unique features of reproduction in stenolaemates may be related to the usually small size of both zooids and colonies, resulting in scarcity of sperm (RYLAND 1996, 2000).

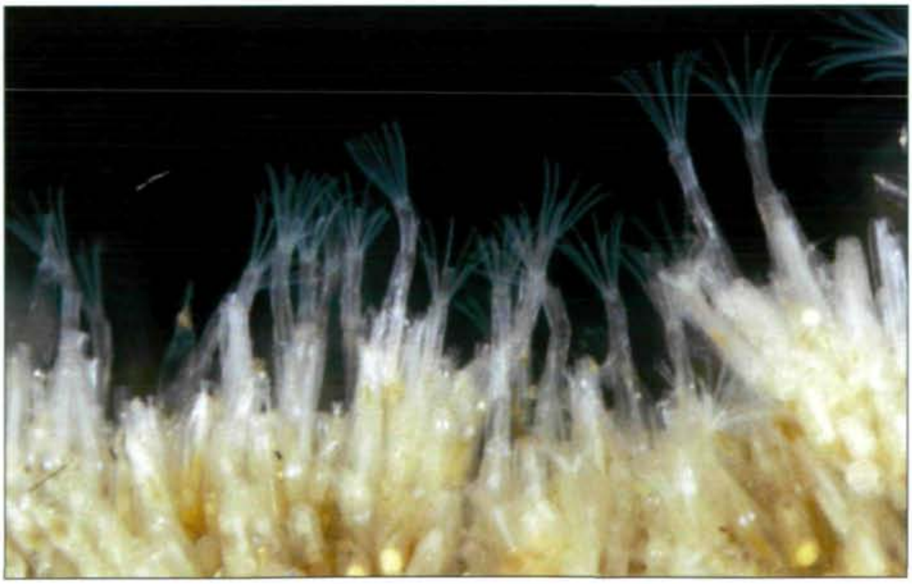
Among the phylactolaemates, the fertilized egg develops in an internal embryo sac; a larva, which already contains the first polypide, is formed there, then liberated. Phylactolaemates also produce asexual statoblasts, which develop on the funiculus, a cord of tissue that links the stomach to the lining of the body wall. As it grows, each statoblast is surrounded by a hard protective case that may also include an air-filled float and slender, hooked spines. Statoblasts usually develop in late summer and are liberated as the colony disintegrates with the ap-

**Fig. 5**: Encrusting colony of *Schizoporella unicornis* (Cheilostomatida). Many zooids in the central band support ovicells, a majority containing pinkish-red embryos. Frame approximately 18 x 12 mm. Origin: west coast of Scotland, May 1996.

proach of winter. Statoblasts survive dry and freezing conditions and can initiate a new colony when favourable climatic conditions recur.

In most gymnolaemates one oocyte at a time enlarges and bursts from the ovary into the coelom, probably then being fertilized by exogenous sperm already present. The oocyte grows and is transferred to a brood chamber. This may be an undifferentiated part of a zooid; in some ctenostomates, for example, one or more late oocytes pass through the supraneural pore into a space created by the tentacle sheath (as in Fig. 1). Usually among cheilostomates, however, each oocyte passes into a special globular or hooded ovicell (or ooecium) – usually, if not invariably, produced from the next distal zooid (Ostrovsky & Schäfer 2003) – in which the embryo develops (Fig. 5). The egg at transfer generally has sufficient yolk to nourish its embryonic development; but in the cheilostomes *Bugula* and *Celleporella* the egg, which is small at transfer, establishes a pseudo-placenta with tissues of the mother zooid and receives nourishment as the embryo develops (general review by Ström 1977). The ciliated larvae, subspherical and often about 0.25 mm in diameter, are liberated when fully developed and may swim first toward the light and thus away from the parent colony; later, however, the larvae avoid light as they seek a place in which to settle (Ryland 1976b, 1977). Metamorphosis of larvae to adults occurs within a few hours after larvae are liberated (metamorphosis and early astogeny reviewed by Zimmer & Woollacott 1977).

**Fig. 6**: Cylindrical zooids of *Bowerbankia imbricata* (Ctenostomatida) with expanded lophophores. Scale not recorded but expanded zooids are about 0.25 mm diameter. Origin: west coast of Scotland, May 1985.



In certain genera (e.g., *Membranipora* and some species of *Alcyonidium*) of the class Gymnolaemata, each zooid sheds many tiny, fertilized eggs directly into the sea. These develop into oval or triangular, bivalved larvae, known as cyphonautes, which for several weeks live among, and feed on, plankton. Larvae from brood chambers (termed 'coronate') and cyphonautes settle in a similar way; i.e., both locate a suitable surface and explore it with sensory cilia (Ryland 1976b). Attachment is achieved by flattening a sticky holdfast, which pulls the larva down on top of it. As metamorphosis proceeds, larval organization degenerates and the first polypide develops – with reversed polarity – inside the primary zooid (Ryland 1976b, 1977; Zimmer & Woollacott 1977).

## Food and feeding

Bryozoans feed on minute planktonic particles that are captured by the (8-30) tentacles, which, in marine species, spread as a funnel with the mouth at its vertex (Fig. 6, 7, 9). The beating of long lateral cilia draws water into the top of the funnel and propels it out between the tentacles. Particles are projected toward the mouth; it was suggested by Strathmann (1973) that those leaving the funnel between the tentacles would be flicked back into it by reversed beat of the lateral cilia, though some of Strathmann's interpretations were unsupported by the work of BEST & THORPE (1983). Recent work suggests, moreover, that the lateral cilia function more as passive sieves (RIISGÅRD & MANRÍQUEZ 1997; NIELSEN & RIISGÅRD 1998; LARSEN & RIISGÅRD 2002). More study on mechanisms is needed. Shorter cilia on the inner face of the tentacles may assist in the transport of food particles toward the mouth without the involvement of mucus; from there they are sucked into the pharynx. Diatom shell valves are separated or broken in the gizzard, when present (MARKHAM & RYLAND 1987). Digestion and absorption occur in the stomach, and indigestible remains are compacted by rotation and expelled as faecal pellets. Freshwater bryozoans generally have more tentacles, disposed in a crescentic lophophore, the ends of which project behind the mouth.

The bryozoan method of feeding, especially in extensively spreading colonies of optimally packed zooids, imposes colonial organization as well as appropriate zooidal behaviour. Filtered water accumulates below the expanded lophophores, which are held above the colonial surface. Hydrodynamics requires that this water, very viscous at the scale of individual zooids and often far from the colony margin, be removed without diluting the food-bearing inflow (GRÜNBAUM 1995; LARSEN & RIISGÅRD 2001). The solution has been the formation of regularly spaced 'exhalant chimneys' first described in the flat spreads of *Membranipora* (BANTA et al. 1974; LARSEN & RIISGÅRD 2001; Fig. 8, 9). Each 'chimney' is essentially a space, sometimes centred on a non-functional zooid (Fig. 9), enlarged by the divergent posture of the surrounding lophophores. Exhalant water enters the base of the 'chimney' and outflows to well above the height of the surrounding lophophores. The efficiency of the system is often enhanced, as in the cheilostomate genus *Hippoporidra*, by the colony surface being regularly mammillated, each summit coinciding with and elevating the 'chimney'. The colony-wide adaptations to feeding have been comprehensively reviewed by MCKINNEY & JACKSON (1989), though further important contributions to our understanding of and the need for and functioning of, chimneys have been made by ECKMAN & OKAMURA (1998), LARSEN & RIISGÅRD (2001), and SHUNATOVA & OSTROVSKY (2002). In a further development, for example in species of *Hippoporidra* and in the ctenostomate *Alcyonidium nodosum*, the hydrodynamic system evolved to promote feeding efficiency has been utilized in reproduction. In both bryozoans the zooids are single sex rather than hermaphroditic, and small male zooids are clustered on the summits of the mammillae, so that sperm are discharged in the strong outflow (RYLAND 2001).

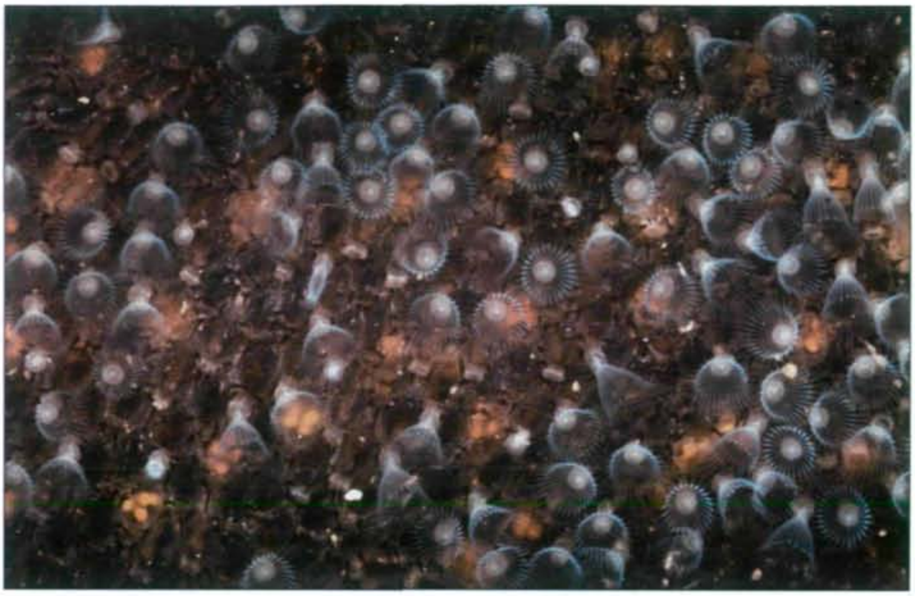
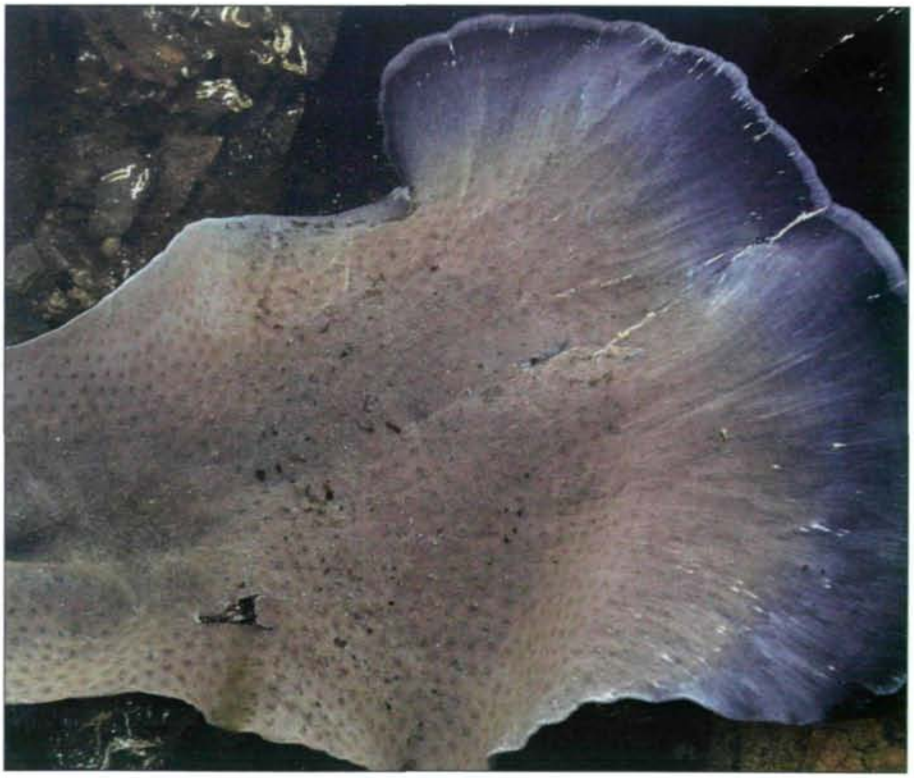


**Fig. 7**: Encrusting colony of *Flustrellidra hispida* (Ctenostomatida) with expanded lophophores. Coast of Wales but no further details recorded; the expanded lophophores have a diameter of about 1 mm to the point of out-curving (bright in the photograph).

**Fig. 8**: Colony of *Membranipora membranacea* (Cheilostomatida) on a kelp (*Laminaria*) frond. The direction of growth is to the right, bounded by a wide marginal budding zone (rapid growth rate). In the older part the regularly spaced darker spots indicate the positions of exhalant chimneys (see text). Actual size not recorded. Locality: Shetland, June 2001.



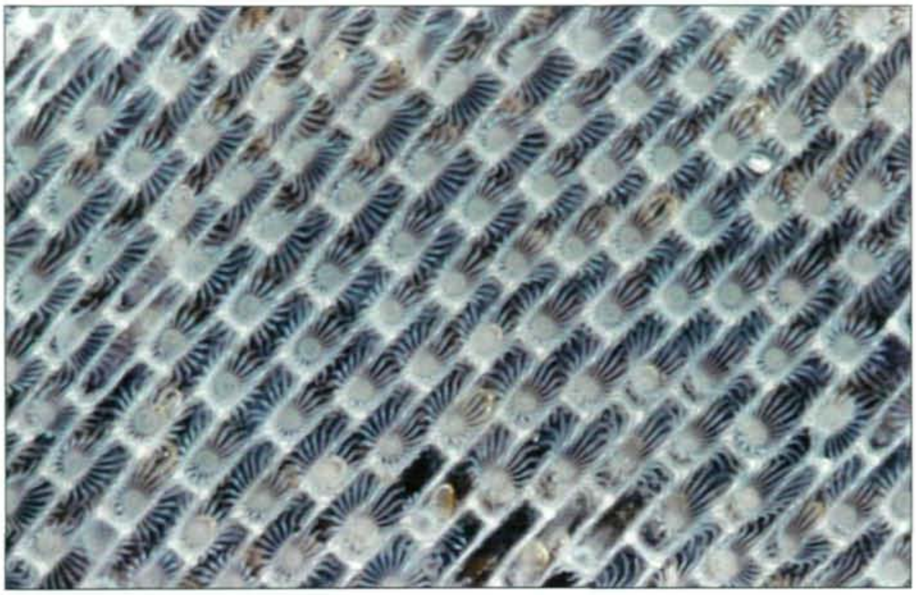


**Fig. 9**: Zooids of *Membranipora membranacea* with expanded lophophores. At the bottom centre is an "empty" zooid which will become the focus of a chimney. Zooids measure about 0.4 mm length. Locality: west of Scotland.

## Distribution and abundance

Bryozoan colonies are found in both fresh and salt waters, most commonly as growths or crusts on other objects (Fig. 3, 10). Freshwater bryozoans live among vegetation in clear, quiet, or slowly flowing water. Marine species range from the shore to the ocean depths but are most plentiful in the shallow waters of the continental shelf. They cover seaweeds, form crusts on stones and shells, hang from boulders, or rise from the seabed. Bryozoans readily colonize submerged surfaces, including ship hulls and the insides of water pipes. A few form free-living or apparently non-attached populations on sandy seabeds.

The zooid walls, which constitute the most permanent portion of the colony, are generally calcareous, giving bryozoans a fossil record that dates from the Ordovician onward (i.e., from about 500 My ago).

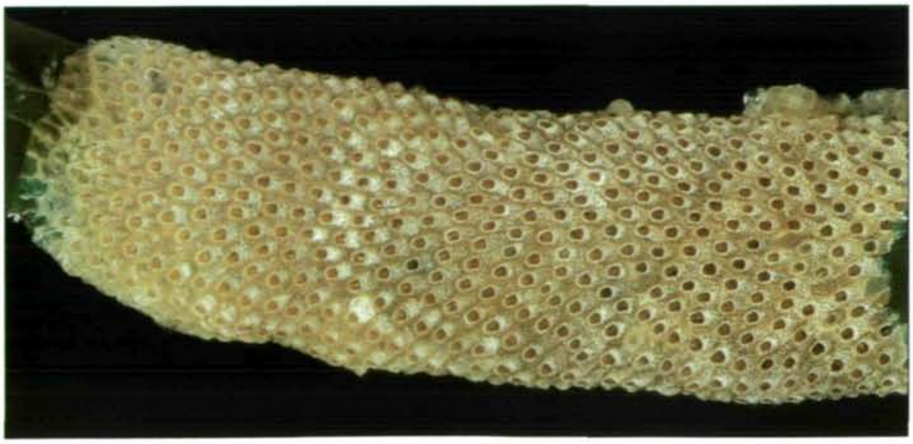


**Fig. 10**: Encrusting colony of *Cryptosula pallasiana* (Cheilostomatida). This species has a porous frontal wall, a very large orifice, and (unusually) lacks ovicells, the embryos developing internally. Zooids approximately 0.8 x 0.4 mm. Origin: west coast of Scotland, May 1985.

## Ecology

**Freshwater bryozoans**. Freshwater bryozoans live mainly on leaves, stems, and tree roots in shallow water. Before drinking water was filtered, they regularly polluted water supply pipes. Though not uncommon, freshwater bryozoans are often inconspicuous in pools, lakes, or gently flowing rivers, especially in slightly alkaline water.

**Marine bryozoans**. The most familiar marine bryozoans are those that inhabit shores, though they occur in greater numbers below tidemarks. Dredge hauls of stones and shells yield colonies in abundance. Colonies also occur on the ocean bed, even at great depths, but the frequently muddy bottom of the oceanic abyss is an unfavourable habitat. A few species tolerate hypersaline or brackish waters. The predominantly marine Gymnolaemata have a few freshwater representatives, e.g. *Paludicella*.

Shallow, sheltered channels that have currents but are protected from severe waves are typical bryozoan habitats. Open coastlines support fewer species, but non-calcareous species (e.g. of *Alcyonidium*, *Bowerbankia* (Fig. 6) and *Flustrellidra* (Fig. 7)) occur abundantly on intertidal algae in temperate waters. A familiar gymnolaemate genus is *Membranipora* (Fig. 8), which is found throughout the world and is well adapted to living on kelp weeds at, and just below, low water mark. Although the zooid walls of *Membranipora* colonies are calcified (Fig. 9), they contain flexible joints, which allow the colony to bend as the alga sways in the waves. *Membranipora*, which may cover large areas with a million or more zooids, always grows predominantly toward the youngest part of an algal frond (Fig. 8). Overhangs, which form when soft rock erodes along a shoreline, floating pontoons, and the shaded pilings of jetties and piers, are other favoured habitats. Since bryozoans do not require light and can grow in dark places, they can avoid competition from algae that could smother them. Opisthobranch sea slugs and pycnogonids appear to be the principal predators of bryozoans.

## Evolution and palaeontology

The Bryozoa have a long history. From the Lower Ordovician (500-430 My ago) onward, most limestone formations, especially those with shale alternations, are rich in bryozoan fossils. The skeletons of calcified bryozoans are easily preserved. Stenolaemates are abundant fossils; and, after their appearance in the Upper Jurassic (140 My ago), cheilostomate fossils also are abundant. The soft-bodied phylactolaemates, on the other hand, have left no fossil record, and fossilized ctenostomates are rare (usually in the form of moulds resulting from immuration; VOIGT 1979) but long antedate the cheilostomates.

The most ancient bryozoans are stenolaemates from the Lower Ordovician of the United States and Russia (Arenig series, about 499 My old); both cystoporate and trepostome stenolaemates have been found. The ceramoporoids, a group belonging to the order Cystoporata, flourished during the Ordovician and evidently were the progenitors of a more advanced group, the fistuliporoids, which were successful until the end of the Permian (280-225 My ago).

Dominant among the early Palaeozoic (570-225 My ago) stenolaemates, however, was the order Trepostomata, which evolved rapidly during the Ordovician and attained its peak during the upper part of the same period. The long, slender zooids of trepostomes grew together to form large, solid, colonies. As a zooid grew longer and longer, diaphragms (or transverse partitions) were deposited. The trepostomes declined in importance after the Ordovician, perhaps as a result of competition from the cryptostomes, and were extinct by the close of the Permian (225 My ago).

Cryptostomes evolved rapidly during the Ordovician. They were similar to the trepostomes but evolved freely erect, leaflike, branching or lacy colonies in the ptilodictyoids, or branching in rhabdomesoids, and were the dominant bryozoans from the start of the Devonian until the Permian (395-225 My ago). For reasons not yet clear, the cryptostomes dwindled and became extinct soon after the end of the Palaeozoic Era (225 My ago).

The Cyclostomatida arose in the Palaeozoic, flourished during the Jurassic (190-136 My ago) and Lower Cretaceous, and still survive.

The ctenostomates (class Gymnolaemata) have left a sparse fossil record. During the Late Jurassic they apparently gave rise to the complex and successful cheilostomes. These had encrusting flat zooids similar to some of their contemporary ctenostomates but with side walls that were calcified. This type of organization, termed anascan (meaning without an ascus), permitted inflexion of the front wall to evert the lophophore but seemed to offer little protection. The ascophoran (ascus bearing) organization evolved in the Late Cretaceous by calcifying the membranous front but preserving its hydrostatic function by a flexible infolding (ascus) below the wall. The parietal muscles attach to the ascus and pull its lower surface into the coelom to evert the lophophore, while the ascus itself fills with seawater.

## Classification

Although both colony type and zooid morphology are used to classify bryozoans, zooidal characters are more reliable. However, the cylindrical zooids of stenolaemates are of rather uniform appearance, making classification difficult; wall structure and the morphology of the embryo chambers are important taxonomic characters. In cheilostomates the skeletal features of the zooids, particularly the presence, extent, and structure of the frontal wall – together with shape of the orifice, type of ooecia, and zooid polymorphism – provide the most important distinguishing taxonomic criteria. A simple division of cheilostomates into two suborders, Anasca and Ascophora, is now recognized as being an over-simplification, though these former taxa certainly represent grades of organization. The Ascophora, in particular, are certainly polyphyletic, the frontal wall-submural ascus combination having evolved in a number of separate ways (GORDON 2000). Among ctenostomates and phylactolaemates, whose zooids lack skeletal features, colony form is more important. Statoblasts are of taxonomic value. Internal characters have been used less but, in ctenostomates, the presence or absence of a. gizzard, number of tentacles, and colour of developing embryos are of taxonomic significance.

## Phylum Bryozoa

Sedentary, aquatic invertebrates that form colonies of zooids by budding; each zooid with circular or crescentic lophophore surrounding a mouth from which slender, ciliated tentacles arise; anterior part of body forming an introvert within which the lophophore can be withdrawn; alimentary canal deeply looped; anus opening near mouth but outside lophophore; excretory organs and a blood vascular system absent; each zooid secretes a rigid or gelatinous wall to support colony; at least 8,000 extant species.

The classification of bryozoans began in 1837 when the freshwater and marine Bryozoa were separated into the classes now known as Phylactolaemata and Gymnolaemata: later a third class, Stenolaemata, was separated from the Gymnolaemata. The cyclostomates and the fossil trepostomes were placed in the new class (for a recent review, see BOARDMAN 2002). In recent years, the cryptostomes have also been placed in the Stenolaemata. The most satisfactory system, therefore, separates the bryozoans into three classes, distinct since the beginning of the fossil record.

Most of the bryozoan orders were named many years ago (though the suffixes have been changed to accord with a more logical hierarchy): Cheilostomatida; Ctenostomatida, and Cyclostomatida in 1852; Trepostomata in 1882; and Cryptostomata in 1883. Cystoporata was introduced in 1964 to include the Palaeozoic ceramoporoids and fistuliporoids.

### Class Phylactolaemata

Zooids basically cylindrical, with a crescentic lophophore and an epistome (hollow flap overhanging mouth); body wall noncalcareous, muscular, used for averting the lophophore; coelom continuous between zooids; new zooids arising by replication of polypides; special dormant buds (statoblasts) are produced; zooids monomorphic; exclusively freshwater; cosmopolitan; apparently primitive, but with no certain fossil record; about 12 genera.

### Class Stenolaemata

Fossil except for some Cyclostomatida; zooids cylindrical; body wall calcified, without muscle fibres; not used for everting the lophophore; zooids separated by septa; new zooids produced by division of septa; limited polymorphism; marine; Ordovician to present; about 550 genera.

### Order Cyclostomatida

Orifice of zooid circular; lophophore circular; no epistome; zooids interconnected by open pores; sexual reproduction involves polyembryony, usually in special reproductive zooids (gonozooids); all seas; Ordovician to present; about 250 genera.

### Order Cystoporata

Zooid skeletons long and tubular, interconnected by pores and containing diaphragms (transverse partitions); cystopores (not pores but supporting structures between the zooid skeletons) present; Ordovician to Permian; about 80 genera.

### Order Trepostomata

Colonies generally massive, composed of long tubular zooid skeletons with lamellate calcification; without interzooidal pores; orifices polygonal; sometimes with numerous diaphragms, zooid walls thin proximally, thicker distally; Ordovician to Permian; about 100 genera.

### Order Cryptostomata

Colonies mostly with foliaceous or reticulate fronds or with branching stems; zooid skeletons tubular, shorter than in trepostomes; without pores; with diaphragms; proximal portions thin walled, distal portions funnel-like, and separated by extensive calcification; Ordovician to Triassic; about 130 genera.

### Class Gymnolaemata

Zooids cylindrical or squat; with a circular lophophore; no epistome; body wall sometimes calcified; non-muscular; eversion of lophophore dependent on deformation of body wall by extrinsic muscles; zooids separated by septa or duplex walls; pores in walls plugged with tissue; new zooids produced behind growing points by formation of transverse septa; polymorphic; mainly marine; all seas; probably Ordovician to present; abut 650 genera.

### Order Ctenostomatida

Zooids cylindrical (Fig. 6) to flat; walls not calcified; orifice terminal or nearly so, often closed by a pleated collar; no ooecia or avicularia; Ordovician (on basis of immured casts; see VOIGT 1979) to present; about 40 genera.

### Order Cheilostomatida

Zooids generally shaped like a flat box, walls calcified; frontal membranous (Fig. 9) or calcified (Fig. 10); orifice frontal; closed by a hinged operculum; specialized zooids, such as avicularia, commonly present; embryos often developing in ooecia (ovicells or brood chambers). Upper Jurassic to Present; at least 600 genera.. A simple subdivision into suborders Anasca and Ascophora is no longer sustainable.

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