

3

General morphology and terminology

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3.1 External characteristics and astogeny

Because of the wide diversity of forms, bryozoan colonies are frequently misidentified as members of other phyla, including sponges, corals, hydroids, foraminiferans, and even calcareous and non-calcareous algae. Many colonies consist of encrusting sheets on rock, shell or algae, often covering them completely. Others are erect and massive, arising from an encrusting base, or are nodular and composed of many layers of zooids. Yet others are delicate and flexible, resembling little trees and attached by rootlet systems, or reticulate and lacy, formed of complex scrolls and tubes. Homeomorphy is common – that is, species from different classes or orders have closely similar colony forms.

Although each colony is the equivalent of a single solitary animal, many of the zooids of which it is composed may also have an almost autonomous existence. Individual zooids may feed and breed with little reference to neighbouring members of the colony. This is particularly the case in ramifying uniserial species of *Plumatella*, *Stomatopora*, *Aetea* and *Hippothoa*, among others. Other colonies, however, are highly integrated structures, formed of zooids whose morphology, physiology and function contribute to, and whose individuality is subordinated to, the common life of the colony. Examples are found among species of *Cristatella*, *Hornera*, *Caberea*, *Selenaria* and *Reteporella*, among others. Zonation of autozooids and

supporting structures, or clustering of autozooids in distinct patterns, is often external evidence for a high degree of integration (Boardman and Cheetham 1973).

A colony may be fragmented by breakage or alien overgrowth (e.g. by another species of bryozoan, or by other organisms, such as algae), resulting in the dispersal of genetically identical colony fragments. Each resultant subcolony may repair the original damage and grow to continue life as a clone of the original colony. Each fragment of the clone is able to 'recognise' other members, and to recombine to form a single colony, should they grow to have contact with one another. In some bryozoans, separation or isolation of special subcolonies, or single zooids, is a distinct, alternative, asexual method of reproduction and dispersal.

All colonies are derived originally from a single individual that is the result of sexual reproduction. The fertilised egg develops into a motile larva, which settles almost invariably upon a substratum, where it metamorphoses to become the primary zooid (ancestrula) or a multizoooidal complex that buds off the next zooid or zooids asexually. Budding is continued to form the colony.

All adult bryozoan colonies, including tiny ones living in the interstices of sediment grains, include at least one feeding zooid (autozooid). Of course, most bryozoan colonies comprise many more (thousands to millions) such zooids. Each

autozoid has a circlet of ciliated tentacles (= tentacle crown) surrounding a central mouth. The gut is U-shaped, the anus opening outside the base of the tentacle crown. Tentacles are extroverted or protruded for feeding, with the cilia of the tentacles producing a current that concentrates particles above the mouth.

The skeletal structures and musculature that evert and retract the tentacle crown differ among the various groups of bryozoans. Essentially, the tentacle crowns are squeezed out of the introvert, which is housed within the body wall, by the displacement of coelomic fluid by different sets of muscles. The mode of withdrawal of the tentacle crown, however, is common to all bryozoans. It is achieved by a retractor muscle that extends from

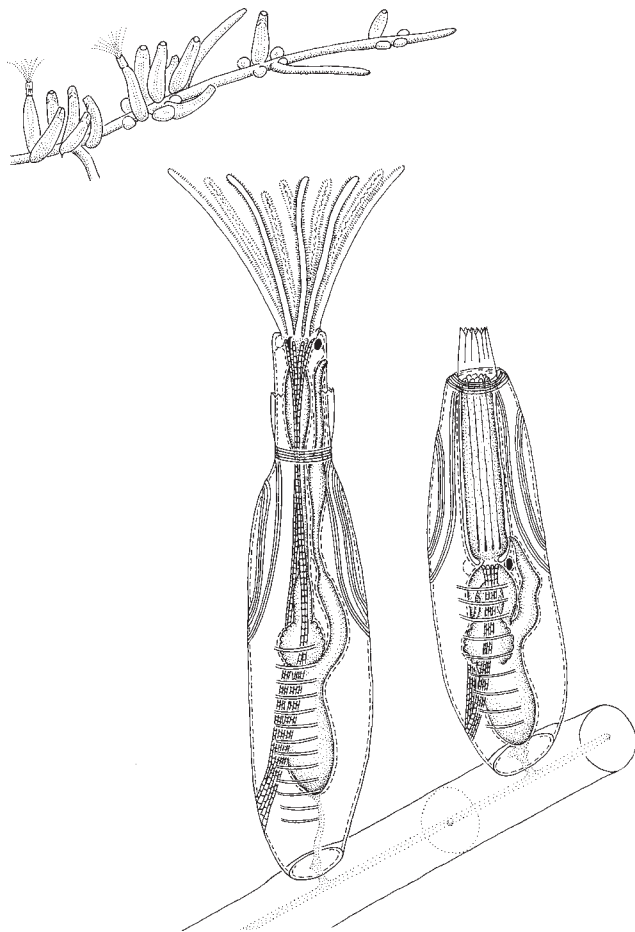


Figure 3.1: An example of the musculature required for everting and retracting the tentacle crown: *Amathia* sp. zooid structure (image redrawn from Hayward 1985).

the base of the tentacle crown to the proximal body wall (Taylor 1981) (Fig. 3.1).

3.1.1 Astogeny

The budding process that allows bryozoan colonies to grow is achieved by expanding the body cavity of developing zooids at the colony margin and then partitioning off the extended part by adding new body wall. Each completed zooid then, whether an autozoid or a polymorph, can be thought of as a little box or tube, depending on its shape. The wall of the box or tube is the body wall, known as a cystid, and it encloses the body cavity (coelom) and any tissues and organs. Budding is unique to colonial animals, such as bryozoans and hydroids, and the process is called **astogeny** (Boardman *et al.* 1983). There are usually changes in zooid morphology and physiology from the ancestrula to the colony margin, referred to as an **astogenetic gradient**. In a similar way, each zooid may pass through a series of ontogenetic changes in morphology and appearance as it develops (see Fig. 3.2). The linear series from ancestrula to colony margin records these changes, which may cease at maturation or continue through colony life. These changes thus also constitute an **ontogenetic gradient**. In this way, the direction and method of budding may be ascertained in fragmented specimens, particularly in fossils (Cheetham and Cook 1983).

In all bryozoans, two major methods of asexual budding occur. The first consists of an expansion of



Figure 3.2: Diagram of a longitudinal section through an encrusting colony, showing zones of astogenetic change and repetition and basic orientation of zooidal walls. Soft parts (e.g. tentacles and gut) are not shown. The zooid at the proximal end of the colony, extreme right, is the primary zooid (ancestrula). As the colony grows, the expanding exterior wall of the budding zone gains enclosed space that is partitioned into zooids by interior vertical walls. The boundary between zooids runs through the middle of the calcareous layer of interior vertical walls. The cuticle is attached directly to skeletal layers of exterior frontal and basal walls (image redrawn from Boardman *et al.* 1983).

cuticle and epidermis outwards from a pore in an existing body wall. The expansion increases in size with transfer of coelomic tissue and nutrients until the bud reaches full size and develops organs within its body wall. This process is discontinuous and is known as **intra-zooidal budding**. The second method involves expansion of a continually differentiating mass of coelomic tissue bounded by a distally elongating body wall; the enclosed chamber (coelom) becomes serially partitioned internally by the sequential growth of transverse walls, each of which develops communication pores as it grows. This method is known as **zooidal budding**. Colonies may grow by one or a combination of these methods (Lidgard 1985).

Morphological differences among zooids of the same astogenetic generation (i.e. zooids that are about the same distance from the ancestrula in a flat circular colony or in branches) are usually attributable to polymorphism, but some may be traced to micro-environmental influences, such as crowding, obstruction, overgrowth, or damage and repair. Because zooids are able to communicate and transfer nutrients within the colony, damage is repaired by new episodes of ontogenetic changes within zooids and astogenetic change among zooids.

Overall, colonies may consist of simple chains of feeding zooids all having the same form (i.e. monomorphic), bounded by exterior walls – their zooids each living almost as an autonomous single animal (Fig. 3.3). At the opposite extreme, entire colonies may consist of one extrazooidal exterior wall, subdivided internally into multizooidal zones of feeding and polymorphic zooids, partitioned by interior walls. The morphologies, positions and functions of all zooids are interrelated and all contribute to colony-wide function, including, in some species, locomotion. Among Bryozoa, all kinds of intermediate conditions may be found, comprising a mosaic of forms (Boardman and Cheetham 1973). A wide range of colony forms may be found within an individual taxon (e.g. superfamily Thalamoporelloidea) or a group may comprise all species having just one kind of colony morphology (e.g. superfamily Aeteoidea).

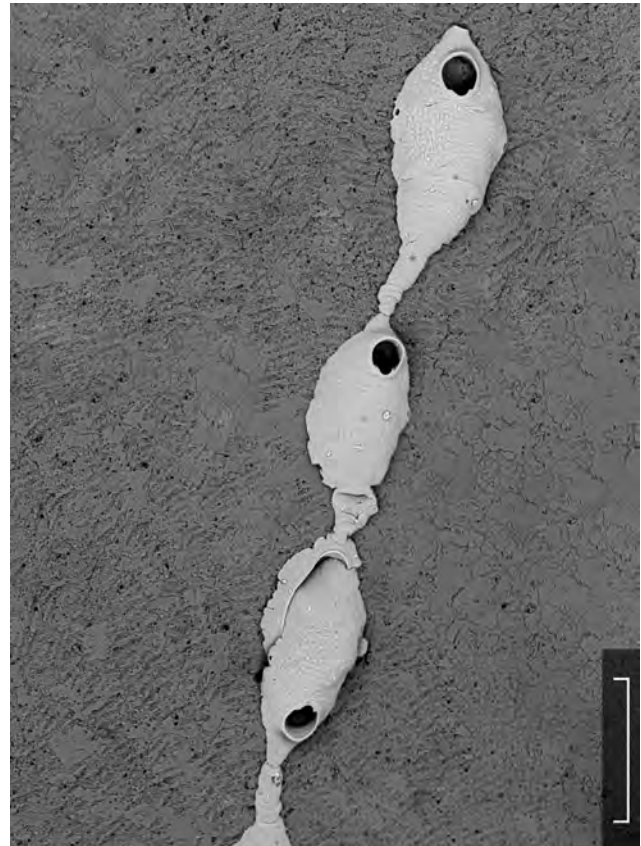


Figure 3.3: A chain of feeding zooids from *Hippothoa* sp. Scale bar = 200 μ m (photo: P. Bock).

3.2 Skeletal system

Each zooid in a colony is delineated and contained by body walls. Walls include an epidermal layer or scattered epidermal cells that secrete an outer covering of cuticle or a gelatinous mixture of proteinaceous and cuticular material. The outer covering layers are impervious to exchanges of fluids. Apart from all Phylactolaemata and gymnolaemates of the order Ctenostomata, some parts of body walls are also calcified.

Calcification allows erect growth and strengthening of zooids and extrazooidal structures, but, whether calcified or not, erect growth permits the extension of feeding zooids further into the surrounding water. Erect colonies may be rigid or flexible. Cuticular joints – which may be formed as kenozooids or as thickened cuticular zooid linings within existing zooids – allow flexibility in colony structure. Non-calcified rootlet-like rhizoids are

also a common feature of erect colonies. They function like the holdfasts of algae. They can also fuse to form a rope-like support that is able to withstand considerable flexing.

The capacity to control calcification is innate in most Bryozoa and is found in particular epithelial cells, whether those adjacent to an outer cuticular layer, which they secrete, or to those that may internally partition a coelom. Bryozoans are generally able to lay down calcite and/or aragonite and, most importantly, to resorb it in small or large specific regions of zooids. In a few species (e.g. some Hippothoidae), zooids are able to erode a calcified external environment, and all species in several families of Ctenostomata can bore into and through mollusc shells and other calcified substrata.

Zooids have two types of walls, which are not completely exclusive of one another. **Exterior walls** extend the body cavities of zooids and protect them from the environment; these nearly always have an external cuticular layer. Where the exterior wall is calcified, it can be considered to be an exoskeleton. **Interior walls** may have a cuticular layer or a calcified layer, or both; such walls partition pre-existing body cavity into zooids or parts of zooids, and can be regarded as endoskeleton. The **orientation** of zooid walls is explained in Box 3.1.

3.2.1 Skeletal ultrastructure

Bryozoan skeletons are constructed of calcium carbonate, with variable magnesium content. Biomineralisational patterns and, especially, processes are poorly understood in bryozoans but are believed to be similar to those in brachiopods and molluscs. However, bryozoan skeletons are more intricate than those of these two phyla. Calcareous skeletons have been acquired independently in two bryozoan clades – Stenolaemata in the Ordovician and Cheilostomata in the Jurassic (Taylor *et al.* 2015).

The skeletons of stenolaemates are exclusively calcium carbonate (CaCO₃). In cheilostomes, skeletons can comprise one of the two common crystal forms of CaCO₃, calcite or aragonite, or both. In bimineralic skeletons the two forms of CaCO₃ occur in different regions. Commonly, calcite is used in the initial skeleton, with aragonite in the frontal superficial layers, although occasionally aragonite can be found in basal thickenings. The different mineralogy can be reflected in ultrastructure – whereas calcite can have a variety of crystal morphologies and arrays, aragonite occurs mostly as elongate needle-like fibres. Cheilostome skeletons developed by different ontogenetic modes show recognisable differences at the ultrastructural level. Because of this, skeletal ultrastructure can be useful in taxonomy if used cautiously within well-defined

Box 3.1. Categories of zooid walls, based on orientation within the colony

Because most bryozoans are colonial, the walls of each zooid are described based on their orientation to the centre of the colony. This categorisation is useful for taxonomy and systematics, where the morphology of the walls is important, but it is also very important to know which wall is which. The categories are:

- The **distal wall** is that furthest away from the origin of the colony.
- The **proximal wall** is that nearest the origin of the colony.
- The **basal wall** is that which encrusts the substratum or is in common with the walls of an opposing layer of an erect colony.
- The **frontal wall** typically bears the orifice.
- The side walls that connect frontal and basal walls are called **lateral walls**.

However, many bryozoan species, and the majority in some groups, such as the Stenolaemata, Phylactolaemata, and Ctenostomata, have more-or-less tubular zooids in which the orifice is coterminous with the distal end of the zooid, and there is no discernible distinction between basal and lateral walls.



Plate 1.2: *Licomia curvata*, an example of a bryozoan tufted colony (photo: K. Gowlett-Holmes).



Plate 1.3: *Membranipora membranacea* growing on the kelp *Macrocystis* (photo: K. Gowlett-Holmes).

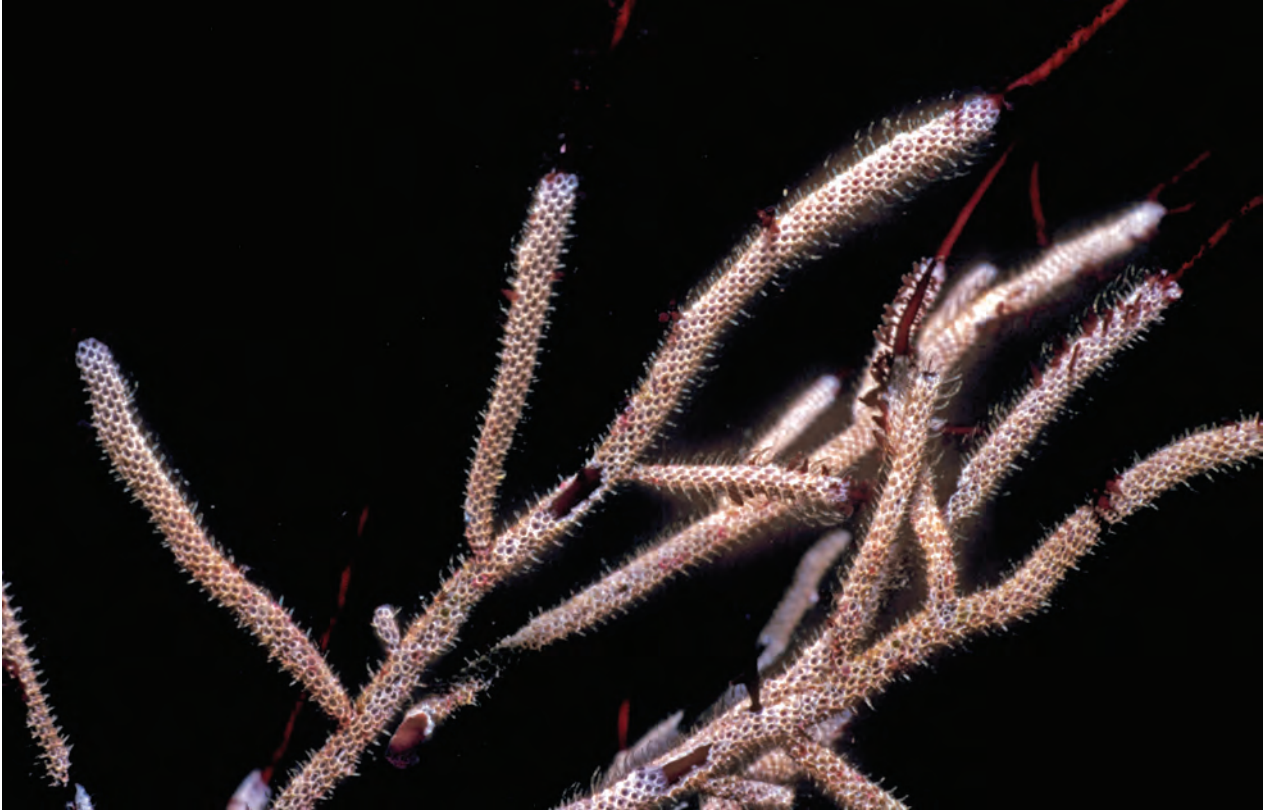


Plate 1.4: *Electra lesueuri* (photo: K. Gowlett-Holmes).



Plate 1.5: *Bugula robusta* (photo: K. Gowlett-Holmes).

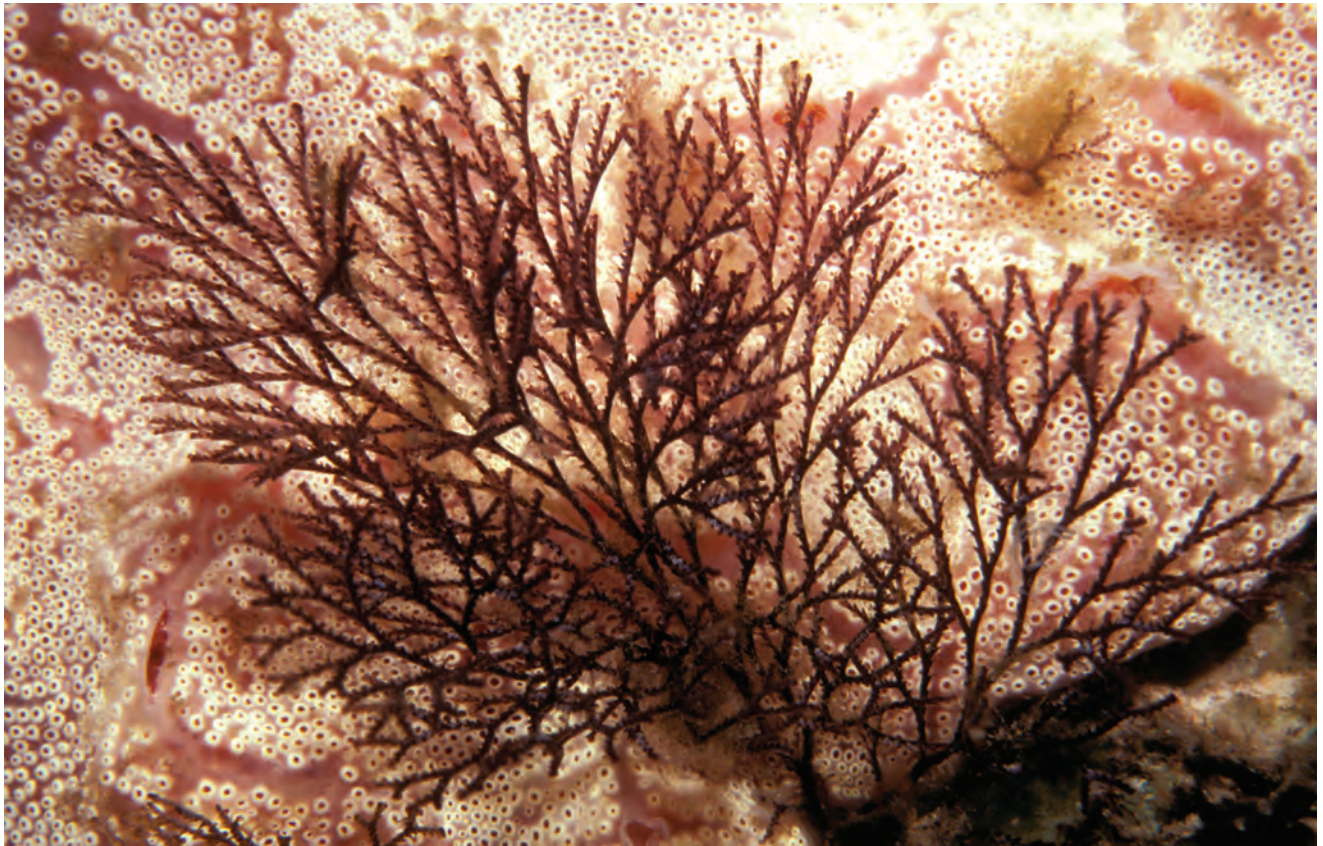


Plate 1.6: The cosmopolitan species *Bugula neritina* (photo: K. Gowlett-Holmes).



Plate 2.1: *Amathia crispa* (photo: K. Gowlett-Holmes).



Plate 4.6: *Iodictyum phoeniceum* (photo: K. Gowlett-Holmes).



Plate 4.7: An example of a robust rigid species, *Adeona grisea* (photo: K. Gowlett-Holmes).

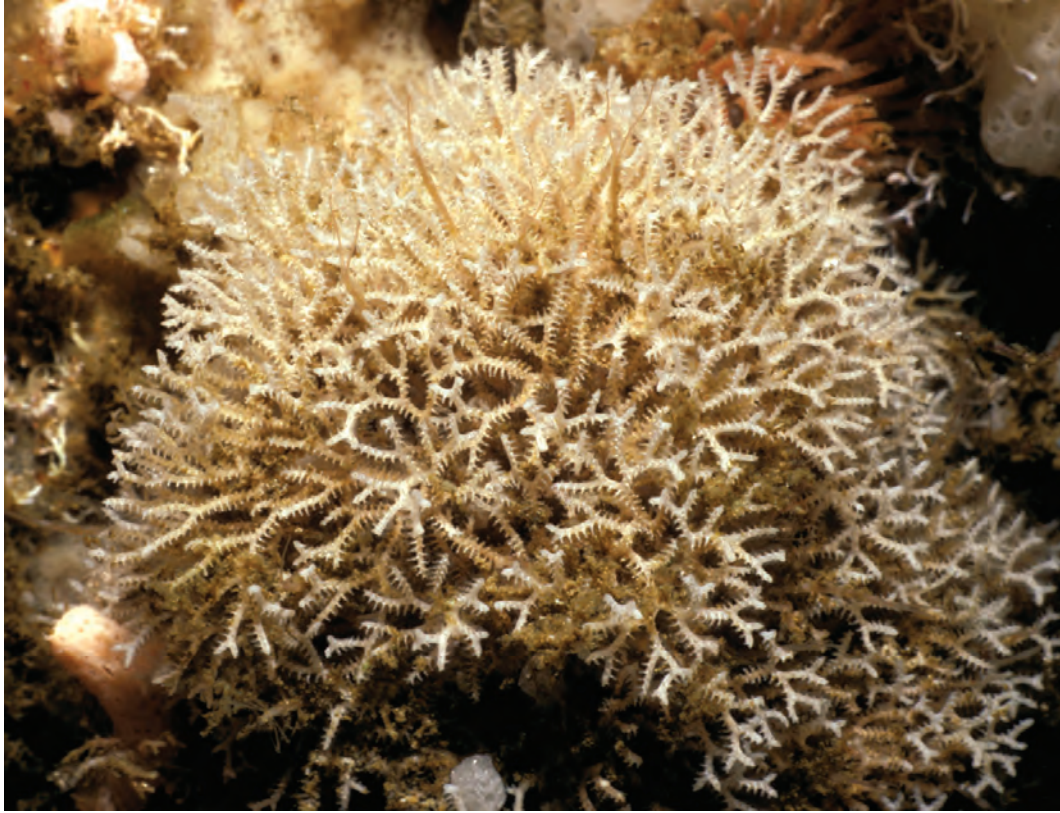


Plate 4.8: An example of a palmate branching species, *Idmidronea* sp. (photo: K. Gowlett-Holmes).



Plate 4.9: An example of a chain-like catenicellid: *Paracribicellina cribraria* (photo: K. Gowlett-Holmes).



Plate 6.3: *Bugula neritina* (photo: K. Gowlett-Holmes).

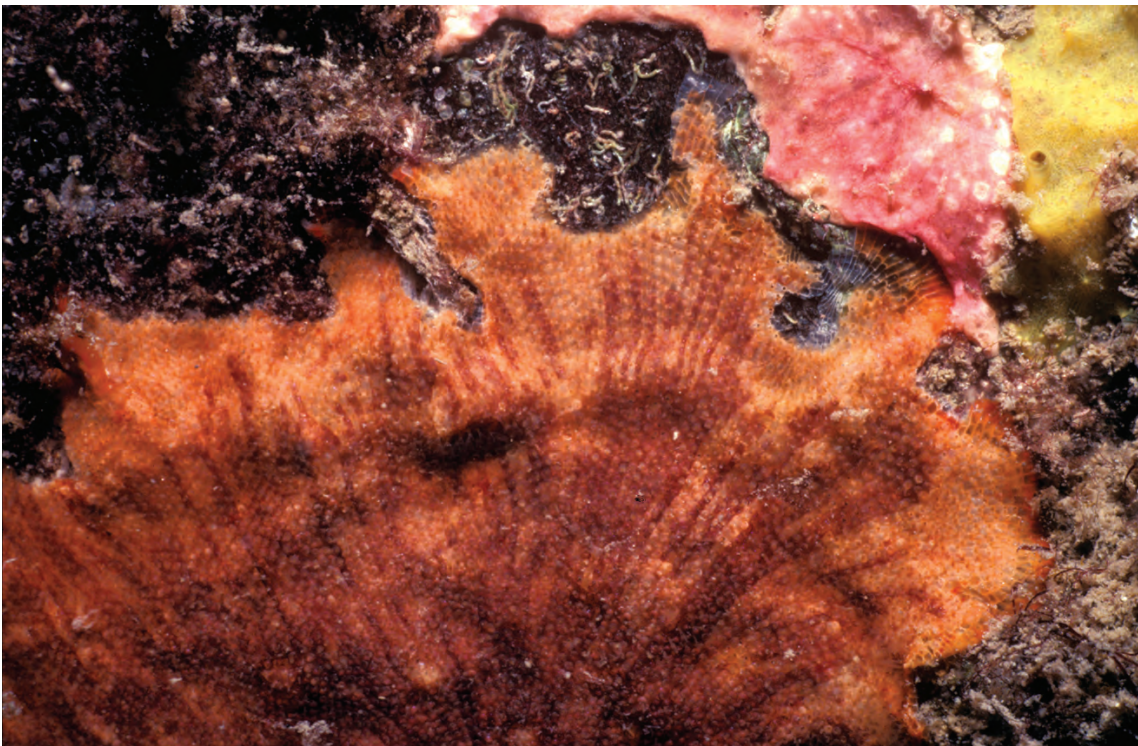


Plate 6.4: *Schizoporella errata* (photo: K. Gowlett-Holmes).