Bryozoan basics[1]

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Bryozoans are a phylum of colonial animals. They first appear in the fossil record during the early Ordovician (~480 million years ago.) Since that time, bryozoans have been a major component of the fossil record and of marine communities. Their colonies are modular, with individual animals, called zooids, forming the building blocks of the colony. There are two primarily marine classes: The **Stenolaemata** and the **Gymnolaemata**. The **Phylactolaemata** are an exclusively freshwater class. Many fundamental discoveries in evolutionary and paleobiology have been made with bryozoans and many more discoveries await.

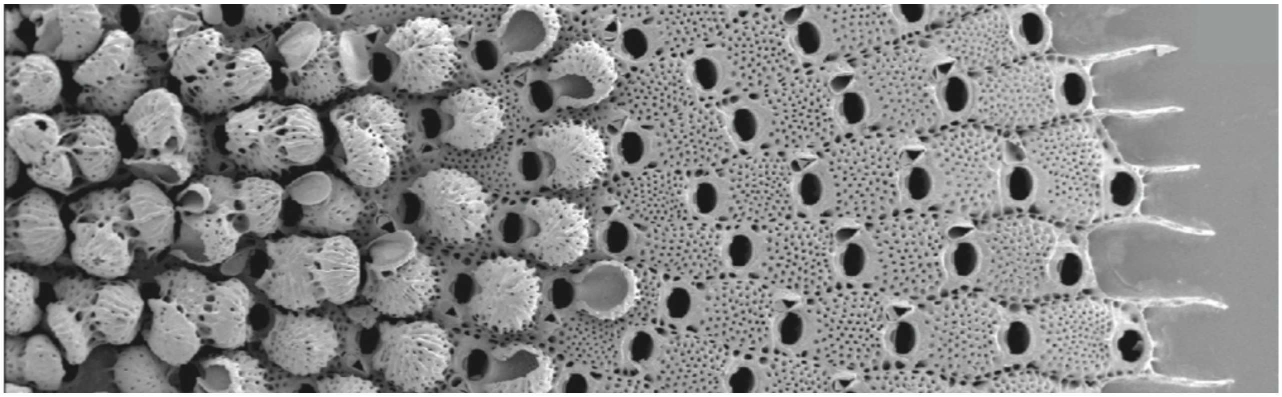

Figure 1: An SEM micrograph of the bryozoan *Schizoporella japonica* showing a radial section through a circular colony. The round structures are zooids that are reproductive specialists called ovicells. These ovicells are located in the center of the colony. Towards the growing edge (on the right) are the approximately rectangular autozooids with an elliptical orifice ● where the feeding structure emerges. Proximal to this orifice is a small teardrop-shaped zooid ● that is a defensive specialist called an avicularium. At the outermost growing edge are the outlines of developing autozooids.

Bryozoan zooids

The basic unit of a bryozoan colony is the zooid. Zooids are homologous to solitary animals, like a worm or a snail. Within a colony, zooids depend on each other for survival. If there is a division of labor within the colony, then the interdependence between zooids is even greater. Zooids are small, no more than a 1mm^3. The modular structure of colonies means that they can be of almost any shape and size. Mature colonies can contain two or three zooids up to millions.

Autozooids are the basic form that a bryozoan animal takes. It contains a feeding unit called the **polypide**. The skeletal element is called the **zooecium** and is secreted by epithelium within a sheath of tissue that encloses the polypide.

Polypides have a U-shaped gut, and a tentacle crown. Tentacles have a coelomic space that connects with other tentacles in the coelomic ring at the base of the tentacle crown. Each tentacle has three compound tracts of cilia. The inner tract passed food particles

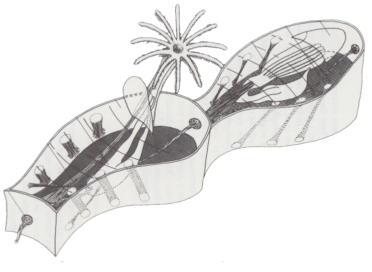

Figure 2: Two adjacent autozooids. The tentacular polypide is in the feeding position in the close zooid and is retracted in the far zooid, from McKinney and Jackson (1991).

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toward the mouth. The other laterally placed tracts are involved in moving water from above the tentacle crown, between the tentacles, to below the tentacle crown.

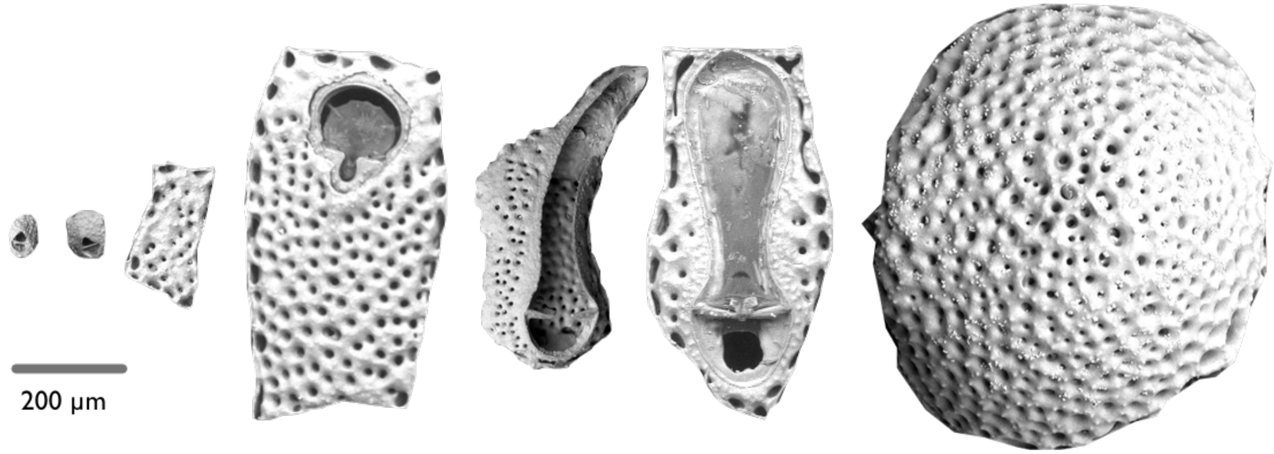

Figure 3: Polymorphic zooid types in a species of the cheilostome *Stylopoma*. From left to right, an oral adventitious avicularia, frontal adventitious avicularia, kenozooid, autozooid, large adventitious avicularia, vicarious avicularia, and an ovicell.

HETEROZOIDS are zooids that deviate from the autozooid form. Heterozoids (or polymorphs) are especially common in the gymnolaemate order Cheilostomata. Heterozoids specialize on functional tasks in the colony, including (but not limited to) defense, reproduction, locomotion, plumbing, structural support, and space filling. Most functions of particular heterozooids are not known.

Because bryozoans are clonal, all heterozooids and autozooids in a colony are genetically identical. How heterozoids evolve is not known. But it is a problem that is similar to the origin and evolution of cellular diversity in metazoans and the origin and evolution of castes in social insects.

Ovicells are heterozooids or even complexes of heterozooids, that specialize on brooding larvae. Ovicells are formed distal to a hermaphroditic or female zooid and sit within or upon the next zooid (see Fig. 1). In some species all autozooids can produce ovicells. But in many others, ovicells are restricted to a subset of zooids (Fig. 4). **Gonozooids** are similar heterozoids that occur commonly in stenolaemate bryozoans.

Variation how many zooids can produce ovicells is a major axis in life-history variation in bryozoans. The frequency of ovicells also correlates with the number of different types of polymorph types[2].

Kenozoids are a diminutive heterozooid that specializes on filling space. Kenozooids lack an orifice and have reduced or lost their polypides. Kenozooids occur often in encrusting species because growing on uneven surfaces sometimes leaves little room for full

Figure 4: A portion of a *Bugula* colony showing ovicells (blackened) concentrated proximal to the tips of the colony, from McKinney and Jackson (1991).

[2] Simpson, C. (2012). The evolutionary history of division of labour. *Proceedings of the Royal Society B: Biological Sciences* 279(1726), 116–121

autozooids. They also occur along the margins of motile species and intercalated among other zooids in erect branching species.

Avicularia are an important type of heterzooid. There are many varieties of avicularia they can be distinguished by their form and their position. Avicularia have modified the hatch-like autozooid operculum and modified or reduced the polypide to a rudiment or sensory organ. The operculum of avicularia (termed the **mandible**) can be shaped like a bristle, a spatula, a hook, or even like a beaked bird's head on a rotatable neck (Fig. 5).

Many bryozoans have **extrazooidal elements**, parts of the colony that are not part of any zooid or heterozooid. These add structural support or fill space.

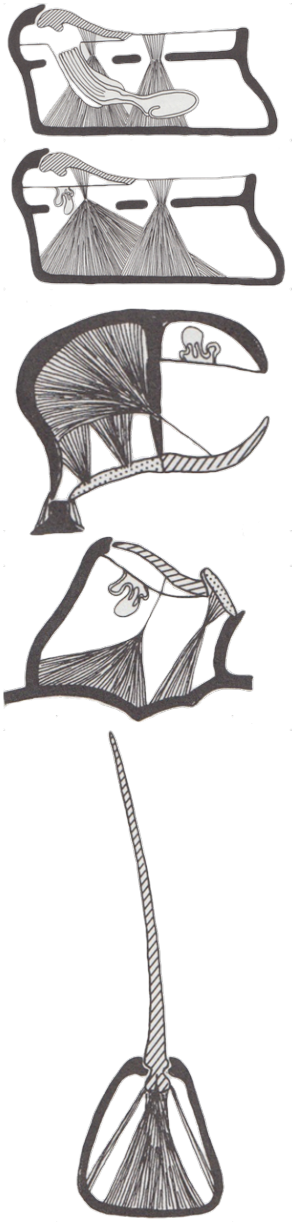

Figure 5: Diagrams of types of avicularia. From top to bottom: Vicarious with polypide, vicarious with reduced polypide, adventitious pedunculate, adventitious sedentary, and vibraculum. The skeleton, membranes, muscles, and polypides are shown. Homologous structures are shown in similar patterns. Operculum (madibles) are diagonally lined. From McKinney and Jackson (1991).

Major taxa of Bryozoa

Stenoleamata range from the Lower Ordovician to the Recent. Zooids are cylindrical or sac-shaped and lengthen through ontogeny, with long axis at an angle to the direction of local colony growth. The basal and vertical walls of the zooecium are rigidly calcified. Communication between zooids is mostly through spaces between outer ends of the vertical walls, but some have pores through the vertical walls. A membrane sac encloses the polypide and is deformed to protrude the tentacle crown through the orifice at the end of the skeletal tube[3].

Order **Trepostomata** — Lower Ordovician to the Upper Triassic. They have encrusting or erect colonies with long autozooids with basal diaphragms. Lots go kenozooids and extrazooidal parts. No communication pores.

Order **Cystoporata** — Lower Ordovician to the Upper Permian. Short autozooids lack basal diaphragms. Long autozooids have them. The outside of zooids are thickened with a strip with different microstructure. Some communication pores between zooids. Species have occasional kenozoids and gonozoids, but abundant extra zooidal parts.

Order **Cryptostomata** — Lower Ordovician to Upper Permian. Colonies are arborescent, or bilaminate sheets. Autozooids are short and some species have basal diaphragms. Zooids lack communication pores. Kenozooids and extrazooidal parts common.

Order **Fenestrata** — Lower Ordovician to Upper Permian. Colonies are erect and have narrow unilaminate branches. Short autozooids, rarely with basal diaphragms. No communication pores between zooids. Gonozoids, nanozooids (polypide reduced to a single tentacle) and other heterozooids occur. Most of the skeleton is made of

[3] The information on the major taxa of bryozoans is based on McKinney and Jackson (1991).

extrazooidal parts.

Order **Cyclostomata** — Lower Ordovician to the Recent. Collins are encrusting or erect. Autozooids are long and some species have basal diaphragms. Many species have zooids with communication pores. Gonozoids, kenozooids, nanozooids, and extrazooidal parts are common.

GYMNOLAEMATA range from the Upper Ordovician until the Recent. Their zooids are box-shaped or sometimes sac-shaped or short cylinders. The long axis of zooids is parallel to the local colony growth direction. Zooid sizes are fixed early in ontogeny. Zooid body walls range from entirely organic to rigidly calcified. Zooids communicate through a funicular network through tissue-plugged pores in vertical walls. The vertical or frontal walls are deformed to protrude the tentacle crown.

Order **Ctenostomata** — Upper Ordovician to the Recent. Zooid walls are membranous or gelatinous. The oriface is terminal and closed in a collar. Kenozooids are the only heterozooids present.

Order **Cheilostomata** — Upper Jurassic to the Recent. The cheilostomes are awesome. They have calcified zooid walls, but some are flexible and others are rigid. The frontal orifice has a hinged operculum. Heterozoids common. The suborders are based on how the tentacle crown is protruded and if the frontal wall is calcified. Ascophorans have calcified frontal walls and the ascus aids in tentacle crown protrusion. Anascans lack calcified frontal walls and the ascus.

Figure 6: *Cristatella mucedo*, a creeping phylactolaemate bryozoan illustrated by Haeckel (1899).

PHYLACTOLAEMATA are uncalcified freshwater bryozoans. They produce **statoblasts** are a mechanisms of asexual reproduction with dispersal. Statoblasts can remain dormant in harsh conditions for long periods of time. These bryozoans only have autozooids. Some of these colonies are motile and can creep along twigs (Fig. 6).

Growth and form

The founding zooid of a colony is called an **ancestrula**. Colonies only grow by adding new zooids and extrazooidal parts. The geometric relationship between new zooids to old zooids determines the colonies growth form. Colony development is called **astogeny**.

ENCRUSTING GROWTH

Many bryozoans grow by encrusting substrates (Fig. 7). They are commonly found on all substrates from algal fronds to corals, and are also common fouling organisms on ships.

Encrusting bryozoans add new zooids along some fraction of the

Figure 7: Encrusting cheilostome colony from the White Sea. Photo by Alexander Semanov, http://clione.ru

margin of the colony. If new zooids are restricted to one spot of the margin, colony growth results in runners or vine-like colonies (Fig. 8).

If zooids are added to a greater proportion of the margin the colonies form sheets (Fig. 7). Some species of cheilostomes are able to **self-overgrow** and may also have zooids that can **frontally bud**. With these abilities, colonies can add layers leading to thickened colonies or large mounds.

Encrusting species are limited by space, so biological interactions and competition are very important. Succession is common among species on large stable substrates and even correlates with the degree of polymorphism (Fig 9).

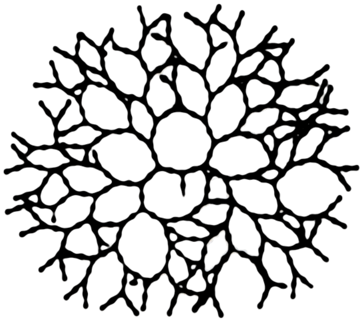

Figure 8: Diagram of a runner-like colony of *Stomatopora*.

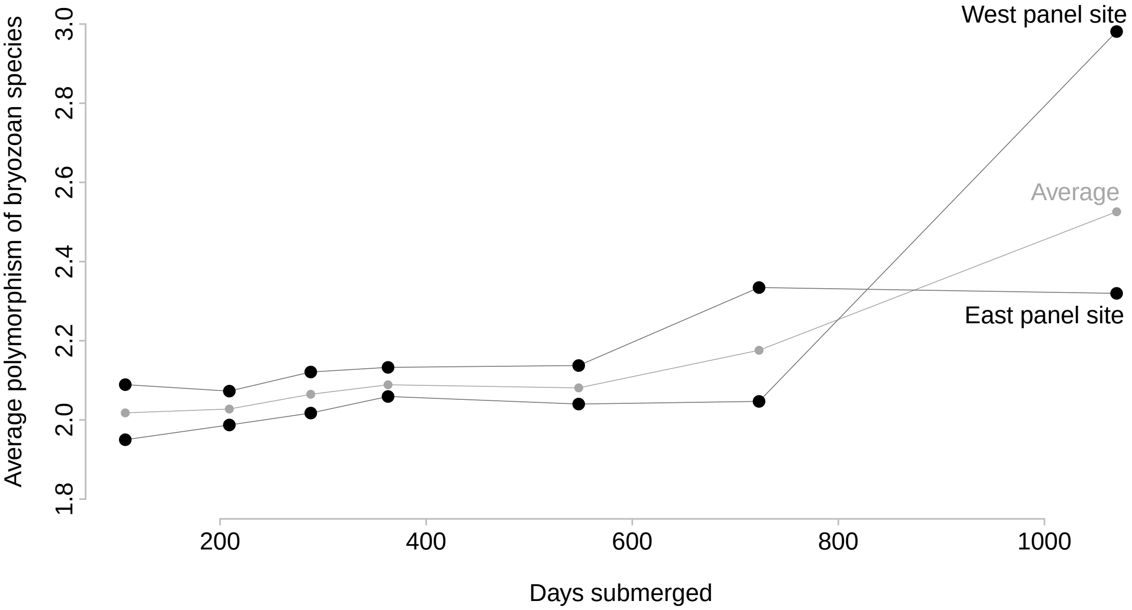

Figure 9: Change in polymorphism over ecological time do to the interaction among 10 species on 15 x 15 cm panels. From Simpson et al. (2016).

McKinney and Jackson (1991) describe a number of important characteristics of encrusting bryozoans.

- Colony size: Large colonies can live longer and can successfully overgrow other colonies.
- Colony thickness: Thicker colonies also resistant to overgrowth and grazers and can regenerate quickly.

- Growth rate: Faster growing colonies take up space easier and leads to overgrowth success.
- Growth flexibility: Some colonies can raise the growing edge, aiding in overgrowth and halting invaders.
- Zooidal morphology: Reef species are heavily calcified. More calcification means more resistance to predators and various forces.
- Specialized defenses: Stolonal outgrowth at the margin can increase competitive abilities.
- Feeding interference: The sizes of tentacle crowns influences currents. Species with larger tentacle crowns can disrupt the feeding of species with smaller tentacle crowns.
- Mutualism: Many species are encrusted by a hydra *Zanclea* which increases the bryozoan's success in overgrowth interactions and protects them from predatory flatworms.

Erect growth

Colonies with erect growth is more complicated. In the simplest mode of erect growth, the growing edge can lift off the substrate.

Commonly, erect colonies have zooids growing back-to-back, so that zooids open on both surfaces. McKinney and Jackson (1991) highlight four processes that go into the growth of branching erect colonies:

- Continuous branch elongation by budding of new zooids.
- Branch widening, which results from multiplication of zooid rows.
- Branch multiplication by division of the growing tip.
- branch thickening proximal to the growing tip, which does not extent the colony into space but contributes to colony strength.

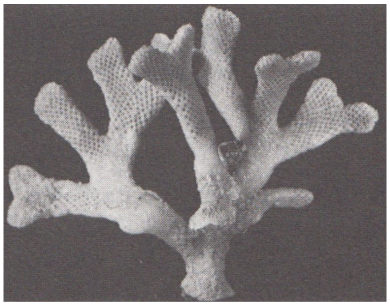

Figure 10: An erect arborescent colony of *Cystisella sachet*. From McKinney and Jackson (1991)

Cheetham (1971) and Jackson (1979) postulated three advantages for erect over encrusting growth (McKinney and Jackson 1991): (a) high tissue area and volume which increase feeding and reproductive capacity per unit area of substratum. (b) increased access to food in the water column. And (c) greater isolation from competitors, predators, and sediments on the substratum.

Free-living growth

Free-living colonies settle on minute substrata and grow in a couple of ways. Colonies can over grow fine sediments. They can concentrically over grow themselves so that the could potentially roll

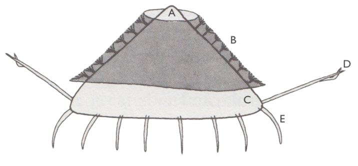

Figure 11: Side view of *Selenaria maculate* showing the donation of functions along the colony. (A) non-feeding zooids around the ancestral. (B) feeding autozooids. (C) brooding zooids. (D) Male zooids with long tentacle sheaths for sperm release. (E) Enlarged peripheral avicularia. From McKinney and Jackson (1991).

about. Most free-living bryozoans are cap-shaped (Figs. 11 and 12) with the convex frontal surface facing up Setae on the frontal surface can sweep it clean of sediment. Colonies can even dig themselves out if they are buried.

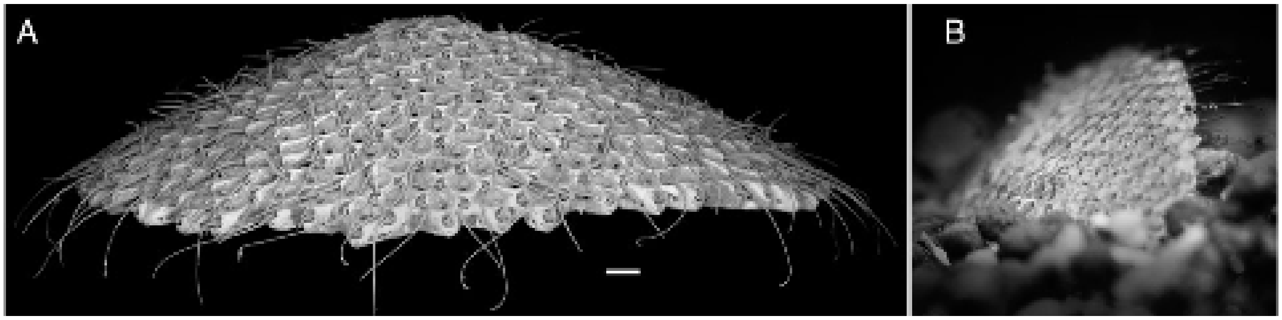

Figure 12: A free-living colony of *Cupuladria biporosa* in life-position (A). The whiskers around the colony are its vibracula. They use these to walk. (B) *C. exframinis* emerging from sediment. Image from O'Dea (2009).

They initially settle on sand grains and form a basal cuticle that is firmly attached to the basal skeleton but extends out it. When the colony outgrows its initial substrate, it starts to extend outward using its basal cuticle beyond the skeletal margin to add new zooids on the periphery. The patterns of growth in free-living bryozoans can vary (Fig. 13). These patterns are important because they can influence the patterns of asexual fragmentation in these bryozoans[4].

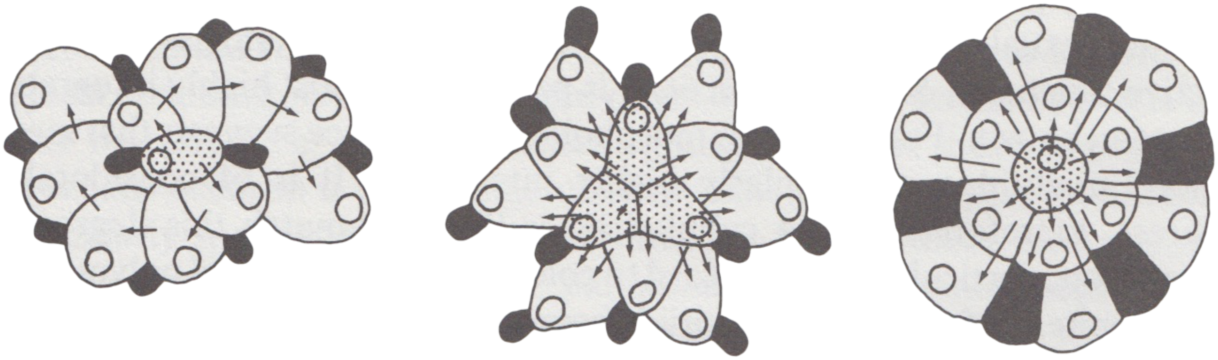

Figure 13: Growth and early astogeny of free-living lunulitiform bryozoans. From McKinney and Jackson (1991).

Rooted growth

Rooted colonies are common members of the interstitial meiofauna. These colonies are rigid and full of structural heterozooids and extra zooidal parts to extend the colony into the sediment and attach to sand grains. They tend to have few zooids and become sexually mature with only a few zooids.

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[4] O'Dea, A. (2009). Relation of form to life habit in free-living cupuladriid bryozoans. *Aquatic Biology* 7(1-2), 1–18

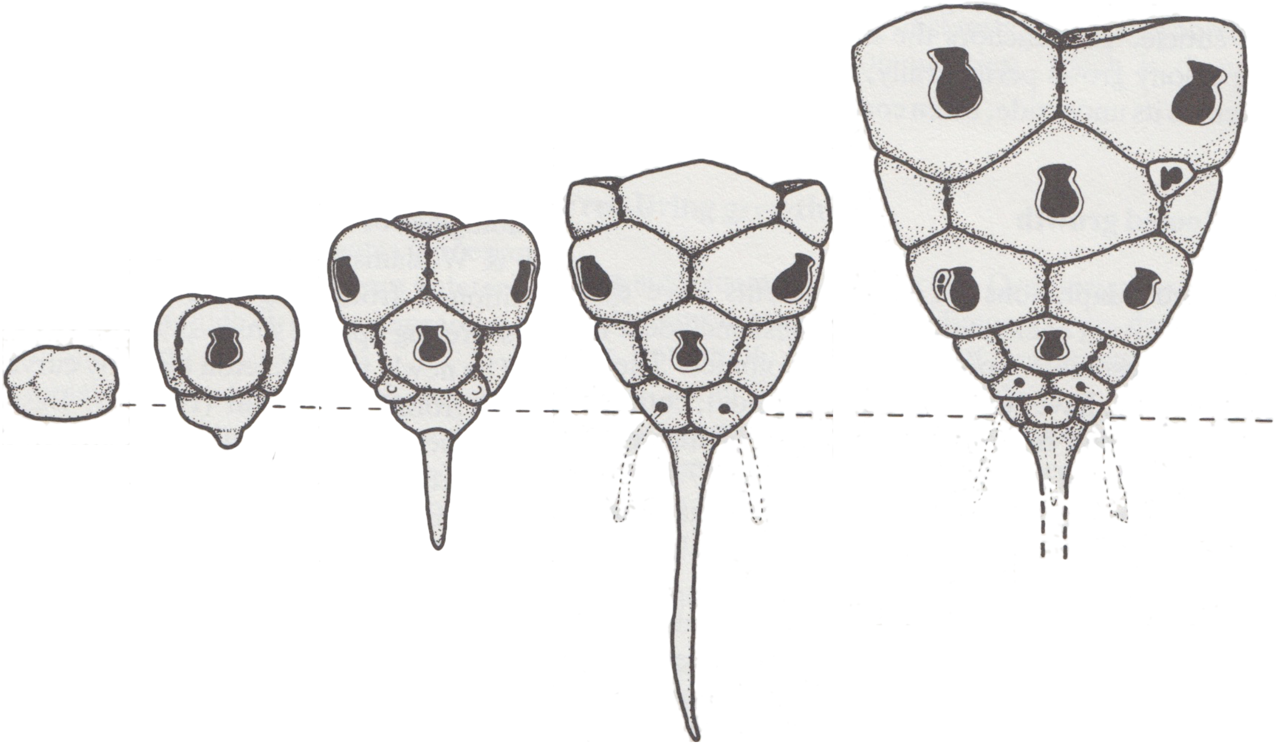

Figure 14: An autogenetic series of rooted conescharellinid cheilostome colonies growing from left to right. The dashed horizontal line represents the sand substrate. Rootlet bearing kenozooids are added proximally. From McKinney and Jackson (1991).

Life History

It gets complicated for clonal and colonial animals. All bryozoans are hermaphroditic. Some ascophorans are dioecious (like in Fig. 11). Some species produce a free-swimming larvae called a cyphonaute. But most bryozoans retain embryos within the colony, commonly in ovicells. These species produce large larvae that are competent to settle upon release. Cyclostomes brood embryos in large female gonozooids and are polyembryonic.

Life-cycles and life-histories are produced by mixing, asexual growth, fission, and fusion, with sex, partial mortality, and death (Fig. 15).

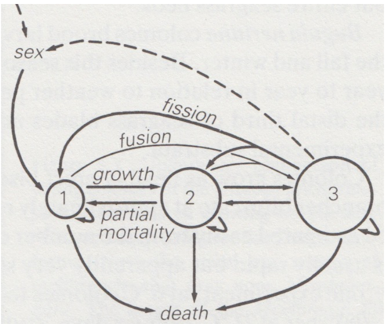

Figure 15: The generalized life cycle of a clonal and colonial animal. From Hughes and Jackson (1985).

Evolutionary trends

The fact that bryozoans posses a modular construction and such an extensive fossil record means that many features about their large-scale evolution are known. Here is the list of trends given by McKinney and Jackson (1991) in Table 10.1:

- Increased diversity and abundance of branched unilaminate erect species relative to other forms.

- Increases in branch thickening rates and bifurcation angles among rigidly erect colonies.
- Increased proportions of cheilostome species with zooidal and frontal budding.
- Increased integration of colonies.
- Improved fit of zooidal elongation, spacing, and polymorphism to predictions of growth form models.
- Shift of rigidly erect species into deeper water.
- Decreased proportion of erect species from Jurassic to Recent in shallow water.
- Increases calcification of zooids with rise of fenestrates; sequential change in relative abundance of anascans, cribrimorphs, and ascopohorans.

Importance for evolutionary biology

Punctuated equilibrium[5] is the macroevolutionary pattern of morphological stasis within species and concentrated bursts of change occurring during speciation. It was proposed as an alternative to the thought experiment of a uniformitarian microevolution that scales up what we see today over the many millions of years observed in the fossil record. When the idea came on the scene in the 1970s it caused massive arguments. When Alan Cheetham decided to test punctuated equilibrium with bryozoans, he was convinced he would be able to reject it. Instead he proved it (Fig. 16).

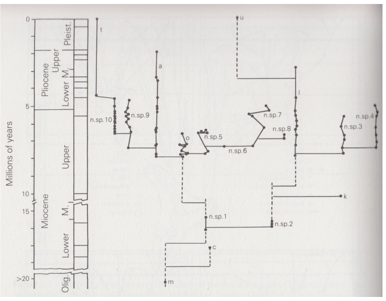

Figure 16: Punctuated equilibrium in *Metrarabdotos*. From Cheetham (1986b).

So much evolutionary biology can be done with bryozoans. How do their polymorphs evolve? How does their life-history influence speciation? Almost any deep question in evolutionary biology can be tested with bryozoans.

References

Boardman, R. and A. H. Cheetham (1973). Degrees of colony dominance in stenolaemate and gymnolaemate bryozoa. In R. S. Boardman, A. H. Cheetham, and W. A. Oliver (Eds.), *Animal colonies: development and function through time*, pp. 121–220. Van Nostrand Reinhold.

Boardman, R. S. and A. H. Cheetham (1969). Skeletal growth, intracolony variation, and evolution in bryozoa; a review. *Journal of Paleontology 43*(2), 205–233.

[5] Eldredge, N. and S. J. Gould (1972). Punctuated equilibria: an alternative to phyletic gradualism. In T. J. M. Schopf (Ed.), *Models in paleobiology*. Freeman, Cooper and Co

Boardman, R. S., A. H. Cheetham, and W. A. Oliver (1973). *Animal colonies: development and function through time*. Van Nostrand Reinhold.

Boardman, R. S., A. H. Cheetham, and A. J. Rowell (1987). *Fossil Invertebrates*. Blackwell Scientific.

Carter, M., D. Gordon, and J. A. Gardner (2010). Polymorphism and vestigiality: comparative anatomy and morphology of bryozoan avicularia. *Zoomorphology 129*(3), 195–211.

Cheetham, A. H. (1971). Functional morphology and biofacies distribution of cheilostome bryozoa in the daniar stage, paleocene, of southern scandinavia. *Smithsonian Contributions to Paleobiology 6*, 1–121.

Cheetham, A. H. (1986a). Branching, biomechanics and bryozoan evolution. *Proceedings of the Royal society of London. Series B. Biological sciences 228*(1251), 151–171.

Cheetham, A. H. (1986b). Tempo of evolution in a neogene bryozoan: rates of morphologic change within and across species boundaries. *Paleobiology 12*(2), 190–202.

Cheetham, A. H. and P. L. Cook (1983). General features of the class gymnolaemata. *Treatise on Invertebrate Paleontology Part G: Bryozoa*, 138–207.

Cheetham, A. H., J. B. C. Jackson, and J. Sanner (2001). Evolutionary significance of sexual and asexual modes of propagation in neogene species of the bryozoan metrarabdotos in tropical america. *Journal of Paleontology 75*(3), 564–577.

Cheetham, A. H. and E. Thomsen (1981). Functional morphology of arborescent animals: strength and design of cheilostome bryozoan skeletons. *Paleobiology 7*(3), 355–383.

Eldredge, N. and S. J. Gould (1972). Punctuated equilibria: an alternative to phyletic gradualism. In T. J. M. Schopf (Ed.), *Models in paleobiology*. Freeman, Cooper and Co.

Haeckel, E. (1899). *Kunstformen der Natur*. Verlag des Bibliographischen Instituts.

Harvell, C. D. (1998). Genetic variation and polymorphism in the inducible spines of a marine bryozoan. *Evolution 52*(1), 80–86.

Herrera, A., J. B. C. Jackson, D. P. Gordon, A. M. Smith, and J. A. Grant-Mackie (1996). Life history variation among “dominant” encrusting cheilostomate bryozoa. In H. Moyano, D. P. Gordon, A. M. Smith, and J. A. Grant-Mackie (Eds.), *Bryozoans in space and time*, pp. 117–123. National Institute of Water and Atmospheric Research Ltd Wellington.

Hughes, D. J. and J. B. C. Jackson (1990). Do constant environments promote complexity of form?: The distribution of bryozoan polymorphism as a test of hypotheses. *Evolution 44*(4), 889–905.

Hughes, T. and J. Jackson (1985). Population dynamics and life histories of foliaceous corals. *Ecological Monographs 55*(2), 142–166.

Jackson, J. (1979). Morphological strategies of sessile animals. In G. P. Larwood and B. R. Rosen (Eds.), *Biology and systematics of colonial organisms*, pp. 499–555. Academic Press, London.

Jackson, J. B. C. and A. H. Cheetham (1990). Evolutionary significance of morphospecies: a test with cheilostome bryozoa. *Science 248*(4955), 579–583.

Jackson, J. B. C. and A. H. Cheetham (1994). Phylogeny reconstruction and the tempo of speciation in cheilostome bryozoa. *Paleobiology 20*(4), 407–423.

Jackson, J. B. C. and A. H. Cheetham (1999). Tempo and mode of speciation in the sea. *Trends in Ecology & Evolution 14*(2), 72–77.

Jackson, J. B. C. and S. P. Wertheimer (1985). Patterns of reproduction in five common species of jamaican reef-associated bryozoans. In C. Nielsen and G. P. Larwood (Eds.), *Bryozoa: Ordovician to Recent*, pp. 161–168. Olsen and Olsen.

Jackson, J. B. C. and J. E. Winston (1981). Modular growth and longevity in bryozoans. In G. P. Larwood and C. Nielsen (Eds.), *Recent and Fossil Bryozoa*, pp. 121–126. Olsen and Olsen.

McKinney, F. K. (1984). Feeding currents of gymnolaemate bryozoans: better organization with higher colonial integration. *Bulletin of marine science 34*(2), 315–319.

McKinney, F. K. and J. B. Jackson (1991). *Bryozoan evolution*. University of Chicago Press.

McShea, D. W. and E. P. Venit (2002). Testing for bias in the evolution of coloniality: a demonstration in cyclostome bryozoans. *Paleobiology 28*(3), 308–327.

Mukai, H., M. Fukushima, and Y. Jinbo (1987). Characterization of the form and growth pattern of colonies in several freshwater bryozoans. *Journal of Morphology 192*(2), 161–179.

O'Dea, A. (2009). Relation of form to life habit in free-living cupuladriid bryozoans. *Aquatic Biology 7*(1-2), 1–18.

O'Dea, A., A. Herrera-Cubilla, H. Fortunato, and J. B. C. Jackson (2004). Life history variation in cupuladriid bryozoans from either side of the isthmus of panama. *Mar Ecol Prog Ser 280*, 145–161.

O'Dea, A. and J. B. C. Jackson (2002). Bryozoan growth mirrors contrasting seasonal regimes across the isthmus of panama. *Palaeogeography, Palaeoclimatology, Palaeoecology 185*(1–2), 77–94.

Okamura, B. and T. Hatton-Ellis (1995). Population biology of bryozoans: correlates of sessile, colonial life histories in freshwater habitats. *Cellular and Molecular Life Sciences 51*(5), 510–525.

Ostrovsky, A. N. (2013). *Evolution of Sexual Reproduction in Marine Invertebrates: Example of Gymnolaemate Bryozoans*. Springer.

Ryland, J. S. (1970). *Bryozoans*. Hutchinson.

Silén, L. (1977). Polymorphism. In R. M. Woollacott and R. L. Zimmer (Eds.), *Biology of Bryozoans*, pp. 184–232. New York: Academic Press.

Simpson, C. (2012). The evolutionary history of division of labour. *Proceedings of the Royal Society B: Biological Sciences 279*(1726), 116–121.

Simpson, C., A. Herrera-Cubilla, and J. B. C. Jackson (2016). Evolutionary determinants of morphological polymorphism in colonial animals. *bioRxiv*.

Winston, J. E. (1983). Patterns of growth, reproduction and mortality in bryozoans from the ross sea, antarctica. *Bulletin of marine Science 33*(3), 688–702.

Winston, J. E. (1984). Why bryozoans have avicularia: a review of the evidence. *American Museum Novitates 2789*, 1–26.

Winston, J. E. (2010). Life in the colonies: learning the alien ways of colonial organisms. *Integrative and comparative biology 50*(6), 919–933.