

Bryozoans in Archaeology

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Summary

Bryozoans (Phylum Bryozoa) are colony-forming invertebrates found in marine and freshwater contexts. Many are calcified, while some others have chitinous buds, and so have archaeological potential, yet they are seldom investigated, perhaps due to considerable difficulties with identification. This article presents an overview of bryozoans, as well as summarising archaeological contexts in which bryozoans might be expected to occur, and highlighting some previous work. It also presents methods and directions to maximise the potential of bryozoans in archaeological investigations.

Features

- Keywords: Bryozoa, environmental archaeology, palaeoecology, biological remains, marine shells, freshwater sediments, marine sediments

1. Introduction

Bryozoans (Phylum Bryozoa), also known as sea mats or moss animals and formerly as Polyzoa or Entoprocta, are colony-forming sessile invertebrates, comprising communities of separate individuals known as zooids. There are around 6000 living species known in the world (Benton and Harper [2009](#), 314). Most are marine, although brackish and freshwater species exist. Generally, they occur on hard substrates such as rocks, shells and the fronds of seaweeds, although there are forms that live on mud and sand. Many are calcified, and others have chitinous buds, and have the potential to be preserved in archaeological contexts, yet they are seldom investigated, perhaps due to considerable difficulties with identification. Considerably more work has been done on geological assemblages and more still on living colonies; however, in general the group is not well known (Francis [2001](#), 106). This article presents a condensed overview of the phylum, as well as a review of archaeological work to date. It also presents directions to maximise the interpretative potential of this under-exploited resource in palaeoecological research.

2. Bryozoan Biology, Taxonomy and Identification

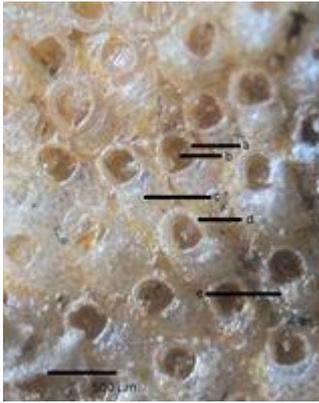


Figure 1: Modern specimen of *Cryptosula pallasiana* (Moll 1803) showing (a) orifice, (b) operculum, (c) calcified frontal wall, (d) peristome and (e) avicularium

Bryozoans form colonies by budding, each colony originating with a primary individual known as an *ancestrula* (Ryland [1995](#), 629). Each unit of the colony is called a *zooid*, and each zooid comprises an outer protective case, the *zoecium*, and the internal living content, the *polypide* (Ryland [1962](#), 34). The colony is more than just a collection of individuals as it has individuality of its own. Two colonies of the same species will not fuse when they meet, whereas two branches of the same colony will (Ryland [1962](#), 34). Bryozoan colony size can vary from a few millimetres to huge masses weighing several kilograms (Francis [2001](#), 105).

Embryos develop within special brood-chambers called *ovicells*. The buds of freshwater bryozoans of the class Phylactolaemata detach from the colony and are encased in a capsule comprising two chitinous valves that may preserve very well and are often identifiable to species level, known as a *statoblast* (Francis [2001](#), 105). Statoblasts have a dorsal valve and ventral valve, and most have another chitinous layer, known as a *periblast*, which overlies the capsule and may form a gas-filled *annulus* that allows flotation (Mundy [1980](#), 9). Statoblasts that float are known as *floatoblasts*, and those that do not are *sessoblasts*. The Plumatellidae produce both floatoblasts and sessoblasts, while the Fredericellidae have only sessoblasts and the Lophopodidae and Cristatellidae have only floatoblasts (Mundy [1980](#), 9-10).

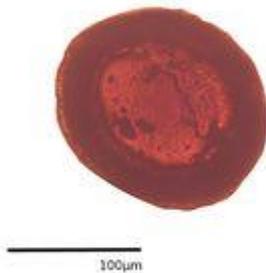


Figure 2: Bryozoan statoblast (floatoblast of *Plumatella emarginata* (Allman 1844), dorsal valve) from Walpole, Somerset, photographed in transmitted light

Bryozoans are suspension feeders that use a specialised feeding and respiratory organ called a *lophophore*, much like Brachiopoda and Phoronida. The lophophore is a U-shaped structure covered by ciliated tentacles that can be withdrawn into the zoecium or extended for feeding (Francis [2001](#), 105). When extended, the tentacles form a funnel with the mouth at its vertex (Ryland [1970](#), 43).

The oldest fossil bryozoans date from the Ordovician, although it is probable that soft-bodied, primitive bryozoans existed during the Cambrian (Benton and Harper [2009](#), 316). Bryozoans are the dominant contributors to temperate water marine carbonate deposits (Clarke [2009](#), 138), forming part of what has been termed 'bryomol' carbonate facies, alongside the shells of molluscs (Nelson [1988](#), table 1).

There are two classes of bryozoan in British marine waters: the Stenolaemata, which have long slender zooids with strongly calcified walls and contains one order, the Cyclostomatida; and Gymnolaemata, with cylindrical or squat zooids. There are two orders of Gymnolaemata, the Cheilostomatida and the uncalcified Ctenostomatida (Gibson *et al.* [2001](#), 321). The freshwater Phylactolaemata are also present in Britain.

Bryozoans are chiefly identified using skeletal characteristics such as spines and other surface structures as well as the form of the pores and the shape and size of the colonies (Smith [1995](#), 231). Archaeological specimens may be damaged, making identification to species level difficult. A complex nomenclature has arisen to describe bryozoans (see Ryland [1995](#), 629). Normal feeding zooids are known as *autozooids*, while specialised forms are called *heterozooids*. Commonly, bryozoans are squat and form an encrusting layer. Such bryozoans have a *basal* surface, applied to the substratum, as well as a *frontal* surface. This distinction also exists in free-standing colonies. The end of the zooid nearest to the origin of the colony is *proximal*, the farthest end being *distal*. The opening through which the polypide emerges is the *orifice*. This is situated near the distal end of the *frontal membrane*, and may be closed by an *operculum*. In some species, this is surrounded by a low ridge or tubular collar called the *peristome*. *Avicularia* are heterozooids found in some bryozoans that do not feed and are usually attached to an autozooid.

A simplified terminology is sometimes used in geology that allows non-specialists to describe growth form (Smith [1995](#), 231; Hageman *et al.* [1997](#), fig. 1). This is based on the mode of attachment to the substrate (cemented, rooted, unattached); colony construction; and colonial geometry (Hageman *et al.* [1997](#), 406). The form of zooids may reflect environment, as both zooid size and colony size decrease with depth (Smith [1995](#), 233), while encrusting forms of colonies tend to dominate over erect ones in shallow water, perhaps owing to increased physical and biological disturbance (Smith [1995](#), 234). Reconstructing past environmental conditions from bryozoan colony forms is not straightforward, however. The same form may occur in different environments; taphonomy may distort the preservation of

different colony forms; and it is possible that environmental distributions of different colony forms have changed through time (Taylor [2005](#), 3).

Bryozoan abundance and species diversity are generally lower under stressful environmental conditions, with distributions most greatly affected by water temperature and phytoplankton availability (Smith [1995](#), 232). Stressful environments may produce greater variability in zooid form within a colony (Smith 1995, 234). Low species diversity is usual in estuaries (Smith [1995](#), 232), although some species are brackish water specialists.

Zooid form may also reflect changes in environmental conditions. In a 15-month survey of modern colonies of *Conopeum seurati* (Canu 1928) at Avonmouth Dock near Bristol, UK, O'Dea and Okamura ([1999](#)) found that zooid length, width and area were strongly related to temperature, with larger zooids being produced during winter months. Water salinity also affected zooid length and area, but not width. Bryozoan zooid size may be used to reconstruct past temperature regimes, though O'Dea and Okamura ([1999](#), 586) note that because zooid size can also be influenced by genotypic factors, it is important that such studies are based on well-studied species and large datasets. Key advantages of performing such studies with bryozoans include the iteration of zooids and the fact that bryozoans are sessile and so reflect a single locality (O'Dea and Okamura [2000a](#)). O'Dea and Okamura ([2000a](#), 326) present an algebraic formula for assessing past mean annual range of temperature experienced by cheilostome bryozoan colonies based on the mean intra-colony coefficient of variation of zooid frontal area.

Certain taxa show morphological responses to specific environmental conditions. Zooids of *Electra pilosa* (Linnaeus 1767), for example, have been shown to grow an extended chitinous spine in high-energy environments (Bayer *et al.* [1997](#)), although this is likely to be poorly preserved in archaeological specimens.

Colonies of *Flustra foliacea* (Linnaeus 1758) grow between March and September, and develop clearly defined growth check lines (GCLs) as a result of winter growth cessation. These have been used by O'Dea and Okamura ([2000b](#)) to investigate seasonal patterns of colony growth. They suggest that the GCLs can be used in association with measurement of zooid size (which is determined by temperature) for retrospective morphometric analyses to infer past environmental changes (O'Dea and Okamura [2000b](#), 1128).

Unlike other marine invertebrates, perhaps most notably Mollusca, no non-native species of bryozoan have been confirmed as present in British waters, although this is likely to result from an absence of evidence, as several species occur only in harbours and may be historical introductions. *Bugula stolonifera* (Ryland 1960) in particular is identified as likely to be a recent arrival (Eno *et al.* [1997](#), 8). Certain subspecies of *Bowerbankia gracilis* (Leidy 1855) might also be recent arrivals (Eno *et al.* [1997](#), 12). The non-

native *Bugula neritina* (Linnaeus 1758) has been recorded in Britain, but was listed by Eno *et al.* ([1997](#), table 2) as no longer established in the wild.

3. Bryozoa and Marine Molluscs



Figure 3: Colony of *Conopeum seurati* (Canu 1928) encrusting an *Ecrobia ventrosa* (Montagu 1803) shell

Bryozoa often occur as epibiont organisms on the shells of marine molluscs, and are often recorded in assemblages derived from food waste. In these cases, the ecological tolerances and geographical range of the bryozoa might give some additional information about the origin of the shells. Published records of bryozoa on marine shells include Buckquoy, Orkney (Evans and Spencer [1977](#), 217); Ardnave, Islay (Evans [1983](#), 356); Chanctonbury Ring, Sussex (Somerville [2001](#), 109); Shapwick, Somerset (Light [2007](#), 928); Whitefriars Street, Norwich (Ayers and Murphy [1983](#), 36); and Gilbert School, Colchester (Murphy [1992](#)). In most of these cases the bryozoa were not identified beyond phylum level, however. The mere presence of bryozoa may give useful information: in a survey of modern shells from Poole in Dorset, Winder ([1997](#), 198) found that encrusting colonies of bryozoa were more frequent on oysters dredged from the harbour than those from the bay. Winder does not offer an explanation for this; however, it may be that there was a wider availability of suitable surfaces for the colonies to encrust in the harbour than on the soft substrate of the bay.

The colonies may reveal information about a shell's likely condition at the time of collection, as the presence of bryozoa on the inside of a bivalve shell shows that it could not have been collected as an intact animal and so is unlikely to be food waste (Thomas [1978](#), 155; Thomas [1981](#), 50; Murphy [1992](#)). This was also the case with the 82,000 year-old perforated *Nassarius gibbosulus* (Linnaeus 1758) (a gastropod) shells from Grotte des Pigeons, Taforalt, Morocco (Bouzouggar *et al.* [2007](#), 9967). Claassen ([1998](#), 149) has suggested that bryozoans on shells may be indicators of seasonality, stating that large quantities of *Conopeum* sp. on bivalve shells are a winter phenomenon. This seems too general a statement, however, as once a bryozoan colony forms on a shell, it is a permanent fixture.

Bryozoans that are often found on shells from European waters are *Bugula flabellata* (Thompson, in Gray 1848), *Bugula plumosa* (Pallas 1766), *Celleporina hassalli* (Johnston 1847), *Conopeum reticulum* Gray 1848, *Conopeum seurati*, Crisiidae, *Electra* spp., *Flustrellidra hispida* (Fabricius 1780), *Membranipora membranacea* (Linnaeus 1767), and *Walkeria* (= *Valkeria*) *uva* (Linnaeus 1758) (Ryland 1962, table 1). Bryozoan colonies may affect the settlement, growth and mortality of shellfish such as oysters (Valero 2006, 4). In addition to encrusting forms, a number of bryozoans leave borings in shells (Boekschoten 1966, 359-67). In the lower Pleistocene crag at Levington (Suffolk), shells of *Neptunia contraria* (Röding 1798), *Glycymeris glycymeris* (Linnaeus 1758) and *Astarte* spp. showed the characteristic borings of *Immergentia* (= *Terebripora*) *orbignyana* (Fischer 1866) (Boekschoten 1966, 360). These are more-or-less cylindrical holes in the shell up to 0.1mm in diameter (called shell pores by Boekschoten) with a slit-like caudal extension, through which the zooid makes contact with the environment. These are connected by stolons within the shell 0.45–0.9mm apart (Boekschoten 1966, 359). As with encrusting forms, the ecological tolerances of boring bryozoans may reveal clues about the source of the shell, and its condition at time of collection.

4. Bryozoa within Sediments

Bryozoa may also be found within archaeological sediment samples. They may be imported to a site attached to seaweed, which has been used widely in the past as fodder, fertiliser and soil stabiliser (Bell 1981). This was the case at Ardnave on Islay where unidentified bryozoans were found among calcareous debris in a sample (Evans 1983, 357) and at Bishopstone in Sussex, where four examples of *Turbicellepora avicularis* (Hincks 1860) were recovered: two from an Iron Age enclosure ditch, one from the bottom of a pit and one unstratified (Bell 1977, 287). Bell (1981, 121) studied modern seaweed from Saltdean, Sussex, and found colonies of *Membranipora membranacea* on the stipes of *Laminaria* sp. Unidentified marine bryozoans were also found during micromorphological analysis of sediments from the Epipalaeolithic to Neolithic site of Ifri Oudadane, Morocco, where they were interpreted as having been introduced by humans (Linstädter and Kehl 2012, 3319).

Where previously intertidal or brackish water deposits are being excavated, *in situ* colonies may be preserved on the surface of rocks, as at Walpole in Somerset. Ongoing archaeological investigations at the Walpole landfill site have revealed a now-buried lias outcrop that would have been an island until late prehistory (Hollinrake and Hollinrake 2002). Samples from this site are the subject of ongoing study by the present author. Recently, a combination of colonies of *Conopeum seurati* and the molluscs *Ecrobia ventrosa* (Montagu 1803) and *Macoma balthica* (Linnaeus 1758) has been found in samples from the south-western edge of this island, suggesting a deposit bearing lithic implements of Mesolithic to Bronze Age date was a

lagoon margin. Statoblasts of *Plumatella emarginata* (Allman 1844) are present in a peat deposit from the same site, suggesting freshwater inputs at the time of peat formation.

Smith and Howard (2004, 118) examined the usefulness of Coleoptera to distinguish low-energy and high-energy fluvial depositional environments. To enhance their method, they suggest studies in parallel with other biological remains, including bryozoa. This does not appear to have been done, although statoblasts are reasonably frequent finds from freshwater sediments. Statoblasts of the freshwater bryozoan *Cristatella mucedo* (Cuvier 1798) have been reported from North Bridge, Doncaster, where they were interpreted as being derived from flood deposits (Carrott *et al.* 1997, 68). Statoblasts of *Cristatella mucedo* and *Plumatella* spp. were also reported from medieval estuarine sediments associated with the River Fleet at 3 Tudor Street, London (Boyd 1981, table 22.1), and statoblasts of *Cristatella mucedo* were recorded from sediments dating to the Hoxnian interglacial (marine isotope stage 11) at Nechells, Birmingham (Shotton and Osborne 1965). The majority of the statoblasts were incomplete, and were identified as dorsal or ventral discs based on comparison of measurements to modern data (Shotton and Osborne 1965, 366). *Plumatella* spp. statoblasts were also recorded in pollen samples from Caldicot, Gwent (Caseldine and Barrow 1997, table 6), and *Lophopus crystallanus* (Pallas 1768) statoblasts in samples from Enkhuizen, The Netherlands (van Geel *et al.* 1983). At Flixton School House Farm, near Flixton in Yorkshire, a decline in the number of *Cristatella* statoblasts before c. 8600 cal BC was attributed to a transition in the depositional environment from permanently to periodically submerged (Taylor 2011, 72). Kenward (2009, 73) lists several examples from north-east England where statoblasts have been recovered in archaeological samples from terrestrial sequences and so are likely to have been introduced by human agency or by flooding.

5. Bryozoa, Ships and Structures

The encrustations may also have considerable economic impact as a fouling organism on the hulls of ships and within sewage outlets and seawater intake pipes. Ryland (1970, 12) reports that at the start of the 20th century some 700 tons of bryozoa were removed from the sewers in Manchester. Wood-boring bryozoans are also known, such as *Bulbella abscondita* Braem 1951, whose borings may be preserved in ship timber or submerged wooden structures (Boekschoten 1966, 359).

6. Isotopic Analysis

It has been shown that most bryozoans precipitate carbonate in isotopic equilibrium with sea water (Smith *et al.* 2004, 809), although bryozoans with internal symbiotic hydroids may not (Smith *et al.* 2004, 813). Bryozoan mineralogy is a complex mix of calcite and aragonite, each of which has

naturally different ratios of oxygen and carbon isotopes, meaning that simple isotopic corrections are difficult (Smith *et al.* [2004](#), 819). Smith *et al.* ([2004](#), 819) found, however, that in modern New Zealand bryozoans, there is a strong trend towards higher isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) in deeper water and at higher latitudes, both related to temperature. Smith *et al.* ([2004](#), 819) further found within a single branch of a colony of *Cinctipora elegans* Hutton 1873, that endozone and exozone carbonate can have different carbon stable isotope ratios, perhaps due to different rates of calcification.

In a three-year study of colonies of *Cellaria sinuosa* (Hassall 1840) off the coast of Roscoff, France, Bader and Schäfer ([2005](#)) found that $\delta^{18}\text{O}$ is incorporated into the skeleton at close to isotopic equilibrium with sea water and documents seasonal changes in temperature, although $\delta^{13}\text{C}$ is characterised by lower relative values than the predicted equilibrium and does not show a seasonal cycle.

7. Recommended Methods

Calcified bryozoan colonies may be preserved in similar situations to molluscs, ostracods and calcareous foraminifera. Chitinous statoblasts may be preserved in similar situations to insects. The most likely scenario in which bryozoans may be encountered archaeologically is as epibiont organisms on marine shells. Encrustations may also occur on artefacts that have been submerged, for example at Walpole in Somerset, where bryozoans were recorded on pieces of fired clay (Figure 4). Shells and artefacts bearing bryozoan encrustations should not be subjected to normal finds washing procedure as this is likely to cause damage to, or even completely deface, diagnostic features. Should any cleaning be required, gentle brushing with a fine sable paintbrush and a pipette of deionised water should be used.



Figure 4: Colony of *Conopeum seurati* (Canu 1928) on archaeological fired clay, Walpole, Somerset, UK

Loose strands of zooids may also be recovered within sediment samples. This was the case at Weston College, Weston-super-Mare, where strands of *Flustra foliacea* (Linnaeus 1758) were washed into a tidal creek or ditch and recovered by the author in samples for molluscan analysis (Figure 5). Techniques for the extraction of bryozoans are essentially the same as for non-marine Mollusca (Evans [1972](#); Davies [2008](#)). A standard weight of air-dried sediment should be selected (1.5kg was used at Weston College and at

Walpole where samples were also processed for Mollusca; much less will suffice for recovery of statoblasts from freshwater deposits). Some sediments may require disaggregation in dilute sodium pyrophosphate. Residues should be washed through a 250 µm mesh sieve and oven dried. Statoblasts of the freshwater Phylactolaemata may be found in freshwater-lain sediments. Use of a 125 µm mesh sieve is recommended where their recovery is sought. Extraction should take place using a fine sable paintbrush or fine forceps under a low-power stereo microscope. Identification of bryozoan colonies relies on the characteristics of the frontal surface, so the basal surface may be mounted with a water-soluble glue or gum tragacanth on black card. Statoblasts should be mounted onto glass slides.



Figure 5: Strands of *Flustra foliacea* (Linnaeus 1758) recovered from samples of a tidal creek or ditch, Weston-super-Mare, UK

Identification should be carried out using a low-powered microscope at 50x magnification with reference to modern specimens (Figures 6 and 7). Francis ([2001](#), 109) notes that some statoblasts of *Plumatella* spp. can only be differentiated using scanning electron microscopy. Zooid and statoblast size may be measured using a micrometer eyepiece (O'Dea and Okamura [2000a](#), 323).

The best general text on bryozoans is still that of Ryland ([1970](#)). A key to British and European freshwater taxa, including statoblasts, has been published by Mundy ([1980](#)), and a thorough review of methods by Francis ([2001](#)). Statoblasts of *Cristatella* spp. decay in a distinctive fashion, and Hall *et al.* ([2003](#), fig. 3) present a decay sequence allowing identification of even poorly preserved specimens. A good starting point for marine taxa is Ryland ([1995](#)), although a number of more detailed texts exist in the Synopses of the British Fauna series (Ryland and Hayward [1977](#); Hayward and Ryland [1979](#); Hayward [1985](#); Hayward and Ryland [1985](#); [1996](#); [1999](#)), as well as two keys in the journal *Field Studies* (Ryland [1962](#); Ryland [1974](#)).

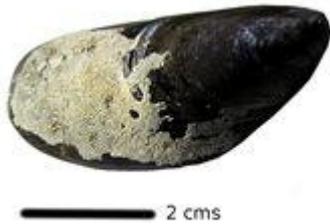


Figure 6: Colony of *Conopeum reticulatum* (Linnaeus 1767) on a modern mussel (*Mytilus edulis* Linnaeus 1758) shell.



Figure 7: Colonies of *Escharella variolosa* (Johnston 1838) on a modern common whelk (*Buccinum undatum* (Linnaeus 1758)) shell.

8. Problems in Bryozoan Analysis

Smith ([1995](#), 238) identified a lack of data about the ecological requirements of modern bryozoans as a potential problem in palaeoenvironmental analysis. As most bryozoans are sessile, microenvironments are essential, meaning that modern surveys must have thorough enough sampling strategies to recognise changes in microenvironment (Smith [1995](#), 238). Taphonomy also presents problems, as key identification features may be destroyed. In archaeological situations, encrusting bryozoa may not survive the finds washing or sample sieving process if due care is not exercised. The turbulent nature of marine processes may mean that bryozoan colonies have been transported and are not autochthonous, although bryozoans that are in life position offer potential for palaeoenvironmental reconstruction (Smith [1995](#), 239). Floatoblasts are, by their nature, unlikely to be found in life position.

Quantification of bryozoa presents a challenge. While two small discrete colonies on an oyster valve may legitimately be recorded as two colonies, clusters of (say) *Membranipora membranacea* found within the residue of a bulk sediment sample may, in life, have been part of a much larger colony. In these cases it is perhaps preferable to simply record presence.

9. Conclusions

Although bryozoa are reasonably common in archaeological sites, especially as epibiont organisms on marine shells, they are seldom identified to species

or even family level. This is unfortunate, as different species can have quite specific preferences with regard to water salinity and tidal level, as well as distinct geographic distributions. The presence or absence of bryozoans, and their colony form, may provide evidence of past habitats and the locations from which marine shells have been sourced, as well as the condition of the shell (occupied or empty) at the time of collection. The size of zooids may reflect palaeotemperature, they may exhibit morphology that allows reconstruction of seasonality, and zooids may be sampled for stable isotope analysis for palaeoclimatic studies. Colonies found in life position have the potential to reveal high-resolution palaeoenvironmental information. Unlike ostracods, foraminifera or molluscs, all of which may be recovered from similar contexts, bryozoans are generally sessile. As with many biological proxies, more study of living colonies and their responses to environmental factors is needed to maximise the palaeoecological utility of bryozoan analysis (bryozoarchaeology?).

Although calcified bryozoa may be well preserved in similar depositional environments to molluscs, ostracods or foraminifera, the colonies are fragile, and may easily be damaged during sample processing or cleaning of shells and other artefacts. This is likely to be a contributory factor to the under-recording of bryozoa in archaeological samples. Statoblasts similarly may be damaged or degraded. As Hall *et al.* (2003, 142) have previously suggested, online sharing of photographs of different grades of preservation may overcome some identification difficulties.

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