



BRYOZOANS AND PALAEOENVIRONMENTAL INTERPRETATION

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ABSTRACT

Bryozoans are locally abundant as fossils in many marine deposits from the Ordovician to the Holocene. The value of bryozoans in palaeoenvironmental interpretation has been widely acknowledged but their application has yet to be adequately developed, mainly because the environmental factors (both biological and physical) controlling the distributions of modern bryozoans are still poorly understood. Simplistic use of bryozoan colony-forms as palaeoenvironmental indicators, as often attempted, suffers from several problems. This essay focuses instead on the potential for using intraspecific variability in palaeoenvironmental studies. Bryozoan species are often plastic in their growth and form, with ecophenotypic variations potentially providing useful information on depositional depth, temperature and other environmental factors. Branch thickness in many erect species, especially bushy cyclostomes, decreases with increasing depth. Zooid size in cheilostomes decreases with increasing temperature. This relationship means that variance in zooid size within a colony can be used as a proxy for seasonality, being greater in more seasonal environments.

Key words: Bryozoans, environmental generalization, ecophenotypic variations, environmental interpretation

INTRODUCTION

This essay, written for the Golden Jubilee volume of the Palaeontological Society of India, reviews aspects of the application of bryozoans in palaeoenvironmental studies (see also Smith, 1995). After some generalizations on bryozoan distribution and a brief critique of the use of bryozoan colony-forms as palaeoenvironmental indicators, I consider how ecophenotypic variations within species can provide useful information about ancient environments. At the outset, it is worthwhile emphasizing that our knowledge of the environmental preferences and responses of bryozoans, living and fossil, is limited compared to many other groups that have been more intensively studied. Not only is there considerable scope for further study, but caution must always be exercised when inferring palaeoenvironments using bryozoans.

Bryozoa are a phylum of aquatic invertebrates which are entirely colonial, each colony comprising a series of interconnected, genetically identical individuals called zooids. Currently classified within the Lophotrochozoa, bryozoans are traditionally regarded as close relatives of brachiopods and phoronid worms with which they share a ciliated organ, the lophophore, for suspension feeding, and a benthic lifestyle. Over 6000 species of Recent bryozoans have been described, most inhabiting shallow water marine environments but some living in the deep sea, brackish- or fresh- waters.

The great majority of living bryozoans secrete calcareous skeletons (Taylor, 1999). In most species, these are built of calcite but some species employ aragonite or mixtures of calcite and aragonite. These calcareous skeletons have endowed bryozoans with an excellent yet imperfectly documented fossil record. In some sedimentary deposits, bryozoans are the dominant fossils, occasionally forming bryozoan limestones. However, the vertical and lateral distributions of bryozoans in sedimentary rock tend to be discontinuous, a pattern in accord

with their epibenthic ecology, dependence on patchily distributed hard or firm substrates for colonization, and generally short-lived larvae that settle very close to parent colonies (philopatry) giving limited dispersal.

No unequivocal bryozoans have been described from the Cambrian, but the phylum is well represented in all subsequent geological periods. Six orders have calcareous skeletons: Cyclostomata (Ordovician-Recent), Trepostomata (Ordovician-Triassic), Cystoporata (Ordovician-Triassic), Cryptostomata (Ordovician-Triassic), Fenestrata (Ordovician-Permian) and Cheilostomata (Jurassic-Recent) (see Taylor, 2005). The skeletal morphology of the zooids is crucial in distinguishing between these orders, colony-form generally having less taxonomic value. Indeed, a striking feature of the geological history of bryozoans has been the repeated evolution in different clades of similar colony-forms. For example, mesh-like colonies have evolved in species belonging to the Fenestrata, Cyclostomata and Cheilostomata, and jointed colonies in the Cryptostomata, Cyclostomata and Cheilostomata.

ENVIRONMENTAL GENERALIZATIONS

All modern bryozoans with fossilizable calcareous skeletons inhabit marine or, less often, brackish waters. Freshwater bryozoans at the present day belong to two groups (Class Phylactolaemata and Order Ctenostomata) that lack mineralized skeletons. The meagre fossil record of freshwater bryozoans (Kohring and Pint, 2005) consists entirely of the organic, seed-like structures (statoblasts) of phylactolaemates which have been recorded back to the Permian (Vinogradov, 1996). As there is currently no reason to suspect that ancient bryozoans with calcareous skeletons ever colonized freshwater environments, the finding of autochthonous fossil bryozoan colonies can safely be used to rule out deposition in a freshwater palaeoenvironment.

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Bryozoans that today inhabit brackish environments, including lagoons and estuaries, exist in low diversity communities largely consisting of unmineralized ctenostomes and cheilostomes with weakly calcified skeletons. The latter are often malacostegans that, unlike most cheilostomes, lack ovicells for larval brooding and have simple skeletal morphologies (Taylor, 1987). Higher diversity (> ca 10 species) communities of robustly calcified cheilostomes, together with occasional cyclostomes which are more strictly stenohaline, epitomise fully marine conditions at the present day and can safely be used to infer such conditions in the geological past. Likewise, the extinct stenolaemate relatives of cyclostomes (trepostomes, cystoporates, cryptostomes and fenestrates) appear to have been stenohaline. Although intertidal bryozoans (e.g. colonies encrusting seaweeds and the undersides of rocks) can be found at the present day, and very shallow water bryozoan communities have been inferred in the geological record (e.g. McKinney *et al.*, 2001), most bryozoan communities live subtidally on the continental shelf. Bryozoans in rock-forming abundance are likely to indicate shelf or ramp settings, occasionally extending onto the upper slope. Deep sea bryozoans do exist at the present day but mostly comprise cheilostomes with small colonies that are rooted into the sediment (Cook, 1981) and often have weakly calcified skeletons with a low fossilization potential. Bryozoan species diversity decreases markedly between 1000 and 2000 metres depth at the present day (Gordon, 1987). While careful analysis of bryozoan assemblages may provide useful information on depth (e.g. Pachut *et al.*, 1995; Kuklinski *et al.*, 2005), individual species often range very widely in depth, from the shallow subtidal to many hundreds of metres (Taylor, *et al.*, 2004). Fossil occurrences of such species furnish little useful information on palaeodepth.

Turbid, muddy environments are generally avoided by bryozoans. Although many of the best preserved fossil bryozoans come from argillaceous deposits (marls), bryozoans tend not to inhabit environments with continuous influxes of fine-grained sediment which expose the colony to the dangers of burial and hamper suspension feeding - high silt loadings have been shown experimentally to decrease feeding activity, possibly through particle impacts causing physical damage to the lophophores (Best and Thorpe, 1996).

Modern bryozoans can be found at all latitudes, from poles to equator. Individual species and some genera, however, do tend to have more restricted distributions, with some characteristic of cool waters and high latitudes, others of warm waters and low latitudes. Bryozoans are occasionally very diverse in tropical environments, including coral reefs, but are typically inconspicuous, low in biomass and generate far less biogenic sediment than do corals, algae and molluscs in these settings. Consequently, bryozoans are minor components of modern warm water, chlorozoan carbonates but are very

common in cool water, heterozoan carbonates (James, 1997). This pattern can be traced back into the Mesozoic based on the palaeolatitudinal distribution of post-Palaeozoic bryozoan-rich carbonates which are almost entirely extratropical (Taylor and Allison, 1998). In contrast, Palaeozoic bryozoan-rich deposits exhibit a panglobal distribution and include numerous examples of tropical bryozoan limestones. The present is not a reliable key to the past in this respect.

COLONY-FORM ANALYSIS: A BRIEF CRITIQUE

Stach's (1936) insightful paper suggesting the use of bryozoan colony-forms ('growth-forms') in palaeoenvironmental analysis spawned a large literature on this topic (see Appendix 1 of Hageman *et al.*, 1997), including examples from India (Guha and Mukhopadhyay, 1996; Guha and Gopikrishna, 2005). Stach defined nine different colony-forms in bryozoans, naming them after cheilostome genera, e.g. membraniporiform (*Membranipora*), cellariform (*Cellaria*) and reteporiform (*Retepora*). He went on to make inferences about the environmental preferences of these colony-forms, based on knowledge of where modern species lived and/or functional morphological deductions. A couple of applications were briefly described in the Cenozoic of Victoria. As recognized by Stach, one of the great appeals of colony-form analysis is that it demands no taxonomic expertise. On the other hand, the complex names coined by Stach, and later added to by Schopf (1969) and others, have proven discouraging to non-specialists and alternative, simpler schemes for categorizing bryozoan colony-forms have been proposed (Nelson *et al.*, 1988; Hageman *et al.*, 1998).

Application of colony-forms to infer palaeoenvironments is not as straightforward as portrayed by Stach (1936) and subsequent authors for various reasons. Firstly, some of Stach's (1936) ideas about the environmental significance of particular colony-forms were incorrect. For example, he regarded mesh-like, 'reteporiform' colonies as '... adapted for life in regions where wave action and currents are strong, these factors being overcome by the rigidity and fenestration of the colony.' (Stach 1936, p. 62). However, Cuffey and McKinney (1982) found the reteporiform cheilostome *Triphyllozoon cuspidatum* Harmer to live in quiet water cryptic habitats on Enewetak Atoll. Carboniferous genera belonging to the order Fenestrata that have reteporiform colony-forms evidently ranged widely in their hydrodynamic tolerances, from low to moderately high energy (McKinney and Gault 1980), and Kelly and Horowitz (1987) regarded them as the least sensitive among Carboniferous colony-forms to either current strength or sedimentation rate.

In many modern and ancient environments, a wide array of different colony-forms are found together. Particular colony-forms may not be precisely and/or uniquely optimised to

specific environments. Instead, they can represent alternative strategies for coping with the same environment. For example, high current velocity environments may be inhabited by heavily calcified colonies that resist stresses or by articulated colonies that take the force by bending at their joints. Furthermore, different colony-forms can be adaptations to the multiplicity of microhabitats (e.g. exposed and cryptic) that are present in one and the same environment.

The common co-occurrence of many different colony-forms demands quantitative analysis. Several methods of quantifying the relative proportions of colony-forms are possible, notably: (1) number of species having each colony-form, (2) number of colonies, (3) number of specimens (e.g. branch fragments), and (3) biomass (volume or weight). Hageman *et al.* (1997) suggested a standardized analytical method combining specimen abundance and species richness data. In fossil bryozoan assemblages, taphonomic factors may significantly distort the original proportions of different colony-forms (Smith and Nelson, 1996). For example, Cenozoic lunulitiform colonies (see below) are invariably aragonitic and will be preferentially lost in the fossil record relative to many other colony-forms. Transportation can also play an important role in high energy environments (Poluzzi *et al.*, 1997). Lagaaij and Gautier's (1965) classic and oft-cited study of the environmental distribution of bryozoan colony-forms off the Rhone delta utilized microfossil-sized bryozoan fragments (150-450 μm and 450-800 μm residues), the authors noting the rarity of live specimens. The extent to which the distributional patterns of these 'sedimentary particles' actually mirrors that of living bryozoan communities is unclear: transportation and time-averaging may both have played a role.

Another difficulty in using bryozoan colony-forms for palaeoenvironmental analysis is that particular forms may occur in more than one environment. An example is provided by the detailed study of Hageman *et al.* (2003) in southern Australia of modern and Cenozoic thicket-forming *Celleporaria* with large colonies that have hollow branches. Thickets form beneath swell wave-base, on muddy-silty substrates experiencing moderate rates of sedimentation and with medium-high mesotrophy. Such conditions pertain in two different settings in the study area: (1) in deep water (>200 m) where upwelling occurs, and (2) in shallow water (<50 m) embayments receiving terrestrial nutrient input.

Evolution has resulted in significant changes in the balance of colony-forms through geological time (see McKinney and Jackson, 1989). While such evolutionary changes may have occurred in concert with shifts in the environments inhabited by bryozoans, it is also possible that the environmental distributions of colony-forms have changed somewhat through time. A pattern of onshore origin of taxa followed by expansion or retreat offshore has been documented in various marine invertebrates (see Sepkoski, 1991) and needs

to be tested for bryozoan colony-forms.

Despite these problems, certain colony-forms do provide useful palaeoenvironmental information. The highly distinctive lunulitiform cheilostomes, with their small, low cone-shaped colonies, are free-living bryozoans that unlike most bryozoans are capable of directly colonizing soft sediments. Most live on fine sand to silt on the continental shelf and are able to tolerate higher rates of sedimentation than is usual for bryozoans (see review by Rosso, 1996). They have been interpreted as indicators of sedimentary instability by Di Geronimo *et al.* (1992).

Depth-related empirical patterns exist in the proportions of major colony morphotypes among modern bryozoans (Schopf, 1969; McKinney and Jackson, 1989). The ratio of encrusting to erect colonies decreases with increasing depth in the Atlantic, as does that of multiserial to uniserial colonies. The first of these relationships was used by Zagorsek (1996) to infer the depth of deposition of Eocene sediments in Europe. However, the extent to which this method can be carried backwards in geological time in the context of evolutionary changes needs to be established before the method is applied in the Mesozoic and Palaeozoic. This is especially so given that the patterns may be driven by biological interactions with predators, etc. which have changed significantly through time.

ECOPHENOTYPIC VARIATIONS WITHIN SPECIES

Given the problems associated with the use of bryozoan colony-forms in fossil assemblages as palaeoenvironmental indicators, an alternative approach worthy of consideration is the use of morphological variations within species. Many species of bryozoans exhibit plasticity in growth and form, at least some of which is ecophenotypic in origin, i.e. the result of environmental rather than genetic differences. Plasticity can occur at the level of the entire colony or its constituent zooids, the latter varying both within and between colonies. A major challenge facing bryozoologists is to identify the exact environmental factors causing intraspecific variations in modern bryozoans and then to apply this knowledge to fossil bryozoans as a means of inferring palaeoenvironments.

Colony-form

Harmelin's (1973) study of the cyclostome *Idmidronea atlantica* (Forbes in Johnston) in the Mediterranean near Marseilles showed how the exact shape of the tree-like colonies varied according to habitat. Colonies growing in caves are slender, infrequently branched and often sinuous, whereas those growing in the open are robust and regularly branched with closer spacings between branch bifurcations (Fig. 1). Colony shape changed from infrequently to frequently branched in colonies growing out from caves and into the open. Factors causing this ecophenotypic variation are

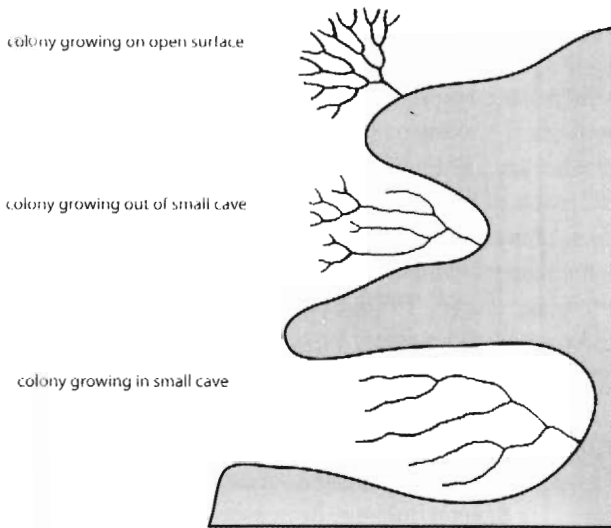


Fig. 1. Variations in the shapes of colonies of the cyclostome *Idmidronea atlantica* (Forbes in Johnston) in the Mediterranean near Marseilles depending on habitat (redrawn from Harmelin, 1973).

unknown but may include the reduced currents and food supply, as well as increased sedimentation rates, that are experienced by cave-dwelling colonies.

Flor (1972, 1973) studied within colony variations among some European Upper Cretaceous cyclostomes with bushy colonies. Branch fragments from colonies that inhabited nearshore sites, as indicated by facies analysis and palaeobiogeography, were found to have thicker mean diameters and to show a greater variability than those from offshore sites. In *Spiropora verticillata* (Goldfuss), which has apertures arranged in whorls, an interesting pattern of covariation was found between branch width and whorl spacing according to environment (Fig. 2). Nearshore populations showed a higher variability of branch diameter than whorl spacing, the reverse being true for offshore

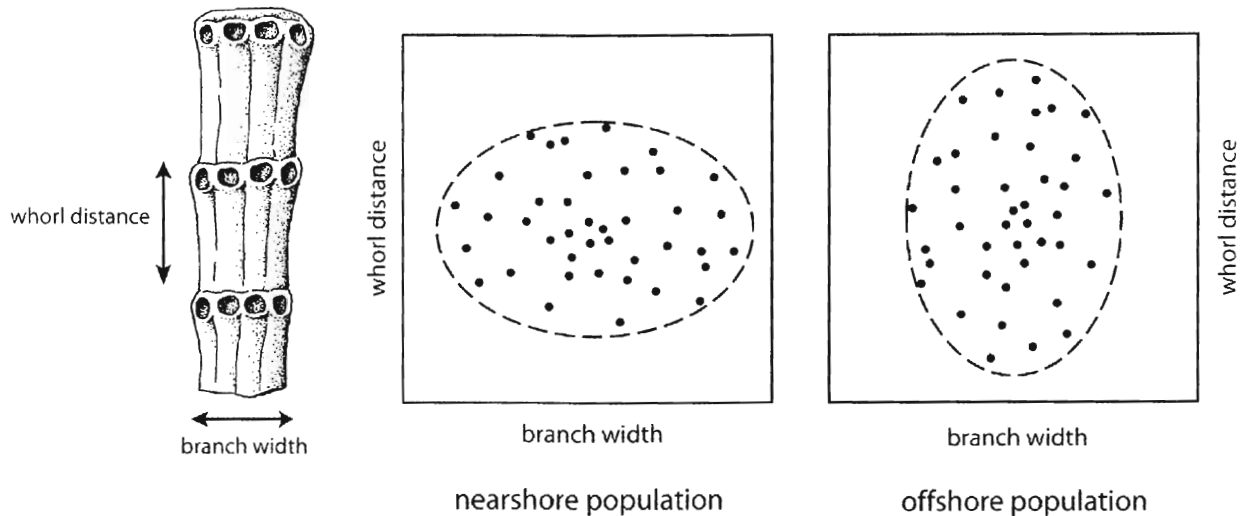


Fig. 2. Differing patterns of covariation in whorl distance and branch width in nearshore and offshore populations of the Upper Cretaceous cyclostome *Spiropora verticillata* (Goldfuss). After Flor (1972, 1973)

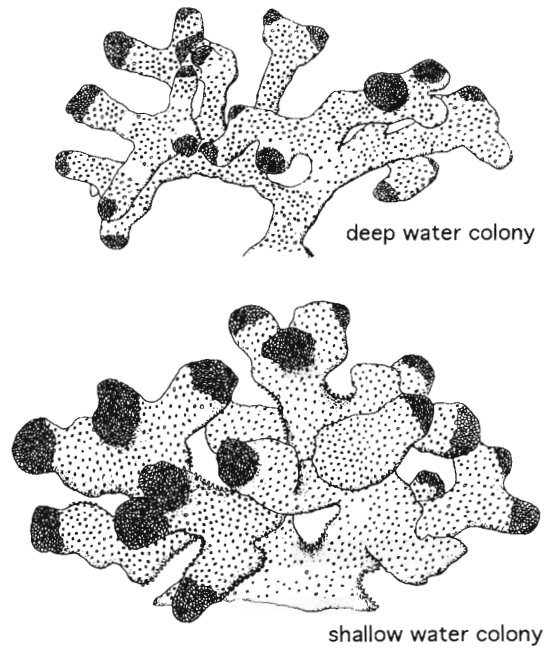


Fig. 3. Contrasting morphologies of deep and shallow water colonies of the cyclostome *Heteropora pacifica* Borg at Friday Harbor (redrawn from Schopf *et al.*, 1980).

populations. Echoing Flor's work, modern branching cyclostome species from East Africa were noted by Brood (1976) to possess gracile variants with narrow branches and widely-spaced zooids in deeper waters.

Schopf *et al.* (1980) studied variations in the branch diameter of the bushy cyclostome bryozoan *Heteropora pacifica* Borg (Fig. 3) at Friday Harbor, Washington State, USA. In 4 separate transects, average branch diameter was found to decrease with increasing depth from 9 to 15 to 30 metres (Fig. 4). While Schopf *et al.* (1980) concluded that this pattern was not related to current strength, they only actually

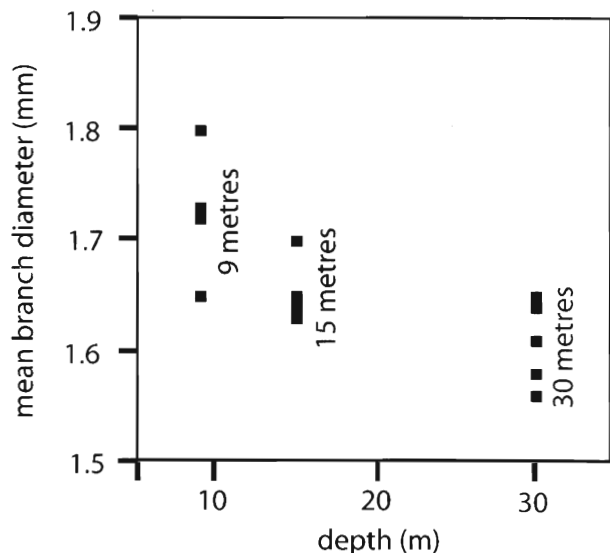


Fig. 4. Depth-related variation in branch diameter in the cheilostome *Heteropora pacifica* Borg at Friday Harbor (based on data in Schopf *et al.*, 1980).

measured current velocities at the 15 metre depth sampling stations and based their conclusion on the observation that branch diameter at one site (Sentinel Island) was similar to three other sites where measured current velocity was much lower. Instead, they believed that light, and therefore food levels, were more important in explaining the decrease in branch diameter with depth. Whatever the causal factor/s responsible, an inverse correlation between branch diameter and depositional depth may be universal or at least widespread among cheilostome bryozoans.

Thomsen (1977) found a strong bathymetrical pattern of branch diameter variation in three of six species of branching cheilostomes he studied from Danian (Paleocene) bryozoan mounds at Karlby Klint, Denmark. Samples of these three species (*Porina salebrosa* Marsson, *Onychocella columella* Berthelsen and *Floridina gothica* (d'Orbigny)) collected from the crest of a mound were found to have thicker branches than those from the intermound regions on either side. Interestingly, branch diameter in bushy sponges, hydrozoan and scleractinian cnidarians has also been shown to decrease with depth (e.g. Kaandorp, 1999).

As already mentioned, mesh-like colonies occur among cheilostome, cyclostome and fenestrate bryozoans. The meshwork and holes (fenestrules) in these colonies may vary within a species. Hass (1948) found smaller fenestrules in colonies of the Mediterranean cheilostome *Sertella septentrionalis* (Harmer) living in more exposed habitats. A related species from the Philippines, *Reteporella graeffei* (Kirchenpauer), was noted by Hillmer (1979) to have short branches with numerous anastomoses when found at 3-17 metres deep and longer, non-anastomosed branches in deeper waters.

The cheilostome bryozoan *Pentapora fascialis* (Pallas) forms erect colonies with bifoliate branches. There are two colony morphotypes in the Mediterranean. A foliaceous (eschariform) morphotype was shown by Cocito and Ferdeghini (2000) to develop in colonies experiencing strong unidirectional current flows, whereas a branched (adeoniform) morphotype appeared to grow in response to multidirectional current flows. Occasionally, the two morphotypes are found on opposite sides of a single colony. Whether or not such ecophenotypic variability is more widespread among bryozoans has yet to be established, although fossil species are known with similar within-species variations in morphotype, as in the Jurassic cyclostome *Multisparsa lamellosa* (Michelin). In another study of *P. fascialis*, Cocito *et al.* (2004) found that colonies living close to freshwater springs ('vruljas') grew larger than those further away from the springs, possibly because of the introduction of nutrients and carbonate by the springs and/or the higher current speeds and decreased sedimentation in their vicinity.

Another cheilostome – *Schizoporella errata* (Waters) – shows striking variations in colony morphotypes according to environmental conditions in the Mediterranean (Ferdeghini *et al.*, 2000; Cocito *et al.*, 2000). The large (up to 30 cm) multilayered colonies vary from mound-like with hummocky outer surfaces, to tree-like with hollow, finger-like branches. End members develop respectively in exposed and quiet water environments (Fig. 5).

Branches of the second morphotype of *S. errata* grow around hydroids or algae that would not normally be fossilized. There are many examples of fossil bryozoan colonies with tubular branches containing narrow axial canals or broader hollows. In some of these growth occurred around a perished substratum, either loosely as in the case of *S. errata*, or in a more tightly encrusting mode such that the surface details of the substratum may be preserved as a bioimmuration. Unfortunately, there has been a tendency in the palaeontological literature to attribute tubular colonies to growth around algae (e.g. Kopajevich, 1978), with clear consequences for the inference of light levels and palaeodepth. This is not justified as alternative cylindrical substrates may be utilized by tubular bryozoans, including hydroids (Cocito *et al.*, 2000), sponges (Hageman *et al.*, 2003), gorgonians (Moissette and Pouyet, 1991) and worm tubes (Hara and Taylor, 1996), as well as sea-grass rhizomes (Hoffmeister *et al.*, 1967).

Winston (1976) showed that cultured colonies of the encrusting cheilostome *Conopeum tenuissimum* (Canu) were small, straggly and had a branched morphology when poorly nourished, but large, compact and sheet-like when well nourished. Diet was also found by Jebram (1980) to have a major effect on experimental colonies of the related *Electra*

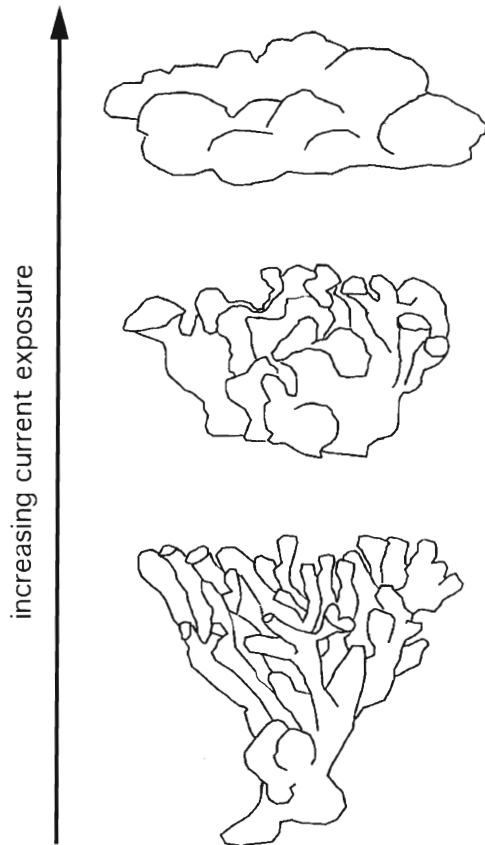


Fig. 5. Variation in colony form of the cheilostome *Schizoporella errata* in the Ligurian Sea between sites experiencing different hydrodynamic exposure (redrawn from Cocito *et al.*, 2000).

pilosa (L.), with some mixtures of algal food stimulating erect colony growth in this normally encrusting species.

Spinosity

A plethora of different types of spines are found in bryozoans. In stenolaemates, spines tend to be solid, well-calcified structures and are sometimes extrazooidal, whereas in cheilostomes they are more often hollow, basally articulated (and hence invariably lost during fossilization) and sometimes uncalcified. Within species variations in spinosity have long been recognized and during recent years some of the factors responsible have been identified among cheilostomes with uncalcified spines. In the cheilostome *Electra pilosa* (L.) long, cuticular spines develop as an inducible response to wave-related abrasion, apparently protecting lophophores from abrasive damage in high-energy environments (Bayer *et al.*, 1997). Spines may also be produced at the margins of colonies of the same species as a defence against being overgrown by spatial competitors (Stebbing, 1973).

Nudibranch predators have been shown to induce spine formation in a related cheilostome *Membranipora* (Yoshioka, 1982; Harvell, 1984). The spines provide an effective defence against these gastropods, at the cost of slowing colony growth rate. It is not known whether the incidence of calcified,

fossilizable spines correlates either with current velocity or the presence of nudibranch predators in cheilostomes but the potential for palaeoenvironmental studies of this ecophenotypic variant would be worth exploring, despite the limitations imposed by preservation of delicate spines.

Zooid size and temperature

The important paper of Menon (1972) studied the effects of culturing cheilostome bryozoans at different temperatures. Zooid size was found to decline with increasing temperature: in *Electra pilosa* (L.) mean zooid length was 686 μm at 6°C, 596 μm at 12°C, 586 μm at 18°C and 577 μm at 22°C; in *Conopeum reticulum* (L.) the same dimension averaged 558 μm at 12°C, 519 μm at 18°C and 500 μm at 22°C. That the inverse relationship between zooid size and temperature in cheilostomes is not an artefact of laboratory culture is clear. For example, Silén and Harmelin (1976) showed a similar decline in mean zooid size between populations of their new species *Haplopoma sciaphilum* inhabiting natural caves in Marseilles, the northern Adriatic and the Skagerrak. The relationship extends beyond feeding zooids (autozooids) to avicularian polymorphs which are thought to have a defensive function. Morphological clines in both autozooid and avicularium size were found in *Schizoporella errata* along the southern shore of Cape Cod by Schopf and Dutton (1976), paralleling sea water temperature changes. Metabolic scaling and oxygen content of the water probably explain the inverse correlation which is observed in other ectotherms (Atkinson, 1994) though not in endotherms where it is known as Bergmann's Rule.

The potential for inferring relative palaeotemperatures using fossil cheilostome bryozoans was demonstrated by Okamura and Bishop (1985). They compared zooid size in 8 species which occurred both at the present-day around the British Isles and in the Coralline Crag Formation deposited in eastern England during the Pliocene when the climate was appreciably warmer. As predicted, the Recent colonies had larger zooids than their Pliocene counterparts. The difference in zooid size was particularly evident when lengths were compared but could also be seen in width measurements.

The zooid size:temperature relationship has so far been documented only for cheilostomes (e.g. Fig. 6). While there is no obvious reason why it should not apply also to other bryozoan orders, work on the soft-bodied ctenostome *Alcyonidium* by Ryland and Porter (2005) failed to find the expected pattern. Factors other than temperature differences were considered by Berning *et al.* (2005) to account for apparent intraspecific variation in zooid size among Miocene cheilostome bryozoans from the Mediterranean and eastern Atlantic. Larger zooid areas in their Mediterranean samples pointed to lower temperatures which, on the grounds of other evidence, seem unlikely. The cyclicity in zooid size detected by Hageman (1995) in the Carboniferous cryptostome

Streblotrypa, with a wavelength of 3-5 zooids, is also unlikely to represent an annual, temperature-driven signal unless growth rates were extremely slow in this bushy, erect bryozoan. Novosel *et al.* (2004) compared zooid size in 14 species of cheilostomes that occurred at two sites - northern and southern - in the Adriatic Sea and found no consistent differences, calling into question the generality of a zooid size:temperature relationship. Comparisons between congeneric ascophoran cheilostomes collected on either side of the Isthmus of Panama yielded results contrary to those expected (Jackson and Herrera Cubilla, 2000): colonies from the cooler waters of the eastern Pacific had smaller zooids than those from the warmer Caribbean Sea. Therefore, despite the studies linking zooid size to temperature, some caution still needs to be exercised when using it as a palaeothermometer as other factors may confound a simple correlation (cf. O'Dea and Okamura, 1999). For example, Okamura and Partridge (1999) showed that zooids of the cheilostome *Membranipora membranacea* (L.) were shorter (and less elongate) in colonies living at sites experiencing greater rates of current flow in a very high energy setting. Cyclical variations in zooid size in the Antarctic cheilostome *Melicerita obliqua* (Thornely), although seasonal, are more likely due to variations in food supply than temperature (Bader and Schäfer, 2004).

Zooid size variation and seasonality

Whereas variation in zooid size between colonies may reflect the different temperature regimes in which the individual colonies grew, variations within a single colony should track temperature changes during the growth of that colony and hence provide an indicator of seasonality. Such intracolony variation in zooid size can be expressed as a coefficient of variation (CV). Colonies in which the CV is small are inferred to have lived in environments experiencing low levels of

climatic seasonality, those in which it is large in highly seasonal environments (O'Dea and Okamura, 2000a, b). This technique, which was fully developed by O'Dea and Okamura (2000b), has the advantage over between colony comparisons in that it does not demand taxonomic certainty in recognizing colonies that belong to the same species. Twenty-nine Recent species inhabiting environments of known temperature range were studied to show a linear correlation between CV and mean annual range of temperature (MART) (Fig. 7). From this, it is possible to obtain a formula allowing MART to be calculated from CV in fossil cheilostomes:

$$\text{MART} = -3 + 0.745(b)$$

where (b) is the mean intracolony CV of frontal area (length x width).

Two applications of this technique were given by O'Dea and Okamura (2000b): (1) eleven cheilostome species from the Pliocene Coralline Crag of Suffolk, England, produced a MART estimate of 6.6°C (range 4.6-8.9°C) which corroborated previous estimates of seasonality; and (2) five species from the Miocene 'faluns' of north-western France gave an estimated MART of 5.4°C (range 4.2-6.9°C), suggesting a more equable climate in this part of Europe than pertains at the present day with an average MART of 8°C in the Bay of Biscay.

Profiling zooid size variations in the proximal-distal direction of colony growth is the best method for collecting CVs from which to obtain MART values (O'Dea and Okamura, 2000c; O'Dea and Jackson, 2002). Assuming a colony grows continuously for an entire year or more, it will 'sample' the full annual range of temperatures and will reflect them in the sizes of the zooids budded at different times.

Ovicell porosity and temperature

Prior to releasing them as larvae, most cheilostome bryozoans brood their embryos in globose, typically two-

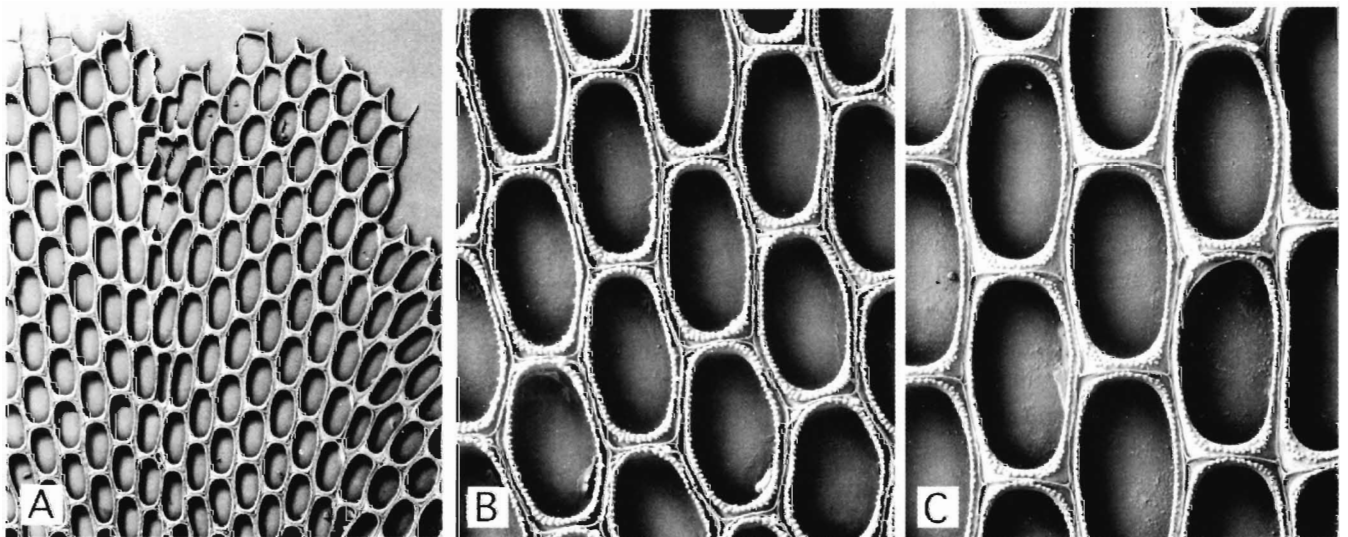


Fig. 6. Scanning electron micrographs of the cheilostome *Conopeum seurati* (Canu) from Avonmouth Dock, near Bristol, UK (see O'Dea and Okamura 1999). A, part of colony with growing edge at top (x 6). B, small zooids budded during the summer (x 50). C, large zooids budded during the winter (x 50).

layered structures called ovicells. Often the outer skeletal wall of the ovicell (ectooecium) contains holes (pseudopores). In Chilean populations of *Celleporella hyalina* (L.), Naverrete *et al.* (2005) found that the density of pseudopores declined from warm to cooler water sites. Laboratory cultures showed that pseudopore density was modulated by water temperature and dissolved oxygen. There is potential for using this correlation as a tool for inferring relative palaeotemperature and/or ancient oxygen concentration. However, very well-preserved material is required as ovicells are fragile and easily destroyed in fossils.

DISCUSSION

For the reasons discussed above, caution should be exercised when using bryozoan colony-forms to interpret palaeoenvironments. Simplistic use of colony-forms to infer ancient environmental conditions neglects the complications caused by the frequent co-occurrence of dissimilar colony-forms in the same deposits as well as taphonomic and evolutionary factors. As an alternative, the same morphological plasticity that so often hampers bryozoan taxonomy makes bryozoans potentially very useful as palaeoenvironmental indicators because within species variants can be correlated with the environment. Notably, erect, tree-like colonies often show variation in branch thickness according to habitat and depth, while zooid size may vary inversely with the temperature at the time the zooid was budded in cheilostomes. Spines in some bryozoan species may be induced by high current velocities or the presence of predators, and the number of pores in ovicells has been shown to correlate with oxygen levels in the water, though neither of these morphological variants has yet been used in palaeoenvironmental interpretation.

As pointed out by Harmelin (1988), bryozoans provide information on microenvironmental attributes which may be insufficient to characterise the environment as a whole. For instance, high energy environments can contain cryptic microenvironments, such as recesses in the rock or the undersides of shells, where bryozoans adapted to quiet water conditions flourish. It is therefore important to consider evidence from all sources before drawing conclusions about palaeoenvironments from bryozoan data.

An emerging research area with palaeoenvironmental implications is the isotopic geochemistry of bryozoan skeletons. Cyclical fluctuations in $\delta^{18}\text{O}$ parallel to growth direction have been used to determine colony growth rates in Recent bryozoans (Pätzold *et al.*, 1987; Brey *et al.*, 1999; Smith and Key, 2004). This technique should also be applicable to fossil bryozoans after taphonomic and diagenetic considerations have been taken into account and the problems of sampling thin (<100 μm) skeletal walls overcome. Variations in bryozoan growth rates may correlate

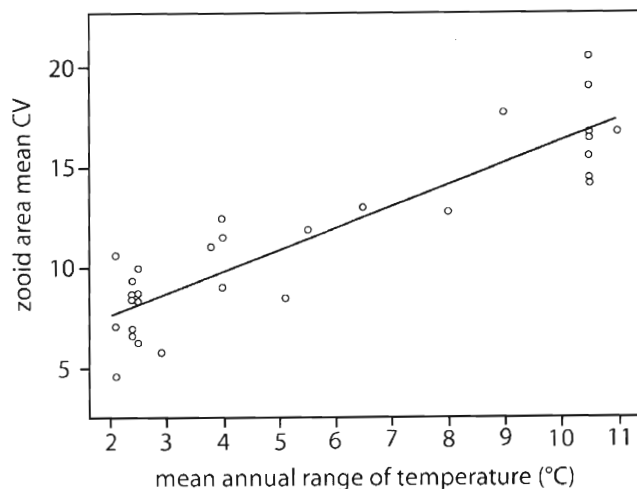


Fig. 7. Correlation between within colony variability in zooid size (expressed as mean coefficient of variation of zooid area) and mean annual range of temperature at collecting site for 29 species of Recent cheilostomes (redrawn from O'Dea and Okamura, 2000b).

with temperature (e.g. Kitamura and Hirayama, 1984) and possibly food levels (e.g. Bader and Schäfer, 2004).

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