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Cover illustration. *Celleporella uberrima* Moyano, 1987, a Recent cheilostome bryozoan from the south eastern Pacific region. [Photograph by H.I. Moyano G]
# Table of Contents

Foreword IX

Life, death and fighting at high latitude: a review 1  
*D.K.A. Barnes*

Late Miocene Bryozoa from the Guadalquivir Basin (SW Spain): eastern 15  
Atlantic and western Mediterranean environment and biogeography  
*B. Beming, F. Moissette & C. Betzler*

Bryozoa of the Romaine and Mingan Formations (Lower and Middle Ordovician) of the 25  
Mingan Islands, Quebec, Canada  
*T.E. Bolton & R.J. Cuffey*

Bryozoan species and roles in small ‘Waulsortian-like’ mud-mound bioherms in the 43  
Mississippian of the American Mid-West  
*R.J. Cuffey*

Lower Carboniferous Bryozoa from some localities in Sauerland, Germany 49  
*A. Ernst*

Bryozoans from the Artinskian (Lower Permian) Great Bear Cape Formation, 63  
Ellesmere Island (Canadian Arctic)  
*A. Ernst & H.A. Nakrem*

Taxonomic composition and structure of bryozoan-associated biofilms from Japan and 69  
New Zealand  
*G. Gerdes, J. Kaselowsky, A. Lauer, S.F Mawatari & J. Scholz*

The cheilostomatous genera of Alcide d’Orbigny - nomenclatural and taxonomic status 83  
*D.P. Gordon & P.D. Taylor*

Oshurkovia: a new genus of Umbonulidae (Bryozoa: Cheilostomata) from the northwest Pacific 99  
*A. V. Grischenko & S.E Mawatari*

Diversity, evolution and palaeoecology of the Tertiary bryozoan assemblages of western 107  
Kachchh, Gujarat, India  
*A.K. Guha & K. Gopikrishna*

Revised biological definition of the Bryozoa 119  
*J.-L. d’Flondt*

A review of non-commensal loxosomatids: collection, culture, and taxonomy, with new 133  
implications to the benefit of commensalism (Entoprocta: Loxosomatidae)  
*T. Iseto*

Gigantism in Permian trepostomes from Greenland: testing the algal symbiosis hypothesis 141  
using $^{13}C$ and $^{18}O$ values  
*M.M. Key, Jr., P.N. Wyse Jackson, E. Hâkansson, W.P. Patterson & M.D. Moore*

Bryozoan mode of life in the high Arctic dynamic fjordic environment, Spitsbergen 153  
*P. Kuklinski*
Bryodiversity on coastal boulders at Spitsbergen
P. Kuklinski & D.K.A. Barnes

161

Cheilostomate Bryozoa of the Bellingshausen Sea (Western Antarctica): a preliminary report of the ‘Bentart 2003’ Spanish Expedition
C. M. López-Fé

173

The potential role of microbial activity and mineralization in exoskeletal development in Microporellidae
P.A. Morris & D.F. Soule

181

Bryozoa of the CIMAR-7 Expedition to the Aysenian fjords and channels, southern Chile
H.I. Moyano G.

187

Some middle Permian bryozoans from Svalbard, Arctic Norway
H.A. Nakrem

197

Morphological differentiation in the Celleporella hyalina (Linnaeus, 1767) complex (Bryozoa: Cheilostomata) along the Chilean coast
A. Navarrete Z., J.M. Cancino, H.I. Moyano G. & R.N. Hughes

207

Submarine freshwater springs in the Adriatic Sea: a unique habitat for the bryozoan Pentapora fascialis
M. Novosel, G. Olujic, S. Cocito & A. Pozar-Domac

215

Ovicell development in the early calloporid Wilbertopora Cheetham, 1954 (Bryozoa: Cheilostomata) from the mid-Cretaceous of the USA
A.N. Ostrovsky & P.D. Taylor

223

Taxonomy and distribution of Bugula (Bryozoa: Cheilostomata: Anasca) in Rio de Janeiro State, Brazil
L. Vieira Ramalho, G. Muricy & PD. Taylor

231

Bryozoans and stratigraphy. Upper Richmondtian (Cincinnatian, Ordovician)
J.R.P Ross & C.A. Ross

245

Bryozoan facies in deep-sea Pleistocene environments of southern Italy
A. Rosso

257

Variation in zooid size in two west European species of Alcyonidium (Ctenostomatida)
J. S. Ryland & J.S. Porter

271

Palaeoenvironments of Eocene Bryozoa, St Vincent Basin, South Australia
R. Schmidt & Y. Bone

281

Infestation of a temperate reservoir by freshwater bryozoans: an integrated research programme
A.M. Smith, M.A. Brunton & PB. Batson

293

Ovicell pores and frontal wall pore sieve plates in eastern Pacific Microporellidae
D. F Soule, P.A. Morris & H.W. Chaney

303

Freshwater Bryozoa of Italy. A survey of some species from the Italian bryozoan collection of A. Viganò with new records
M. I. Taticchi & G. Pieroni

317

Preliminary overview of the cheilostome bryozoan Microporella
P.D. Taylor & S.F. Mawatari

329

A biogeographical analysis of Indo-West Pacific cheilostome bryozoan faunas
K. J. Tilbrook & S. De Grave

341
<table>
<thead>
<tr>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Some remarkable Bryozoa from the Neogene of Moravia (Czech Republic)</td>
<td>351</td>
</tr>
<tr>
<td>N. Vávra</td>
<td></td>
</tr>
<tr>
<td>The higher phylogeny of Phylactolaemate bryozoans inferred from 18S ribosomal DNA sequences</td>
<td>361</td>
</tr>
<tr>
<td>T.S. Wood &amp; M.B. Lore</td>
<td></td>
</tr>
<tr>
<td>The distribution of freshwater bryozoans in Austria</td>
<td>369</td>
</tr>
<tr>
<td>E.R. Wöss</td>
<td></td>
</tr>
<tr>
<td>A bryozoan fauna from the Carboniferous (Mississippian, Late Viséan) of the Velbert Anticline, Germany</td>
<td>375</td>
</tr>
<tr>
<td>PN. Wyse Jackson &amp; H.M. Weber</td>
<td></td>
</tr>
<tr>
<td>A bryozoan and foraminifera association from the Miocene of Podbrezice, south Moravia (Czech Republic): an environmental history</td>
<td>383</td>
</tr>
<tr>
<td>K. Zágorsek &amp; K. Holcová</td>
<td></td>
</tr>
<tr>
<td>List of participants</td>
<td>397</td>
</tr>
<tr>
<td>Taxonomic index</td>
<td>401</td>
</tr>
<tr>
<td>Author index</td>
<td>411</td>
</tr>
</tbody>
</table>
Foreword

This volume contains 37 papers presented at the 13th International Conference of the International Bryozoology Association (IBA) held in Concepción, Chile from the 11th to the 16th of January, 2004 and hosted by Universidad de Concepción and Universidad Católica de la Santísima Concepción. In addition we include the last paper on bryozoans to be written by Tom Bolton before his death in 1997. Tom was a palaeontologist with the Geological Survey of Canada and a long-time member of the IBA. The publication of his paper is a worthy memorial.

This was the second time an IBA conference has been held in the Southern Hemisphere - the previous one had taken place in New Zealand in 1995, and the second conference to be held in a Spanish speaking country. The first was that held in Panama in 1998.

In spite of Concepción being located far away from the various centres of bryozoological research in Europe, the USA, Australia, New Zealand and Asia, there was a total attendance of 71 delegates and 12 accompanying members, who represented 22 nationalities. The opening ceremony of the conference was held in the Fine Arts House (Casa del Arte) of Universidad de Concepción which contains a splendid Mexican-Chilean mural that was inspired by a verse penned by the Chilean Nobel laureate Pablo Neruda. This verse and the mural itself poetically sing to Latin America from Mexico to Patagonia and in front of it the delegates were entertained with songs and dancing from Chilean folklore and its various geographical regions.

The Conference was held in an academic and friendly environment in the Aula Magna of Universidad Católica de la Santísima Concepción, adjacent to the main square of Concepción. The programme and the Abstracts of the Conference were published in December 2003 as Volume 74 of the Boletín de la Sociedad de Biología de Concepción, edited by H.I. Moyano, J.M. Cancino and M.C. Orellana. At the Conference a total of 65 papers, arranged in 16 sessions were presented orally, and 25 posters were displayed. The scope of the papers covered seven thematic subjects: Ecology and life strategies (13 papers); Australasian Realm: past and present (3); Arctic and Antarctic: past and present (13); Geology and Palaeontology (6); Freshwater bryozoans (6); Evolution and Diversity (17); and Mediterranean-Tethyan Realm (7). The high quality, originality and the up-to-date methods and techniques used in the papers presented are demonstrated in the contents of the present proceedings. Frequently number of posters presented at the IBA International Conferences is less than 15; at the Chile conference however, the number increased to 25. It is also worth mentioning that a large number of young bryozoologists attended the Conference, and this can only be interpreted as a good sign for the future of the International Bryozoology Association. Also noteworthy was the fact that a fair number of papers were presented at the conference that examined fossil and Recent bryozoans from Brazil, Argentina and Chile - this is a topic hardly explored in South America. Hopefully this Conference and the present proceedings might help to increase and foster bryozoological studies in South America.

As is usual for an IBA Conference the mid-conference trip provided delegates and companions with a unique opportunity to visit an area of natural beauty close to the conference centre. The group became familiar with the Chilean natural environment and its people when it visited the Nahuelbuta National Park where they walked through the forest dominated by magnificent *Araucaria araucana* and *Nothofagus dombeyi* trees that tower over the dense forest and reach up 40-50 m high. From this visitors came away with a personal experience of what the cold and low diversity old rainy-forest of austral South America looks like. They also observed Andean volcanoes from the vantage point on top of a huge granite boulder in the park.

Chile which extends from 17°S to 56°S includes all the climates on Earth except tropical. The preconference and post-conference trips allowed delegates to become acquainted with the diversity of landscapes, ecology, geology, weather and culture of the country. The pre-conference trip was organised by Juan M. Cancino, Hugo I. Moyano, Maria Cristina Orellana, with assistance from Patricio H. Manriquez of Pontificia Universidad Católica de Chile, Luis Figueroa of the Universidad de Antofagasta and Dr Guillermo Chong of the Universidad Católica del Norte, Antofagasta. The 26 participants travelled from the dry deserts of the north, across the semi-desert into the Mediterranean areas of central Chile and finished at the doorsteps of the humid cold-temperate area of southern Chile. Nearly 2500 km was travelled by bus from Calama, ca 22° 30’S to Concepción ca 36° 40’S. The highlights of this trip included visiting the old Village of San Pedro and Salar de Atacama with its flamingos and lizards, that is surrounded by the driestmost inland warm desert on Earth; the landscape of the
coastal desert of Pan de Azúcar National Park, with its large diversity of cacti and wild foxes, which contrasted with that of La Campana National Park, known to the world since the visit by Charles Darwin in 1835, with its forest of Chilean palms and southern beech (*Jubaea chilensis* and *Notophagus obliqua*, respectively). Finally, there was time for a short visit to Valparaiso, its hills, and the house of the Chilean poet Pablo Neruda, after which the party made its way to Concepción across the green valleys of the Mediterranean Chile amid myriad of orchards and vineyards where high quality wines are produced.

The post-conference trip was attended by 30 delegates and organized by Hugo I. Moyano with help from Juan M. Cancino and Maria Cristina Orellana. This trip crossed the forests, lakes and austral ice lands from Concepción to the Magellan Strait at 56°S. Lakes, water cascades volcanoes and forests with *Philesia magellanica* and *Fitzroya cupressoides*, one of the most long living trees in the world, were visited around Puerto Montt. The Vicente Perez Rosales National Park and the sailing trip across Todos los Santos lake with its emerald coloured waters (close to the border with Argentina) will certainly be remembered by delegates. The second part of the post-conference trip started in Punta Arenas and visited the Magellan Strait, Bulnes Fort, Port Famine, the penguin nesting areas at Seno Otway (Otway Inlet) and the Milodon cave before travelling to Torres del Paine National Park with its majestic mountains, glaciers and rich flora and fauna, including condors and many species of birds and South American camellids. The trip ended with a day sailing on the Ultima Esperanza (Last Hope) fjord with its glaciers at Mount Balmaceda and O’Higgins National Park.

The 13th International Conference of the IBA was made possible thanks to the collaboration of many people and institutions. Many thanks are due to the host Institutions, the Universidad de Concepción and the Universidad Católica de la Santísima Concepción, who made all their facilities and personnel available to the service of delegates and accompanying persons, and which made the Conference possible and achieve its objectives efficiently. Special thanks are due to Maria Cristina Orellana for her help with organising the Conference, to Magdalena Jofré and Matilde Mella for their secretarial assistance, to Patricio H. Manriquez, Roger Sepúlveda, Maria Cecilia Pardo, Nelson San Martin and Arturo Navarrete for their help during the conference in Concepción. Finally, the hosts of the Conference in Chile thank the International Bryozoology Association for trusting us with the organisation of the present Conference, and especially thank all fellow bryozoologists who attended and/or presented papers in the Conference, which have led to the publication of *Bryozoan Studies 2004*. This volume is a good example of an international collaborative enterprise to the benefit of scientific knowledge, and we hope that the readers of the volume will be encouraged to make future contributions to bryozoological knowledge.

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Life, death and fighting at high latitude: a review

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ABSTRACT: Nearshore animals living in the two polar regions have much in common, they experience extreme light climates and associated primary productivity, freezing sea temperatures and seasonally intense ice disturbance and UV irradiation. Arctic and Antarctic shallow water environments and their communities have important differences from each other, though, as well as from those in low latitude. Life is tough on land and on the shore, the fauna is small and scarce but not so in the sea. Bryozoans are highly ecologically successful in shallow waters in terms of species richness, abundance and biomass. In this paper critical influences on life and death of polar bryozoans are reviewed as well as the importance of competition. Closer inspection of seemingly barren boulders reveals a bustle of pioneer species fighting for their undersurfaces. The organisation of these battles is extremely hierarchical: at any given locality one species is overgrown by all others and one species overgrows all others - everyone else occupies a rigid rank in between. With no keystone predators to remove competitive dominant species only the catastrophically destructive power of ice and waves prevents monoculture of certain species. In ice-sheltered areas, such as crevices the end point of classically envisaged ‘succession’ can be seen. In these shallow water environments many animal populations display exactly the converse of characters typically associated with the polar regions. The most abundant species of many clades are the rarer broadcast spawners with pelagic larvae, that grow and reproduce fast (for polar animals) are small and have but brief lifespans. Many of these contrasts can be seen in the representatives of just one phylum - the Bryozoa. Rather than the predicted K selected species of deeper waters the shallows are ruled by lightly calcified pioneers. Here ecological and evolutionary success have become very much decoupled. A ~2°C rise, predicted in polar waters, could be enough to transform this unique zone in our lifetimes.

1 INTRODUCTION

In Earth’s history, having two frozen polar regions is unusual, but icy coasts are not marginal habitats. Coastlines currently experiencing freezing sea temperatures or floating ice constitute ~30% globe and ~50% during the last glacial maximum (Bond et al. 1992). The two polar regions not only experience freezing sea temperatures but also seasonally intense UV irradiation and most obviously extreme light climates and associated primary productivity (see Dayton 1990). At these high polar latitudes severe wind speeds, wave action, ice scour and anchor ice (as well as massive fresh water runoff and localised anoxia in the Arctic) make the nearshore environment the most disturbed anywhere (Amtz et al. 1994, Gutt & Pipenburg 2003). On land, in fresh water and in the intertidal zone there are few colonist species but just a few metres deeper in the sea there can be rich, diverse and abundant benthos even in shallow water (Dick & Ross 1988, Bames 1995a, Bames & Kuklinksi 2003). In comparison with other major regions of the globe the Arctic does appear to be species poor, though this may simply be due to its youth and being still in the process of invasion (Dunton 1992). In contrast there is no evidence that the Antarctic benthic environment is impoverished compared with other latitudes (Clarke 1992) and some shelf areas are highly rich (Galeron et al. 1992, Brey et al. 1994). Amongst the most abundant shallow water benthos are lithophyllic polychaetes, cheilostome and cyclostome bryozoans, sponges and, in the arctic, barnacles. Although these taxa occur elsewhere at lower latitudes there is a very distinct polar fauna in many ways. Firstly, to the casual observer life between the tides seems to have disappeared and that below the tides seems very still: most animals are sessile or sedentary - even predators are mainly sluggish (Amtz et al. 1994). Secondly, some unusual animal types such as brachiopods and pycnogonans are very well represented, others such as the gastropods and especially the decapod and balanomorph crustaceans are not (Clarke & Johnston 2003). Thirdly, most Antarctic (though not Arctic) species are endemic, nowhere-else are levels of endemism as high. Fourthly, representatives of some taxa are giant compared to elsewhere - due to the...
high oxygen levels in the cold well-mixed water (Chapelle & Peck 1999). The chemistry, kinetics and physiology of these strange animal assemblages are quite different to those at low latitudes (Peck 1998, Pörtner 2002a, b) and this is easiest seen in the pace of life. Recruitment and growth of such polar ectotherms is typically very slow (Arntz et al. 1994, Stanwell-Smith & Barnes 1997). In combination with high rates of disturbance, slow colonisation results in only small proportions of available space, on shallow substrata, being occupied. There has, therefore, been a prevailing view that competition would be of no great importance in structuring communities at high latitudes, given that space (seemingly in abundance) is required to be limiting (Connell 1978).

The organisation of sessile animals is extremely hierarchical: at any given locality one species is overgrown by all others and one species overgrows all others - everyone else occupies a rank in between (Barnes 2002a). With no keystone predators to remove competitive dominant species only the catastrophically destructive power of ice and waves prevents monoculture of certain species (Barnes 2002b). The nature of bryozoans, compared to most other taxa, conveys many advantages in investigation of pattern across scales, especially including those examining competition. Just over last decade alone studies of bryozoans have given powerful insight into large-scale patterns in time and space (Jackson & Cheetham 1990, McKinney 1995, McKinney et al. 1998, Clarke & Lidgard 2000. Sepkoski et al. 2000, Barnes 2002a). Since Winston’s (1983) pioneering ecological work on high Antarctic cheilostomes, the ecology of this taxon has received increasing attention in the southern polar region (see Winston & Hayward 1994, Moyano 1996, Barnes & Clarke 1998, Brey et al. 1999a, b, Bader2001. Cancino et al. 2001). Arctic and subarctic bryozoans have, in contrast received little study, other than recording of species presence (but see Dick & Ross 1988, Schäfer 1994, Kuklinski et al. 1998, and Barnes & Kuklinski 2003). Nevertheless bryozoans are clearly abundant and ecologically important in the northern polar region and frequently seems to be substantial constituent of Arctic macrobenthic assemblages (see Różycki & Gruszczynski 1986, Gulliksen et al. 1999, Lippert et al. 2001). In the current study bryozoans are used as a model taxon to examine polar nearshore communities relative to non-polar equivalents mainly by reference to the last decade of polar bryozoological research.

Many features of polar benthic ecology and benthos can be illustrated with reference to just one taxon: the bryozoans. Characteristics of high latitude life in boulder communities, mainly using the bryozoans as an example taxon, are reviewed here together with levels of mortality and the implications these have. In the main part, though, this article discusses competition for space between polar species in terms of how this structures communities, past, present and future. I start by outlining principal factors shaping life in high latitude shallow water communities: seasonality, temps of life processes and disturbance.

2 LIFE ON THE ROCKS

2.1 Seasonality and longer time scale variability

Seasonality of light climate becomes similarly stronger polewards in the northern and southern hemispheres. Although the two polar regions differ in many respects, water surrounded by land or visa versa, age and history, isolation, bathymetry and types of substrata, a dominant feature of the lives of organisms in both is intense seasonality. Sea surface temperatures (SSTs), fast-ice (frozen sea surface) formation and breakup, disturbance and primary productivity (and, therefore, secondary productivity) all change sharply between summer and winter (Clarke 1988, Dayton 1990). Polar SSTs generally have a greater degree of constancy than at lower latitudes, varying throughout the year by as little as a fraction of 1°C. The seasonal pattern of SST is typically a long period at near freezing (—1.8°C) followed by a sharp rise to positive temperatures, then a return to near-freezing levels. In the Antarctic this varies from a 3–4°C annual variation at Signy Island (Clarke 1988) to a tenth of a degree in the Ross Sea (Dayton et al. 1970). In the Arctic annual variation is generally a bit higher, even at 77–79°N (Svalbard) annual range is approximately -1.8 to +4°C (Swerpel 1985, Weslawski et al. 1988). Such relative constancy rather than the extreme low temperatures of the environment has resulted in a biota which is highly stenothermal and, in the Antarctic, strong patterns of temperature-dependent biogeography (Peck 2002. Pörtner 2002a, b). Although some annual variability of sea temperature is known (Clarke et al. 1988), there has been no obvious signal of climate change in SSTs in the way there has in air and lake temperatures in both polar regions (Quadfasel et al. 1991, King & Harangozo 1998, Quayle et al. 2002). The level of error in predictions of the better climate models to date has been of the same order of magnitude as the predicted change, due to the complexity of buffering (Murphy & Mitchell 1995).

Disturbance to the water column and shallow benthos from wave action, currents and floating ice is also highly seasonal. Gouging and scraping (icescour) from floating ice during summer months contrasts with a frozen sea-surface (fast ice) and the stillest, most clear, sea-water anywhere during winter. The duration of fast ice varies from place to place: in the arctic it extends further and stays longer on west Atlantic and Pacific coasts than east and in inner fjords areas for longer than the central and outer parts (Weslawski et al. 1988,
Ice-loading of surface waters has been found to change with supra-annual periodicity (Dayton 1989, Murphy et al. 1995), climate warming through disintegration of ice shelves (Doake & Vaughan 1991) and possibly with longer term phenomena, such as Milankovich cycles. Like sea surface temperatures, near-boron salinities vary very little (usually 33-35 p.s.u.). At the surface, in contrast, there are big seasonal salinity decreases in the Arctic summer (especially around the many rivers discharging around it) whereas the lack of Antarctic rivers results in little brackish influence.

Dictated by light climate, high latitude primary productivity is concentrated around just a few months of the year (Clarke & Leakey 1996). The level of seasonality does alter with the type of primary producers, Clarke & Leakey (1996) showed the abundance of the larger diatoms to be much more seasonal than the nanophytoplanktonic ciliates and flagellates. This explains why some animals, such as holothurians, limpets and echinoids feed for just a few months a year (Barnes & Clarke 1995, Brockington et al. 2001, Fraser et al. 2002) - these are mainly diatom feeders. Some other animals, in contrast, seem able to feed near year-round or in extreme cases do not stop. The example taxon focussed on here, Bryozoa, encompass species which almost cover the entire cross-section of strategies. This is possible as most utilise the smaller nanophytoplanktonic fraction of food (Winston 1977). The seasonal signal of feeding can be fairly predictable between years even at places hundreds of miles apart (Fig. 1). Most animals, which lay down non-moulted skeletons, display some evidence of the seasonality of their uptake of food. This is most obvious in some polar bryozoans, brachiopods and bivalve molluscs (Winston 1983, Brey et al. 1995a, Brey & Mackensen 1997). Certain representatives of these taxa produce banding, often referred to as growth checklines. Intuitively these were assumed to be annual in periodicity (Winston 1983) and in the bryozoans have proved to be so (Barnes 1995a, Brey et al. 1999a, Brey & Mackensen 1997). Of the few polar bivalve molluscs investigated to date (with respect to periodicity of growth banding) the same has been found (Brey & Mackensen 1997); however brachiopods have been found to produce similar bands at anywhere between 1-1.9 years (Brey et al. 1995a, Peck & Brey 1996). In cheilostomes each band is formed during periods of change in feeding activity, such that in years when there is two pulses of nanoplankton a feint additional band is apparent (Barnes 1995a). Banding is extremely useful to ecological investigation of organism responses to environmental conditions as interannual variability in growth can be easily examined and compared with reproductive investment, feeding duration and nanoplanktonic food availability if appropriate data is collected. In addition such banding enables investigation of age structure of populations and patchiness of mortality. Perhaps the most obvious primary use of band production data in polar marine organisms has been to compare growth rates of polar organisms with those in the temperate and tropical regions. Data from cheilostome bryozoans was the first data collected from modularly colonial animal types and remains the only data for this sort of animal structure despite hydroids, soft corals, octocorals, didemnid ascidians being abundant and widespread in polar benthos.

2.2 Tempos of activity, metabolism, growth and reproduction

Few polar invertebrates do anything quickly when compared with equivalents from low latitudes - existence at high latitude does seem to be life in the slow lane (Pearse et al. 1991, Peck 1998). Even predators chasing prey, for example nemertean worms after limpets, have to be watched on greatly speeded up time-lapse film for pursuit to be obvious. Sessile suspension feeders and sedentary deposit feeders are very successful (Dayton 1990, Amtz et al. 1994, Gili & Coma 1998, Gullikson et al. 1999, Barnes & Kuklinski 2003). It has been speculated on that sloth and being mainly skeleton or ‘bone idle’ (Emson 1985) is a key facet of high latitude success. Whether low ambient temperatures, food levels or another factor is primary in influencing such inactivity is debateable. Low activity levels are reflected in the metabolic rates of polar species. Two decades ago little was known of high latitude basal metabolic rates or aerobic scope, except in molluscs (Ralph & Maxwell 1977, Houlihan & Allan 1982) and isopods (White 1975, Luxmoore 1984). From the late 1980s measurements were made of a broader spectrum of animals e.g. brachiopods (Peck et al. 1987) and ascidians (Kuhne 1997, Sahade et al. 1998). Recent measurements of Antarctic bryozoan metabolic rates (Peck & Barnes 2003) have little equivalent data to compare with from low latitudes: only two previous studies on bryozoans have been carried out (Murfoz & Cancino 1989, Cancino et al. 1991). For echinoids, in contrast, specific metabolic rates have been measured for a range of localities and oxygen usage is lowest in those at high latitude (Brockington 2001). Overall it seems that oxygen consumption in Antarctic (and Arctic, see Lehtonen (1996), Schmid (1996)) invertebrates is low. The biggest range in values within a higher taxon is in the bryozoans, despite that of only three species being measured to date (Peck & Barnes 2003). This flexibility may be important in explaining the ecological and evolutionary success of bryozoans in the polar oceans.

In general polar ectotherms grow slowly (Amtz et al. 1994). This can vary from nearly comparable
Figure 1. Sea ice thickness, sea temperature, nanophytoplankton standing crop and feeding by the bryozoan *Isosecuriflustra tenuis* Kluge, 1914 with time and locality. Signy Island data are from Barnes & Clarke (1994), Adelaide Island data are from the Rothera Time Series (RaTS) long term monitoring project.
with temperate species to very slowly (Pearse et al. 1991). A couple of Antarctic sponges (Dayton 1989) and ascidians (Rauschen 1991) have been recorded to accumulate tissue quite quickly but when compared with the faster growing low latitude species in their respective taxa (that is their ecological equivalents elsewhere) the polar species remain slow. Many sponges specimens and species, investigated over a number of years, showed little or no growth and even negative growth (Dayton et al. 1970, Dayton 1989). Antarctic bryozoans are not an exception to the general rule, those measured to date grow slowly - though their range of structures and strategies is considerable (Winston 1983, Winston & Heimberg 1988, Barnes 1995a, Brey et al. 1999a, b, Bader 2001, Barnes & Arnold 2001). Much less is known of the relative growth performance of arctic bryozoans (but see Schäfer 1994), or other northern polar marine invertebrates. Investigating the timing of growth may be very important to understanding why rates are depressed - certainly amongst the cheilostomes when they are actually growing they are doing so at comparable pace to temperate ones (Barnes 1995a, Brey 1999a). But this growth period only lasts for 3 or 4 months so the annual mass increments are small. Furthermore despite growing slowly representatives of a number of taxa obtain great size, most obviously isopods and pycnogona. This ‘polar gigantism’ has in amphipods been found to be purely due to dissolved oxygen levels (Chapelle & Peck 1998). Temperature is only of influence in that cold water can hold more gas, and thus have higher oxygen levels. Amongst the largest bryozoan colonies to occur anywhere also occur in polar waters: those of Arachnopusia inchoata Hayward & Thorpe, 1988 reach more than 2 m in diameter (and 50 cm height) at 25 m depth at Signy Island. Below the depth of ice scour or in protected environments such as caves polar invertebrates also tend to live very long lives and may reach considerable age before becoming reproductively active. Echinoids (Stereochinus neu-rayneri Meissner, 1900), brachiopods (Magellania fragilis Joubin, 1914 and Lithothyrella uva Broderip 1833) and bivalves (Yoldia eightsi Couthouy, 1839) may all live to be more than 50 years old, maybe much more (Brey 1991, Brey et al. 1995b, Peck & Brey 1996). Again bryozoans follow the general trend, celarinnellids and flustrids have been found at estimated ages of up to 25 years (Winston 1983, Barnes 1995a) and these were probably restricted by periodic ice scouring events. Strikingly in bryozoans the polypide recycling time is massively longer than has been found in temperate species: 7-9 months rather than just weeks (Barnes & Clarke 1998, Dyrinda 1981, Dyrinda & Ryland 1982). Little work has been carried out on Antarctic bryozoan reproduction and almost nothing on those in the Arctic. The state of knowledge at the moment is confined to the period of brooding, timing of larval release and settlement (Moyano 1984, Stanwell-Smith & Barnes 1997, Barnes & Clarke 1998, Cancino et al. 2001). Amongst other taxa, particularly the echinoderms (Pearse et al. 1991, Brockington 2001) a huge amount of work has been carried out on reproductive (vs somatic) allocation, periodicity, development times and modes of larval stages. Thorson’s rule (Mileikovsky 1971) once thought to be one of the few valid generalities for latitudinal comparisons of reproductive mode and timing does not seem to hold for some taxa (Pearse et al. 1991). Furthermore, a principal prediction of Thorson’s rule that planktonic larvae would be rare seems to have been negated by the finding of larvae from many taxa throughout the year at Signy Island (Stanwell-Smith et al. 1998). Other major advances have included the contrasting ecological vs evolutionary success of brooding species vs those with planktotrophic larvae (Poulin et al. 2002). Most echinoid species in shallow Antarctic waters are brooders but the most abundant species have planktotrophic larvae. The most notable bryozoan group with planktotrophic larvae, the ctenostomes, are nearly absent from Antarctica, except for one spectacular find (Peck et al. 1995). The progress in polar reproductive biology in general has been reviewed in detail by other authors and since little is still known of bryozoan strategies it will not be covered further here.

2.3 Disturbance

Polar benthos may live in many extreme conditions, such as temperatures and food availability but communities can be highly diverse (Brey et al. 1994), have high levels of abundance and biomass (Amtz et al. 1994) and live to great age as already discussed. In shallow waters, however, these are all restricted because of one pervasive factor: disturbance. Disturbance to marine communities, like those on land or in freshwater environments comes from a variety of sources at a variety of scales. Of the non-anthropogenic sources wind force, wave action and currents are probably the most ubiquitous across the world’s oceans. Although these do not have a linear relationship with latitude, they are highest at 50-70° North and South (Barnes 2002a, data from Bentamy et al. 1996). In addition to these high wind and wave forces, polar benthos above ~ 1 km depth, experiences some of the most destructive forces known, ice scour (Conlan et al. 1998, Gutt 2001, Gutt & Pipenburg 2003). This is the scraping and gouging of the sea-bed by floating ice when it grounds out. In very shallow water this can be similar in effect to the bashing of the shoreline by logs (see Dayton 1971) or in deeper water by trawling (Thrush & Dayton 2002). Megafauna, such as Walrus and Gray Whales, also dig pits when foraging in spring and summer, though this is on a somewhat smaller scale (Nerini & Oliver 1983). Arctic benthos...
in shallow water also has to contend with considerable chemical, as well as mechanical, disturbance. A massive incursion of freshwater occurs in the Arctic spring from a number of large rivers discharging as well as the melt of snow and glaciers directly (Dayton 1990). When the sea surface is frozen (fast-ice) most of these forms of disturbance are minimized but other forms increase. Where fast-ice meets the shoreline, the coast becomes encased in several metres of ice (the ‘ice-foot’) and below the surface supercooled water can nucleate around organisms (‘anchor ice’). Anchor ice forming on shallow objects and organisms grows until eventually its buoyancy rips animals or algae off the bottom and carries them to the surface (Ellis & Wilce 1961, Dayton et al. 1970, 1974, Dayton 1989). The cumulative result of all this disturbance is denuded shorelines and impoverished and young communities in shallow waters.

3 DEATH ON THE ROCKS

3.1 Denudation and zonation

The early marine biological polar pioneers noticed that at high latitudes the intertidal biota started to become scarce and in many places disappeared altogether. For decades it was widely thought most of the Antarctic shoreline was denuded apart from a few sporadic places where limpets and a few other itinerant species (e.g. amphipods) occurred (Hedgepeth 1969, Shabica 1972). In the southern hemisphere the littoral regions of Cape Horn, the Falkland/Malvinas islands and to a lesser extent some of the sub-Antarctic archipelagos are the most southerly occurrences of year-round and developed shore macrobiota (de Villiers 1976, Barnes & Brockington 2003). Beyond this at ~56°S there are rare sporadic places where severely impoverished intertidal faunas do exist, examples include Shallow Bay, Signy Island (Barnes et al. 1996) and Thorgersen Island, Palmer Archipelago. In the northern hemisphere the situation is more complex in that severe ice scour denudes western coasts to much lower latitudes than eastern ones. Even at 79°N in Spitsbergen (Svalbard Archipelago) there are some bays with macroalgae and accompanying fauna (Weslawski et al. 1988, 1993). Bryozoans are one of the few, but not the only, colonial taxa represented on extreme high latitude shores, albeit just a few cheilostome species (Barnes et al. 1996, Kuklinski 2002a, b). All colonies found to date seem to be less than a year old; for sessile animals that cannot move to avoid scour or encasement by the winter ice-foot the intertidal must be recolonised each year.

Ice scour, the principal cause of removal of macrobiota (and so zonation) from polar littoral zones, is however one of the major creators of zoning high latitude sublittoral. The frequency and intensity of scraping must alter with depth as there are many small pieces of ice but few very large ones, in the same way that wave action effects drop off rapidly with depth. Dayton et al.’s (1970, 1974) pioneering work at McMurdo Sound in the high Antarctic described a strongly zoned fauna, though they principally ascribed anchor ice as the main cause. Like Dayton et al.’s (1970, 1974) studies, but in the Peninsula region of Antarctica Gruzov & Pushkin (1970) also reported three fairly distinct zones in shallow water. Since then a more detailed picture of biotic zonation has been built up in and around the Arctic, Antarctica and the archipelagos surrounding both (see Dayton 1990). Such depth zonation is apparent in many aspects of communities - richness, diversity, biomass and changes in abundance of specific taxa. Some higher taxa, or even individual species (e.g. the limpet Nacella concinna Strebel, 1908 or the echinoid Sterechinus neumayeri), illustrate such zonation in their population structures (Brockington 2001). Bryozoans are well represented amongst high taxa in shallow waters in both the Arctic (Osburn 1955, Kluge 1975, Dick & Ross 1988) and the Antarctic (Hayward 1995, Barnes & Brockington 2003). As such bryozoans are extremely useful as an indicator of general zonation patterns; they can be defined fairly clearly using changing cheilostome morphologies or abundances alone (see e.g. Dick & Ross 1988, Barnes 1995b). Colony form for example, from 0 to 6-10 m is all encrusting, at 6-10 m foliaceous forms appear (e.g. Arachnopusia inchoata in Antarctica) and only at about 20 m do the first erect flexible (flustrid) forms typically start. Deeper still, at ~40 m rigid erect forms occur but only become common at about 100 m depth. At a bigger scale, and unrelated to ice scour, it seems that in the Antarctic at least, bryozoological biogeographic provinces (Moyano 1982, Barnes & De Grave 2000) correspond well with the general biotic patterns as put forward by Hedgepeth (1969) and Dell (1972). The small-scale zonation and patchiness patterns in shallow water, in biota in general and bryozoans, seem to be largely dictated by the processes of scouring and recolonisation.

3.2 Survivorship rates, animal size and latitude

Iceberg impacts onto hard or soft substratum leave few survivors (Conlan et al. 1998, Gutt 2001), even amongst the meiofauna (Lee et al. 2001). Where icebergs happen to ground and scrape will to some extents be random for a given depth but few large/old sessile animals have been reported above 20 m depth in polar waters. For millions of years life in shallow waters at high latitudes has involved a repeating cycle of colonising new space (which is constantly becoming available) and growing somatic and reproductive tissue fast enough to ensure survival before being
scoured. With increasing scouring frequencies, i.e. decreasing depth, species which have (a) flexible larval settlement, (b) fast (relative to other polar species) growth rates, and (c) early onset of larval production should be favoured. In general polar environments are characterized by K selective species (Clarke 1988), yet shallow waters seem to be populated by r strategists. Survivorship rates on high polar littoral zones is probably rarely greater than a year but little hard data exist. In the southern Atlantic Falkland Islands and Tierra del Fuego, Barnes and Lehane (2001) found cheilostome annual mortalities to be 85-97% in the intertidal and 65-92% in the subtidal. Further south beyond the Polar Frontal Zone fauna have not been demonstrated to survive encasement in the ice foot, which hags the coastline, though limpets may migrate up and down - so returning to the intertidal year after year. In shallow Antarctic waters bryozoan (and probably other sessile animal) mortality ranges from 85-99% (Barnes & Arnold 2001, author’s unpublished data). Similar mortality levels have been described from ice scour's of soft substratum - Peck et al. (1999) found a single scraping of one site to remove all of 6 taxa and 96% of the remaining two taxa. The existence of echinoids (S. neumayeri) in excess of 20 years old in the same localities as encrusting species that rarely avoid being scoured for more than a year is a strong demonstration of the selectivity in killoffs by iceberg grounding. Nevertheless the effect of ice scour on communities and populations on benthos in both polar regions is usually catastrophic (Gutt et al. 1996, Gutt & Pipenburg 2003). Even in demersal fishing activity, probably the source of disturbance most analogous to ice scour at low latitudes, would typically have associated mortalities of 40% per event (Jenkins et al. 2001). Although dredging frequencies can like ice scour be very high (~8 per year), the fast pace of recolonisation possible at low latitude reduces the severity of overall impact compared to ice scour in the polar regions.

Polar benthic species often have the capability of reaching considerable size given the raised dissolved oxygen levels (Chapelle & Peck 1998) and longevity of species (Amtz et al. 1994). In shallow waters though high mortality leads to animals rarely reaching maximum size (even mobile species such as S. neumayeri - see Brockington 2001), populations not being unimodal and in taxa capable of extensive regeneration (such as bryozoans) - growth from fragments. There has been little study of relative attained sizes of animals in the polar regions to date, although some of the largest colonies known (2 m diameter) have been found in Antarctica. The finding of decreased survivorship with increasing latitude in bryozoans (Barnes & Arnold 2001 ) should suggest that the mean size of colonies should also decrease. Complexity is added, however, by findings of increased growth with increasing latitude in the same study. Thus some bryozoans may actually change very little due to faster growth but higher mortality. Certainly many individuals from a number of species seem to grow from fragments rather than sexually originated ancestrulae (Winston 1983, Barnes & Lehanen 2001). Though not noted in bryozoan populations, many soft sediment benthos seem to bear evidence of losing cohorts (presumably through ice scour). Bivalve populations, for example, at several localities have been found to be strongly bimodal (Peck & Bulloough 1993, Urban & Mercuri 1998). Non unimodal population structures have rarely been reported elsewhere in the world (except in fished populations). So high latitude environments have a fairly characteristic mortality signal, caused by ice scour, and with the exception of multimodality, bryozoans are a useful indicator taxon of polar mortality patterns. The combination of the high mortality described and slow tempo of colonization and growth might suggest little role for competition being either frequent or important in structuring communities but this is probably only true in very shallow water and the littoral.

4 FIGHTING ON THE ROCKS

Competition is a widely studied phenomenon in biology and is regularly invoked to be causal or influential of major evolutionary and ecological trends. Given the level of importance attached to competition in time and space and the intensity in which it is studied in tropical and temperate environments the near absence of polar studies seems remarkable. In part this may have been because in the marine environment much of the work concerning competition has been carried out in the intertidal zone, which is of course mostly denuded at polar latitudes. Yet from the subtidal zone to shelf depths, it has been known for some time that rich and abundant sessile biota occurred (see Dayton 1990, Amtz et al. 1994, Brey et al. 1994). Even in shallow water of 6-12 m depth competition is common and on boulders of just 100+ cm² surface area almost certain in either polar region (Fig. 2). The potential for intra- and interspecific competition would seem to be high: amongst bryozoans alone many species occur in close proximity in Arctic (Dick & Ross 1988, Gulliksen et al. 1999, Barnes & Kuklinks 2003) and Antarctic localities (Hayward 1995, Bames et al. 1996, Brey et al. 2003) and pioneer species can be highly dense (Bader 2001, Bames & Clarke 1998, Brey et al. 1999a, b). So competition may be common in polar communities, as it is elsewhere at lower latitudes, but is it important? I argue it is important to investigate competition at polar latitudes for several reasons: (1) the high disturbance regime typical of glaciated...
Figure 2. Probability of competition on high latitude boulders with boulder area and locality. Spitsbergen data are from Barnes & Kuklinski (2003), that for other localities is author’s unpublished data. Curves are logistic regressions but fitted solely for ease of interpretation of pattern.

areas has resulted in poor preservation conditions so we know little about competition in the past relative to at other regions, (2) latitude is strongly implicated as a major (often cited as the most important) factor influencing species diversity and reproductive patterns, so is this the case with competition, (3) interpretation of patterns over geological time can only have real context if trends in space are reasonably well understood, (4) as on land polar environments have advantages for interpretation of ecological experiments due to the greater simplicity of systems, and (5) differential levels of disturbance (by ice scour) across small spatial scales provide a ‘natural experiment’ to compare the effects of competition with different intensities of disturbance.

There are few, probably no, taxa more suited to the investigation of spatial competition in the sea than bryozoans. Unlike many taxa, bryozoans are ubiquitous in shallow water as well as being abundant and speciose from tropics to poles (McKinney & Jackson 1991). In addition competitive interactions occur relatively slowly so encounters between two or more competitors can easily be followed in time and even preserve well giving ‘snapshots in time’ of fossil competition. In the last few decades there has been a number of studies of competition in tropical (Jackson & Buss 1975, Jackson 1979) and temperate (Lopez Gappa 1989, Turner & Todd 1994) bryozoan communities as well as many of general encrusting communities of which bryozoans were a major part (Russ 1982, Sebens 1986). Recently spatial interactions have now been measured in both Arctic and Antarctic encrusting communities (see Barnes 2002a, Barnes & Kuklinski 2003). Such studies have revealed intraspecific competition to be very common, mostly resulting in tied outcomes, but also that many species are involved in competition which tends to be structured in a hierarchically hierarchical manner. So to address the first of the reasons suggested for the importance of study high latitude competition: we can not know that this was also the way it has been in the past in the polar regions and glaciated coastline, but the fact that it is similar from place to place within polar regions (Barnes 2002a) and between the polar regions would suggest this is likely (Barnes & Kuklinski 2003). The influence of latitude (second suggested reason for studying polar competition) does indeed seem to be highly correlated with many aspects and outcomes of spatial competition. Competitive interactions in tropical bryozoan assemblages involve many reversals in outcome between each competitor pairing and high ranking competitors can be beaten by some low ranking ones (see Jackson & Buss 1975, Jackson 1979). In striking contrast competition in high latitude bryozoan communities is organized in a highly hierarchical manner, that is with a fairly rigid pecking order in which one species is overgrown by nearly all others on nearly all meetings. These weakest (pioneer) species are typically *Harmeria scultulata* Busk, 1855 in the Arctic (Fig. 5 A) and *Fenestrulina rugula* Hayward & Ryland, 1990 (Fig. 5 B) in the Antarctic. At the opposite end of the spectrum there are competitive dominants, which overgrow nearly all other species or nearly all meetings. These strongest species are typically *Tegella arctica* d’Orbigny, 1850 in the Arctic (Fig. 5 C) and *Bania erecta* Waters, 1904 (Fig. 5 D) in the Antarctic. Unlike many aspects of ecology for which latitude is sought to be a strong explanatory factor, such as species richness, the described relationship with competitive outcomes is demonstrable in both hemispheres (Barnes 2002a). As well as how hierarchical competition becomes, latitude has also been found to have a strong relationship with the proportion of competition which is intraspecific (cf interspecific), the proportion of tied (cf won/lost) outcomes of competition and the competitive ranking of the most abundant species (Fig. 3). With increasing latitude the ranking (competitive performance) of the most common species decreases from typically good competitors at low latitudes to the poorest ones in the polar regions.

Geographic variability of competition has important implications in the context of interpreting the fossil
record and future climate change. Palaeontologists and ecologists have long sought to explain the success of some clades and the decline of others. The post-Palaeozoic rise of the cheilostomes and bivalve molluscs has been contrasted with the dissimilar performance of ‘ecologically similar’ taxa the cyclostomes and brachiopods respectively (Gould & Calloway 1980, McKinney et al. 1998). Communities on hard substrata are ideal for the study of macroevolutionary trends in time and space particularly because many features of assemblages, amongst them competition, preserve well in fossils (Taylor & Wilson 2003). The review by Taylor & Wilson (2003) provides the most comprehensive review on hard substratum community development over geological time and processes that influence them. In the case of the two bryozoan clades, these at least definitely compete for space, regularly and have done for millions of years though whether this has been cause of the differential success remains to be shown. McKinney (1995) found that over the last 100 million years cheilostomes have been superior competitors, overgrowing cyclostomes in 66% of encounters. Although he found that cheilostomes were superior, they were consistently superior - that is there had been no escalation in performance differential. This historical data had all come from assemblages in shallow warm seas and analysis of modern interactions between cheilostomes and cyclostomes, in similar environments, revealed similar relative performances of the two clades (Fig. 4). Data from modern high latitude assemblages, however, reveals very different relative performances of the two clades and, as importantly, much greater variability. Such a finding puts the historical performance differential in a very different perspective. Being beaten consistently in some environments is survivable if, in other environments, cyclostomes are not inferior spatial competitors. This is clearly an example of how understanding spatial patterns can aid interpretation of temporal patterns and also perhaps one of high latitude variability being a refuge. What is missing from the picture is what happened at high latitudes in the past when it has been cold and had floating ice - the fossil record is poor because ice smashes things up reducing chances of preservation. Future (predicted) climate change has a different but important context to the outcomes of competition at high latitudes. The arctic ice and snow are disappearing - fast and ice shelves are collapsing in western Antarctica (Quadfasel et al. 1991, King & Harangozo 1998). If Scotia Arc lake temperatures continue rising at the rate they have been in the last decade (Quayle et al. 2002) they will not be freezing soon. Change in SSTs is harder to predict because of buffering, but if seas do warm by 2°C as predicted (Murphy & Mitchell 1995), the change in polar benthos will probably be massive. Polar ectotherms are extremely stenothermal (Peck 1998, 2002, Pörtner 2002a, b), such a rise will probably not kill many faunal elements but it may severely or totally reduce their functional capability to feed, escape predators or sedimentation. As competition is highly hierarchically structured in polar seas, a succession of species overgrowth could ultimately result in just one or two species monopolizing space: Tegella arctica (Fig. 5 C) or Tegella retraversa Kluge, 1952 in the Arctic and Beania erecta (Fig. 5 D) in the Antarctic. This does not happen, but only because of the severe disturbance regime of wave action, ice scour and anchor ice (Less competitive bryozoans may be able to survive overgrowth for limited periods (Todd & Turner 1988) but this is of no consequence.

**Figure 3.** Competitive rank of the most abundant species in assemblages with latitude and hemisphere. Points represents the competitive rank of the most abundant species in assemblages from different localities. The fit and significance of the regression line are indicated on the plot as are northern vs southern data. Data are from Barnes & Kuklinksi (2003) and references therein.

**Figure 4.** Success of cheilostomes in competition with cyclostomes for space with time and latitude. Y axis is proportion of wins by cheilostomes, each point represents a different assemblage. The fossil data is from McKinney (1995) and the low and high latitude data from living assemblages is from Barnes & Dick (2000) and references therein.
when the overgrower is removed, so is the overgrown colony as the rock is scraped clean by ice-scour). With the disappearance of ice from northern seas, which is a distinct possibility in our lifetimes will come a profound change in the Arctic benthos - a prediction based on existing competition data is that carpets of *Tegella* sp and colonial ascidians could monopolise encrusting faunas. In the southern polar region the Scotia Arc and Antarctic Peninsula coastal looks like it might face the same monoculture future.

5 CONCLUSIONS

Recent studies of hard substrate communities are revealing powerful insights into large scale trends in time and space (Taylor & Wilson 2003). Ecological data and concepts in high latitude communities, albeit in the last few decades, are proving to have a major role in the interpretation of these. High latitude communities experience some of the highest levels of constancy in environmental conditions, e.g. temperature and salinity. They are subject to the calmest and greatest water clarity during the polar winter but conversely the most extreme disturbance (from ice scour) and intense summer blooms. In some senses the environment for the benthos is so predictable, e.g. light climate and SSTs, in others so unpredictable, e.g. where ice will scour next. They are truly more than just season and cold environments but the most extreme and variable ecosystems. Our view of the processes that shape the benthic species and kill them is increasing rapidly as is the climate that surrounds them. Studies of bryozoans, as much as of any taxon, offer strong possibilities to interpret the past of polar regions, the relationship of high to low latitudes and how benthos may respond to an environment that is changing so fast.

DEDICATION

This paper is dedicated to the late Kirsty Brown, a bright young scientist with an inspirational attitude with tremendous *joie de vivre* who was at the cutting edge quantifying iceberg scour in time and intensity.
and its direct effect on polar benthic communities. Bryozoology and Science is a poorer place without her.

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Late Miocene Bryozoa from the Guadalquivir Basin (SW Spain): eastern Atlantic and western Mediterranean environment and biogeography

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ABSTRACT: Even 30 years after the discovery of the latest Miocene desiccation of the Mediterranean Sea, the circumstances of the Messinian Salinity Crisis (MSC) are a subject of much debate. New cheilostome bryozoan data from the eastern Atlantic Guadalquivir Basin (south-western Spain), which remained unaffected by the MSC, allow us to address questions concerning the late Tortonian biogeography in concert with environmental conditions before onset of the crisis. The great similarity between this eastern Atlantic and the Mediterranean faunas suggests that, other than today, surface water exchange occurred in both directions, and that environmental conditions of the Guadalquivir Basin were sufficiently similar for Mediterranean species to survive the MSC. However, comparison of environmentally controlled autozooid morphometry of eastern Atlantic species with nearly coeval Mediterranean representatives reveals generally smaller autozooid dimensions in Atlantic specimens, thus indicating a certain dissimilarity in physical parameters between these regions.

1 INTRODUCTION

The isolation and desiccation of the Mediterranean Sea during the latest Miocene, an episode known as the Messinian Salinity Crisis (MSC), represents one of the most dramatic oceanographic events in the Neogene. Collision of the African and European plates induced vertical movements of the southern Spanish and northern Moroccan regions and resulted in a progressive shallowing and closure of the Mediterranean-Atlantic connections, the Betic and Rifian corridors, respectively (e.g. Esteban et al. 1996, Hodell et al. 2001, Kouwenhoven et al. 2003). Prior to and during the main phase of desiccation in the late Messinian (5.96 to 5.33 Ma) evaporites up to 3 km in thickness were deposited in the main Mediterranean basins, followed by brackish sediments of the Lago Mare facies (Hsiu et al. 1973, Krijgsman et al. 1999). Re-flooding was most likely initiated by the opening of Gibraltar Strait and Mediterranean-wide normal marine conditions were re-established by the earliest Pliocene (Blanc 2000, Spezzaferri et al. 1998). The event has been thoroughly studied throughout the last three decades, yet many difficulties remain in reconstructing palaeoceanographic conditions of the connecting gateways, late Neogene biogeography of the eastern Atlantic and Mediterranean region, or the impact of the MSC on Mediterranean biota.

Owing to their great diversity and abundance in Neogene sediments, bryozoans have already played an important role in deciphering evolutionary and biogeographical consequences of the crisis to Mediterranean benthic faunas (Moissette & Pouyet 1987, Taylor 2000). Well over 400 Neogene to Recent species are described and numerous monographs have been published especially on the Western Mediterranean fossil fauna (e.g. Moissette 1988, El Hajjaji 1992, Pouyet & Moissette 1992, Haddadi-Hamdane 1996, Pouyet 2000). However, few data exist from the immediate eastern Atlantic side of the corridors (Reguant 1993, Pouyet et al. 1999, Sefian et al. 1999) despite the fact that this region is crucial to the understanding of environmental conditions and biogeographic patterns before, during and after the MSC. In past attempts to
explain the paradox of a desiccated Mediterranean Sea and relatively low late Messinian extinction rates in several benthic invertebrate groups the authors proposed either the existence of an extra-Mediterranean refuge (Ruggieri & Sprovieri 1976, Sabelli & Taviani 1984, Harmelin 1992), or the persistence of marine conditions within the Mediterranean or peripheral basins during the crisis (Moissette & Pouyet 1987, Saint-Martin et al. 2000, Goubert et al. 2001, Néraudeau et al. 2001).

In order to shed light on this issue, and to ascertain Mediterranean/Atlantic current systems and palaeoenvironmental conditions, we collected bryozoan-rich samples from the Guadalquivir Basin in Andalucía, southern Spain (Figure 1), which was connected to both the eastern Atlantic and the Mediterranean Sea during late Tortonian time. 51 cheilostome species from the Calcarenita de Niebla Formation were identified which, together with other pre-MSC bryozoan data available from the Moroccan Atlantic side (Sefian et al. 1999), form the basis of our investigations.

2 GEOLOGICAL SETTING

The Guadalquivir Basin in south-western Spain is the northern foreland basin of the Betic Cordilleras (Sanz de Galdeano 1990). It displays a roughly triangular shape, tapering towards the NE and opening towards the Atlantic (Figure 1). The late Tortonian Calcarenita de Niebla Formation (Clauss Klamp & González Regalado 1993, Civis et al. 1994, Baceta & Pendon 1999) of the north-western margin of the Guadalquivir Basin proved to comprise the best preserved and most abundant bryozoan faunas.

This formation consists of calcarenites and calcirudites with varying abundances of fine grained matrix, coralline algae, bryozoans, bivalves (large pectinids and ostreids), echinoids (Clypeaster) and large benthic foraminifera (Heterostegina). The fauna described here was extracted from samples taken from the friable lower part of the Niebla Calcarenite which is especially abundant in coralline algae (similar to the Crustose Pavement facies [after Bosence 1983]) and has a high content of fine grained matrix, preventing excessive cementation of the biogenic grains. The limestone was deposited on the inner part of a low gradient homoclinal ramp (Baceta & Pendon 1999) and, according to Sierro et al. (1990b), represents a part of the transgressive systems tract of the global sea level cycle 3.2 of Haq et al. (1987). Lateral facies variation is due to the local presence of autochthonous coralline algal and bryozoan patches within areas of bioclastic accumulation (Baceta & Pendon...
1999). Depth of deposition is estimated to have been less than 50 m and the faunal composition indicates a warm-temperate to subtropical environment. The presence of *Neogloboquadrina humerosa* (Takayanagi & Saito 1962) in the lowermost part of the Niebla Calcarenite suggests a late Tortonian age (Sierro et al. 1990a).

The Neogene Guadalquivir Basin opened and deepened towards the eastern Atlantic and was additionally, during late Tortonian times, connected with the Mediterranean Sea via the Granada Basin (Esteban et al. 1996) in its south-central part (Figure 2), and via the Guadix Basin in the north-eastern region (Soria et al. 1999). The knowledge of late Neogene geography and morphology of the Atlantic/Mediterranean connections has greatly increased and thus inevitably changed the assumptions underlying the attempt to reconstruct the regional water exchange by Benson et al. (1991). However, no improved oceanographic model nor field data exist to test their hypothesis that during the late Tortonian influx of Atlantic surface water and outflow of deeper Mediterranean water occurred through the Rifian Straits, whereas Mediterranean surface water passed through the Spanish gateways into the Atlantic Guadalquivir Basin. Understanding the Atlantic/Mediterranean water exchange system is of particular importance when discerning the migration of species and, as a result, establishing biogeographical patterns.

### 3 RESULTS

Although the investigation of the Niebla Calcarenite bryozoan fauna has not yet been completed, 51 cheilostome species have already been identified and their morphological characters measured. The preliminary results presented here are based upon the presence/absence of species in different regions, their variation in colonial morphology, and a morphometric analysis. A more detailed description of the sampling location, methods, bryozoan taxonomy and morphometry, and results will be published elsewhere.

#### 3.1 Palaeobiogeography

Based upon known (palaeo)geographic occurrences, the identified late Tortonian bryozoan species can be grouped into cosmopolitan, eastern Atlantic/Mediterranean, and Mediterranean endemics. Additionally, the genus *Emballotheca*, represented by *E. longidens* (Cipolla, 1921) (Figure 3 A), is the only taxon with an Indo-Pacific affinity. Cosmopolitan species [among others: *Chorizopora brongniartii* (Audouin, 1826), *Escharina dutertrei* (Audouin, 1826), *Microporella ciliata* (Pallas, 1766)], which today occur around the world but are generally absent from polar waters, make up about 16% of the total. Taxa known to occur in both the eastern Atlantic and the Mediterranean Sea predominate the fauna (45%) and comprise species like *Calloporina decorata* (Reuss, 1848), *Schizoporella longirostris* Hincks, 1886, and *Figularia figularis* (Johnston, 1847). A large part of the fauna (39%) is composed of fossil and extant species rarely or never found outside the Mediterranean Sea and thus are considered to be endemic, such as *Steginoporella cucullata* (Reuss, 1848), *Mollia circumcincta* (Heller, 1867) and *Myriapora truncata* (Pallas, 1766).

#### 3.2 Palaeoenvironment

Most of the species identified (57%) are extant, enabling us to rank them according to their Recent distribution patterns. The Niebla fauna is, species-and specimen-wise, mainly composed of taxa that today occur in warm-temperate to subtropical environments [e.g. *Mollia patellaria* (Moll, 1816), *Schizotheca serratimargo* (Hincks, 1886)]. In addition, taxa of both tropical (*Emballotheca, Steginoporella*) and cooler water affinities (*Escharella octodentata* (Hincks, 1880), *Escharoides coccinea* (Abildgaard, 1806)) are present in the samples. All of the Recent species of the Niebla fauna are characteristic of an inner- to mid-shelf environment, such as the stenobathic species *Hagiosynodos latus* (Busk, 1856) and *Onychocella angulosa* (Reuss, 1848), whereas species indicative of outer shelf environments are absent. Specimen-wise, the assemblage is dominated by fragments of *Schizotheca serratimargo* followed by *Rhynchozoon monoceros* (Reuss, 1848), *Myriapora truncata*, *Buffonellodes incisa* (Reuss, 1874), *Hippoporella pauper* (Reuss, 1874), as well as poorly preserved and small (usually < 1 cm in
diameter) celleporiform colonies represented by sev-
eral species. Another indirect sign of shallow-water
conditions is displayed by the faunal predominance of
membraniporiform species (78%) over all other growth
forms (adeoniform 8%, celleporiform 4%, vinculari-
iform 4%, cellariiform 4%, reteporiform 2%).

3.3 Variations in bryozoan zooidal and zoarial
morphology
Following the approach of Jackson & Herrera Cubilla
(2000), who investigated differences in zooid size
from opposite sides of the Isthmus of Panama, an esti-
mation of the surface area (length times width of the
mean values) was calculated for each identified
species from the Niebla Calcarenite. Only species of
which the dimensions of at least ten autozooids could
be measured were included in this study. We then cal-
culated the zooid area for the same species occurring
in the late Tortonian-early Messinian of the western
Mediterranean using data published in Moissette
(1988) and El Hajjaji (1992) and related these values
to the Guadalquivir Basin specimens (Table 1). Given
that the species are correctly identified, and despite a
great inherent variability in intracolonial zooid length
and width as well as significant intra-Mediterranean
differences in zooid area (e.g. Hagiosynodos latus,
see discussion), zooidal surface area is, in most
species, notably larger in the Mediterranean Sea than
in the eastern Atlantic. For example, Hagiosynodos
latus (+111%), Hippoporella pauper (+94%) or
Aplousina bobiesi (+74%, see Figure 3B) display
much larger zooid surface areas on the Mediterranean
side of the connecting corridors, whereas Watersipora

Figure 3.  (A) Emballotheca longidens (Cipolla, 1921), late Tortonian, Guadalquivir Basin. (B) Aplousina bobiesi (David & Pouyet, 1974), late Tortonian, Guadalquivir Basin. (C) Variation of branch diameter in Myriapora truncata (Pallas, 1766), left: late Tortonian, Agua Amarga Basin, SE Spain; middle: Recent, collected onshore Cabo de Gata, SE Spain; right: late Tortonian, Guadalquivir Basin.
Table 1. Late Tortonian Guadalquivir Basin (eastern Atlantic) mean autozooid surface area (SA, in mm\(^2\)) for 33 cheilostome species in comparison with representatives from the Mediterranean late Tortonian/early Messinian Morocco (data from El Hajjaji 1992) and early Messinian Algeria (Moissette 1988). Proportional differences are given in positive (larger surface area in relation to Guadalquivir specimens) and negative values (smaller surface area in relation to Guadalquivir specimens).

<table>
<thead>
<tr>
<th>Species</th>
<th>Guadalquivir Basin</th>
<th>Morocco</th>
<th>Difference (%)</th>
<th>Algeria</th>
<th>Difference (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aplousina bobiesi</td>
<td>0.231</td>
<td>0.396</td>
<td>+71</td>
<td>0.403</td>
<td>+74</td>
</tr>
<tr>
<td>Bufonellaria divergens</td>
<td>0.131</td>
<td>0.146</td>
<td>+11</td>
<td>0.145</td>
<td>+11</td>
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<tr>
<td>Bufonellodes incisa</td>
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<td>0.136</td>
<td>+42</td>
<td>0.090</td>
<td>-6</td>
</tr>
<tr>
<td>Calliopora decorata</td>
<td>0.288</td>
<td>0.370</td>
<td>+28</td>
<td>0.354</td>
<td>+23</td>
</tr>
<tr>
<td>Cheiloropora campanulata</td>
<td>0.207</td>
<td>0.302</td>
<td>+46</td>
<td>0.297</td>
<td>+43</td>
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<tr>
<td>Chorizopora brongniartii</td>
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<td>0.082</td>
<td>-2</td>
<td>0.112</td>
<td>+33</td>
</tr>
<tr>
<td>Ellisina gutierii</td>
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<td>.</td>
<td>0.088</td>
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<tr>
<td>Emballotheca longidens</td>
<td>0.403</td>
<td>0.308</td>
<td>-24</td>
<td>0.311</td>
<td>-23</td>
</tr>
<tr>
<td>Escharella grossa</td>
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<td>.</td>
<td>.</td>
<td>0.480</td>
<td>+44</td>
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<tr>
<td>Escharella peachi</td>
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<td>.</td>
<td>0.194</td>
<td>+17</td>
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<tr>
<td>Escharella reussiana</td>
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<td>0.238</td>
<td>-1</td>
<td>0.270</td>
<td>+13</td>
</tr>
<tr>
<td>Escharina dutertrei</td>
<td>0.239</td>
<td>0.227</td>
<td>-5</td>
<td>0.289</td>
<td>+21</td>
</tr>
<tr>
<td>Escharoides coccinea</td>
<td>0.192</td>
<td>0.201</td>
<td>+5</td>
<td>0.231</td>
<td>+20</td>
</tr>
<tr>
<td>Escharoides megalota</td>
<td>0.372</td>
<td>0.409</td>
<td>+10</td>
<td>0.400</td>
<td>+8</td>
</tr>
<tr>
<td>Figularia figuralis</td>
<td>0.242</td>
<td>0.402</td>
<td>+66</td>
<td>0.286</td>
<td>+18</td>
</tr>
<tr>
<td>Gephyrotes fortunensis</td>
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<td>.</td>
<td>.</td>
<td>0.201</td>
<td>-1</td>
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<tr>
<td>Hagiosynodos latus</td>
<td>0.107</td>
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<td>+111</td>
<td>0.123</td>
<td>+15</td>
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<tr>
<td>Herentia monenati</td>
<td>0.310</td>
<td>0.427</td>
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<td>Hippoleaurerifa sedgwicki</td>
<td>0.447</td>
<td>0.479</td>
<td>+7</td>
<td>0.558</td>
<td>+25</td>
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<tr>
<td>Hippoporella pauper</td>
<td>0.110</td>
<td>0.213</td>
<td>+94</td>
<td>0.170</td>
<td>+55</td>
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<tr>
<td>Microporella ciliata</td>
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<td>0.192</td>
<td>-20</td>
<td>0.288</td>
<td>+20</td>
</tr>
<tr>
<td>Microporella coronata</td>
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<td>0.273</td>
<td>+31</td>
<td>0.279</td>
<td>+34</td>
</tr>
<tr>
<td>Myriapora truncata</td>
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<td>0.394</td>
<td>+9</td>
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<tr>
<td>Onychocella angulosila</td>
<td>0.176</td>
<td>0.168</td>
<td>-5</td>
<td>0.178</td>
<td>+1</td>
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<tr>
<td>Poricella bugei</td>
<td>0.193</td>
<td>0.222</td>
<td>+15</td>
<td>0.207</td>
<td>+7</td>
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<tr>
<td>Prenantia cheilostoma</td>
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<td>0.416</td>
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<td>.</td>
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<tr>
<td>Rhynchozoon monoceros</td>
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<td>0.124</td>
<td>+16</td>
<td>0.072</td>
<td>-33</td>
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<tr>
<td>Schizobrachiella sanguinea</td>
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<td>0.413</td>
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<td>-20</td>
</tr>
<tr>
<td>Schizotheca serratimargo</td>
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<td>0.106</td>
<td>-20</td>
<td>0.146</td>
<td>+10</td>
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<tr>
<td>Smittina messiniensis</td>
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<td>0.131</td>
<td>+77</td>
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<tr>
<td>Stegnoporella cucullata</td>
<td>0.553</td>
<td>0.673</td>
<td>+22</td>
<td>0.747</td>
<td>+35</td>
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<tr>
<td>Trypostega rugulosa</td>
<td>0.087</td>
<td>0.135</td>
<td>+55</td>
<td>.</td>
<td>.</td>
</tr>
<tr>
<td>Watersipora goniostoma</td>
<td>0.410</td>
<td>0.244</td>
<td>-40</td>
<td>0.416</td>
<td>+1</td>
</tr>
</tbody>
</table>

goniostoma (Reuss, 1848) (—40%), Rhynchozoon monoceros (—33%) and Emballotheca longidens (—24%) are some of the few species producing substantially larger surface areas on the Atlantic side (Table 1).

In addition, a conspicuous difference in zoarial morphology between the Niebla Calcarenite fauna and the Mediterranean Sea was detected in Myriapora truncata. The branch diameter of this erect robust species varies considerably not only in the two late Neogene regions we investigated, but also differs from the one measured in Recent specimens (Figure 3C). In the late Tortonian Niebla Calcarenite specimens the branch diameter varies between 2.0 and 3.4 mm (mean: 2.65 mm, N: 30, SD: 0.335) whereas branches of nearly coeval Mediterranean

4 DISCUSSION
4.1 Palaeobiogeography
Although environmental conditions during the main desiccation event were, due to evaporation of the deep
basins and the following brackish episode, evidently unsuited for marine benthic organisms of the Mediterranean Sea to survive the MSC, many of the assumed endemic taxa are found in post-MSC deposits throughout the Mediterranean. For instance, Moissette & Pouyet (1987) estimated that 17% of the Mediterranean endemic Cheilostomata survived the crisis. These observations led some authors, working on different groups of organisms, to infer that either the main Mediterranean Basin or some peripheral basins were always in contact with the eastern Atlantic during the MSC (Moissette & Pouyet 1987, Saint-Martin et al. 2000, Goubert et al. 2001, Néraudeau et al. 2001). A great obstacle hampering the effort to obtain a consensus in this regard is caused by the scantiness of works on marine faunas from the immediate surroundings of the Mediterranean Sea before or during the MSC, i.e. from the eastern Atlantic SW Spanish or NW Moroccan coasts. Combining the available data on eastern Atlantic cheilostome bryozoans from the study of Sefian et al. (1999) and our own, 86 of the 89 species from this region are found in the Mediterranean basins, some of which have never been reported from outside the Mediterranean before. This faunal similarity to the Mediterranean, which is also evident in bivalve distribution (Lauriat-Rage et al. 1999), thus supports the suggestion that the eastern Atlantic region might have served as a refuge for marine taxa to survive the MSC (Ruggieri & Sprovieri 1976, Sabelli & Taviani 1984, Harmelin 1992).

Furthermore, the study of marine organisms from the Atlantic side of the corridors enables us to address questions concerning late Tortonian geographic dispersal of species in concert with the prevailing current system. Today, a westward migration of shallow water Mediterranean bryozoans is hindered by a constant inflow of surface water from the Atlantic through Gibraltar Strait (Harmelin & d'Hondt 1993). Outflowing intermediate water is formed in too distant regions (e.g. Gulf of Lion, Adriatic Sea) for non-planktotrophic larvae of shallow water bryozoan species to survive this lengthy transport and to reach the Atlantic. Furthermore, a physiological barrier is produced by the hydrological characteristics of the intermediate water (high oligotrophy, warm temperature) which prevents bryozoans from living in these depths (Harmelin & d'Hondt 1993). A one-way biogeographic boundary is thus created by the current regime, producing the Mediterranean province of the Atlantic-Mediterranean subregion (López de la Cuadra & García-Gómez 1994). In contrast to the modern situation, the occurrence of a great number of shallow water Mediterranean species on the eastern Atlantic side of the corridors in late Tortonian times implies the presence of a westerly surface water current flowing towards the Atlantic and thus blurring the biogeographic boundary in this time interval. Investigating ostracodes and foraminifers of the Rifian Corridor, Benson et al. (1991) suggested that surface water influx was through the Rifian Corridor whereas the Spanish gateways were assumed to have served as outflow. Although the biogeographic reconstructions of the southern Iberian region, and thus the oceanographic mechanism producing the current pattern modelled by Benson et al. (1991), have significantly changed since then (see Esteban et al. 1996), this scenario of surface water exchange is supported by our observations. The most likely southern Spanish locations for the connecting straits are the Granada and Guadix Basins (Figure 2); however, a detailed reconstruction of these gateways, especially that of the northern margin of the Granada Basin, is impeded by the scarcity of outcrops due to uplift of the Betic Cordillera. The Guadix Basin was connected to the Guadalquivir Basin and displays marine sediments until the latest Tortonian when the region was uplifted (Soria et al. 1999). Evidence for current direction has not been found for either of the late Tortonian connections; yet one such gateway, the Spanish Guadalhorce Corridor, in which sedimentary structures are preserved that indicate a westerly surface water flow, has recently been established for the early Messinian by Martin et al. (2001).

4.2 Palaeoenvironment

The large proportion of extant species occurring in the Niebla Calcarenite provides the means to apply an actualistic approach in order to reconstruct late Tortonian environmental conditions in the northwestern Guadalquivir Basin. The presence of several stenothermic taxa suggests conditions to be sufficient for a range of tropical to cool water species to thrive in the eastern Atlantic. The majority of the extant Niebla bryozoan species live in warm temperate to subtropical waters, a temperature estimate supported by the abundant occurrence of coralline red algae and the large foraminifera Heterostegina as well as the presence of Clypeaster. Whereas reefs are not reported from the eastern Atlantic southern Spanish and northern Moroccan coast, faunas of similar composition are found in distal positions of coeval Mediterranean reef complexes (Esteban et al. 1996). The absence of reefs in the Guadalquivir Basin might be explained by a high nutrient supply and cooler temperatures: although the main diatomite depositional episodes in the Guadalquivir Basin were over by the late Tortonian (Bustillo & López García 1997), the region might have been influenced by highly productive and slightly cooler water due to the mixing of Mediterranean outflow with Atlantic water, thus preventing growth of reefs and maintaining a diverse bryozoan fauna. Similarly, late Tortonian benthic and planktic foraminiferal assemblages from the NW
Moroccan coast record subtropical conditions and eutrophic water masses (Barbiéri 1998).

Judged by the depth distribution patterns of Recent species occurring in the Niebla Calcarenite, a distal inner- to mid-shelf depth of origination of the coralline algal-rich sections can be estimated. The high amount of fine grained matrix and an excellent state of preservation of the bryozoan specimens, owing to little transport of the grains, are further indicators of deposition below fair weather wave base. Coralline algae and bryozoans are interpreted to have formed patches of build-ups on a low gradient ramp sheltered by the presence of small islands (Baceta & Pendón 1999). An analogy to this Guadalquivir Basin fauna might be the Messinian Crustose Pavement facies from Malta (Bosence & Pedley 1982, Bosence 1983) in which coralline algae form fragile frameworks of sheets and branches providing a large surface area for bryozoans to settle upon as well as small cryptic habitats. The faunal predominance of membraniporiform species in the Niebla Calcarenite might thus not be related to a high energy subtidal environment, as is usually inferred, but might rather be a consequence of the special (and spatial) conditions offered by the coralline algal framework.

4.3 Variations in bryozoan zooidal and zoarial morphology

Although environmental conditions in the late Tortonian Guadalquivir Basin were sufficiently similar for Mediterranean species to thrive, the observed variation in zooidal and zoarial morphology displayed by several species indicates the presence of substantial environmental differences between these regions. Earlier morphometric studies of bryozoan zooids have shown that there is a correlation between temperature and zooid size (see references in O’Dea & Jackson 2002) and the results have been used to derive proxies for seasonality or to contrast environmental regimes (O’Dea & Okamura 2000, Jackson & Herrera Cubilla 2000, O’Dea & Jackson 2002). However, previous studies mostly lack a comparison of intraspecific variability expressed in different natural environments.

Our results show that in most species the mean zooid area is larger in the Mediterranean Sea than in eastern Atlantic representatives (Table 1). If zooid size decreases with increasing temperature (Okamura & Bishop 1988) it follows that the late Tortonian eastern Atlantic Guadalquivir Basin experienced warmer temperatures than the western Mediterranean Sea. However, faunal evidence suggests that this was not the case: late Tortonian hermatypic coral reefs are absent from the eastern Atlantic shore while they flourish in western Mediterranean peripheral basins and the connecting gateways (Esteban et al. 1996); *Heterostegina* is the only large foraminifer to occur in greater abundance in the Niebla Calcarenite, a genus occurring in warm temperate (as in the easternmost Mediterranean Sea today) to tropical conditions (Betzler et al. 1997), whereas other tropical foraminifera are absent; and the bryozoan fauna there only includes the genera *Emballotheta* and *Steginoporella* as a truly tropical component.

It is thus questionable that temperature was the only or main parameter controlling bryozoan zooid size in these contrasting environments. However, other explanations seem equally contradictory: an increase in productivity in upwelling regions were responsible for zooid size deviation, the surface area should be larger in the Guadalquivir Basin due to the increase in nutrients and the related decrease in water temperature brought about by the upwelling of cooler water. If an increase in productivity occurred without a decrease in temperature (e.g. nutrient input from continental runoff) and turbidity would have prevented reefs from growth, the bryozoan fauna should be composed of many more tropical taxa. Salinity should not play a role either because the western Mediterranean Sea and eastern Atlantic experienced a much greater water exchange than today. Furthermore, the fact that there is a great range of zooid size differences in the data, and that several species do not show any reasonable variability in zooid size at all (Onychocella angulosa), as well as the display of a larger surface area in Guadalquivir Basin specimens, indicates that bryozoan species do not show a uniform response to environmental change.

It must be noted, however, that our bryozoan specimens only characterise the conditions of this very facies of the Niebla Calcarenite and are, of course, not representative of the eastern Atlantic as a whole. The same holds true for western Mediterranean bryozoans used for comparison, where it is not known from which environment (e.g. reefs vs. temperate-type platform carbonates) the measured specimens were taken by Moissette (1988) and El Hajjaji (1992). The measurement of specimens from different environments might thus explain the frequent occurrence of large intraspecific differences in zooid size within the Mediterranean as, for example, in *Hagiosynodos latus* (Table 1), as well as some of the differences between the eastern Atlantic and Mediterranean locations. The results, interpretations and generalisations must therefore be taken with caution.

Regarding zoarial variability, *Myriapora truncata* shows the most obvious aberration (Figure 3C). Considering the minimum and maximum value measured (0.2 mm and 0.66 mm, respectively), the branch diameter is subject to more than a threefold increase in some Mediterranean locations compared to those of the Niebla Calcarenite. Due to the indistinctness of zooidal margins, resulting in a great inaccuracy when
measuring zooid dimensions, the negligible difference in surface area between eastern Atlantic and Mediterranean specimens (Table 1) might be an artefact. Comparison of orifice surface area, with a mean value of 0.05 mm² in the Mediterranean (El Hajjaji 1992) and 0.034 mm² in the Guadalquivir Basin, suggests that variance of the branch diameter might in fact be related to zooid size. While large branch diameters are commonly observed in late Neogene *M. truncata* in the main Mediterranean basins, slender branches similar to those from the Guadalquivir Basin are also found at its northern limit of distribution, the Badenian Paratethys (N. Vávra, pers. comm.). As for zooid size differences observed between the Atlantic and Mediterranean sites discussed above, the reason for this change in branch thickness is unclear; however, it seems unlikely that it is caused by current energy. Figure 2 in Harmelin (1988) indicates that whereas branch segments between two bifurcation points become shorter with increasing current energy the branch diameter remains unaffected. The wide range of variation in branch thickness within faunas, and a notable change in diameter even within single branch fragments, suggests that these morphological variations are environmentally induced. If, by conducting experiments with Recent colonies, the causal relationship of environment and branch diameter could be accomplished, *M. truncata* might be used as an indicator of palaeoenvironmental and seasonal change. 

5 CONCLUSIONS

The fact that a great number of the Atlantic-influenced Guadalquivir Basin fauna are bryozoan species which were formerly thought to be endemic to the Mediterranean Sea implies that during the late Tortonian surface water transport occurred from east to west through either the Spanish gateways or the Rifian corridor. Since it has been suggested that an eastward flowing Atlantic surface water mass was present in the Rifian corridor (Benson et al. 1991), our data support the assumption that the westward outflow of Mediterranean surface water, carrying bryozoan larvae into the Guadalquivir Basin, occurred through the Spanish corridors (Figure 2). Due to the exchange of species, and in contrast to the modem situation, a clear distinction between a late Tortonian eastern Atlantic and western Mediterranean shallow water bioprovince can thus not be made.

The presence of numerous Mediterranean species on the Atlantic side of the corridors furthermore shows that, prior to the beginning of the MSC, environmental conditions in this region were sufficiently similar to the Mediterranean Sea. This paper thus presents evidence for the hypothesis that many of the Mediterranean ‘endemic’ species were able to survive the MSC in an extra-Mediterranean refuge provided by the eastern Atlantic Guadalquivir Basin and the NW African coastal area. The presence of a large number of extant species in the Niebla Calcarenite and in NW Morocco also suggests that the eastern Atlantic accommodated the founder population for the post-MSC resettlement of the Mediterranean Sea.

However, despite the uniform faunal composition, the development of generally smaller zooid and, in *Myriapora truncata*, zoarium dimensions in Guadalquivir Basin species in contrast to Mediterranean representatives demonstrates that late Tortonian environmental conditions were notably different in these regions. The qualitative and quantitative environmental disparity between the eastern Atlantic and western Mediterranean have yet to be investigated to be fully understood.

An important conclusion which can, nevertheless, be drawn from our morphometry data is that species classifications (partly) based upon zooid or zoarial dimensions should be avoided. An over twofold increase in surface area as in *Hippoporella pauper*, or a branch diameter that varies more than threefold as in *Myriapora truncata*, strongly suggests that morphological measurements should not be taken as an argument to delimit species. Further research should concentrate on contrasting zooidal and zoarial morphology in modern environments differing in physical parameters to test for environmental variance in bryozoans.

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REFERENCES


Bryozoa of the Romaine and Mingan Formations (Lower and Middle Ordovician) of the Mingan Islands, Quebec, Canada

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ABSTRACT: Biohermal and biostromal beds, and to a lesser extent interreefal strata, in the early Middle Ordovician (Chazyan or Llandeilian) Mingan Formation on the Mingan Islands along the north shore (Quebec) of the Gulf of St. Lawrence yield common bryozoans in frame-building and frame-strengthening roles. Overall, 13 species representing 5 orders or suborders were recovered and are described herein. Two species are new: the encrusting ceramoporoid Ceramoporella adamarhombica and the bifoliate ptilodictyoid Chazydictya rossae. In addition, a 14th species occurs very rarely in the Lower Ordovician Romaine Formation below.

TOM BOLTON
Thomas E. Bolton (1924-1997) (Nowlan & Smith 1998) was an early member of the International Bryozoology Association, and contributed a number of significant studies of Early Paleozoic Bryozoa in the course of his long and productive career with the Geological Survey of Canada, based in Ottawa. This present paper represents several years of cooperative collaboration, and will probably be Tom’s last bryozoan paper. He also published extensively on many other taxa, Ordovician and Silurian faunas, and stratigraphy all across Canada. He was honored by election to be President of the Paleontological Society (1991), receipt of the Billings Medal of the Geological Association of Canada, and by the great respect and admiration of those of us fortunate enough to have worked with him.

1 INTRODUCTION AND PURPOSE

Bryozoan-built reefs began in the Ordovician, but have been significant at relatively few times and places in their long geologic history (Cuffey 1977, 1985). It is therefore important to investigate their taxonomic composition and paleoecology wherever possible, and that is the purpose of this present paper.


2 MATERIALS AND METHODS

2.1 Localities and stratigraphy

The Mingan Islands are approximately 15 small carbonate-bedrock islands close to the north shore of the Gulf of St. Lawrence (Fig. 1). Over 100 m of Ordovician dolostone and limestone (Fig. 2) are exposed there, as illustrated by Desrochers & James (1989) and Twenhofel (1938). Two formations are recognized in the Mingan Islands Archipelago (Twenhofel 1938; Desrochers 1983a,b, 1985, 1988; Desrochers & James 1989). The Romaine Formation of Early Ordovician (late Canadian/Ibexian; British late Arenigian) age consists of 2-3 m of sandstone, unconformably lying on the Precambrian, succeeded by 58 m of dolostone. Locally, a thin (3-4 m) limestone
unit is present at the top of the Romaine. The overlying Mingan Formation of early Middle Ordovician (Chazyan; British Llandeilian) age consists of a 6m thick basal sandstone and shale unit, separated from the Romaine by a major paleokarst surface, succeeded by limestones, both lithographic and crystalline-granular (Desrochers & James, 1989; Rigby & Desrochers, 1995). A second major intra-paleokarst unconformity or ravinement and numerous local paleokarst surfaces are displayed within the limestone sequence (Shaw, 1980, p. 229; Desrochers & James, 1987, p. 185).

The Appendix at the end of this paper gives details of the exact collecting localities (also see Fig. 1). In the systematic descriptions and figure captions, only the locality number and its island name are given, to avoid unnecessary repetition.

2.2 Bioherms and biostromes

The upper limestones, the Mingan Formation, contain a number of reefs or build-ups, some mounded bioherms, others tabular biostromes (Desrochers & James 1989). These were constructed in part by bryozoans, accompanied by tabulate corals, lithistid sponges, and solenoporacean algae.

2.3 Bryozoan abundance and roles

Bryozoans are common in the biohermal/biostromal beds of the Mingan Formation and rarer in the
interbiohermal beds. Most are found either as composite intergrowths of Ceramoporella and Batostoma encrusting associated coral coralla, or as concentrations of ramose colonies of Batostoma, Jordanopora, Champlainopora and Lamottopora. These Bryozoa play frame-building (accompanied by other taxa) and frame-strengthening constructional roles here (Cuffey 1977). This is similar to their participation in the higher Chazyan reefs in the Lake Champlain district (Pitcher 1964, 1971), but represents a reduction from their dominating involvement in lower Chazyan reefs there (Cuffey 2002b, 2003; Mehrtens & Cuffey 2003).

2.4 The Mingan bryozoan fauna

Overall, we encountered 13 bryozoan species among 5 orders or suborders in reefal and interbiohermal beds within the Mingan Formation, as listed as follows:

TREPOSTOMIDA:
Batostoma chazyensis Ross, 1963
Batostoma adhaerens (Billings, 1859)
Jordanopora heroensis Ross, 1962
Champlainopora chazyensis (Ross, 1962)
Lamottopora duncanae Ross, 1963
Nicholsonella aff. acanthobscura McKinney, 1971*
Nicholsonella aff. irregularis Loeblich, 1942
Nicholsonella aff. parafondifera McKinney, 1971

CERAMOPORINA:
Ceramoporella adamarhombica sp. nov.

FISTULIPORINA:
Constellaria islensis Ross, 1963

FENESTRINA:
Phliloporina incepta (Hall, 1847)

PITILODICTYINA:
Chazydictya rossae sp. nov.
Eopachydictya aff. gregaria Ross, 1963
Stictopora cf. fenestrata Hall, 1847

A 14th species (marked * above) was found in the Romaine Formation below, noteworthy because so few undoubted Bryozoan have been found in Lower Ordovician strata on this continent.

Type and figured specimens are reposited with the Geological Survey of Canada (GSC).

Several additional bryozoan species, not encountered in the present study, were reported from Mingan strata by earlier workers:
Stenopora fibrosa (Goldfuss) by Billings (1859, p. 427); Phylloporina or Chasmatopora aspera (Hall) by Ulrich (1890, PI. 53, Figs. 4a-c) and Twenhofel (1938, p. 42), respectively; Chasmatopora sublaxa (Ulrich), Eridotrypa aedilis (Eichwald), and Favositella miganensis Twenhofel (Twenhofel 1938, p. 42-44, PI. 6, figs. 1, 2. PI. 7, fig. 2).

2.5 Biostratigraphic implications

The majority of the Mingan bryozoan species are based on material originally described from the type Chazyan beds of the Lake Champlain area of Vermont and New York state, many from the Crown Point and Valcour formations (Ross, 1984, Fig. 2). A mid to late Chazyan age is further supported by the associated brachiopods (Cooper, 1956, p. 14), ostracods (Copeland, 1989, personal communication), and condonts (Nowlan, 1981).

According to Ross (1964, Table 1; 1981) and Pitcher (1964), the bryozoan assemblages within the reefs of the Laval Formation in the Montreal, Quebec, region again establish a correlation with the Crown Point and Valcour formations (Crownian and Valcourian stages) of the Lake Champlain region. A similar though less diversified fauna (Batostoma chazyensis, B. lanensis, Champlainopora chazyensis and Ceramoporella adamarhombica) has been described from the Chazyan Laval Formation farther west in the Hawksbury region, southeastern Ontario (Bolton et al. 1991) that is correlated with the same beds. Champlainopora chazyensis has also been reported from the Middle Ordovician Whiterockian McLish and Tulip Creek formations, Simpson Group of Oklahoma (Key 1990, p. 701).

3 TAXONOMY AND SYSTEMATICS

Order TREPOSTOMIDA Ulrich, 1882
Genus Batostoma Ulrich, 1882

Type species: Monticulipora (Heterotrypa) implicatum Nicholson, 1881 (by monotypy).

Batostoma chazyensis Ross, 1963 Fig. 3 (1,2)
Batostoma adhaerens (Billings, 1859)
Jordanopora heroensis Ross, 1962
Champlainopora chazyensis (Ross, 1962)
Lamottopora duncanae Ross, 1963
Nicholsonella aff. acanthobscura McKinney, 1971*
Nicholsonella aff. irregularis Loeblich, 1942
Nicholsonella aff. parafondifera McKinney, 1971

Batostoma chazyensis Ross 1963d, p. 859, PI. 106, figs. 1-5, 7.
Batostoma chazyensis Ross 1963d, p. 863, PI. 106, figs 6, 8; PI. 107, figs. 8,10; PI. 108, fig. 9; PI. 109, figs 1-10; PI. 110, figs. 1-10.
Batostoma chazyensis Pitcher 1964, figs 12, 22, 24, 41,45.
Batostoma chazyensis Finks & Toomey 1969, PI. 1, fig. 2.
Batostoma chazyensis Pitcher 1971, fig. 3.
Batostoma chazyensis Toomey & Nitecki 1979, p. 161, fig. 79'.
Batostoma chazyensis Ross 1981, figs 1-8.
Batostoma chazyensis Bolton, Steele-Petrovich & Munro 1991, p. 7, PI. 1.1, figs 1-3, 9, 10; PI. 1.2, figs 1-3,10; PI. 1.3, figs. 1,2,11; PI. 1.4, fig. 1.
Batostoma chazyensis Cuffey et al. 2002a, p. 206, figs 3D-E.
Batostoma chazyensis Mehrtens & Cuffey 2003, fig. 6B.
Figure 3. Bryozoa, Mingan Formation. 1, 2: *Batostoma chazyensis* Ross. 1: Tangential section displaying both large and normal size acanthorods, latter indenting the zooecial walls; specimen GSC 94735, X32; GSC locality 96701, île Saint-Charles. 2: Longitudinal section (lower quarter) displaying abundant short acanthorods; GSC 94735a, X8; intergrown with *Ceramoporella adamarhombica* sp. nov., paratype, GSC 94756; same locality as Fig. 1; (also see Fig. 6(4)). 3-5, 7: *Batostoma adhaerens* (Billings). 3, 4: Tangential and longitudinal sections with few acanthorods present in the thin zoarium, holotype, GSC 1004, X16; Mingan Islands Archipelago (not further specified). 5, 7: Tangential section with abundant small acanthorods, zooecia well separated, and longitudinal section displaying abundant mesozooecia and long acanthorods in a thicker zoarium, GSC 94739, X16, GSC locality 96703, île Saint-Charles. 6, 8: *Jordanopora heroensis* Ross. Deep tangential section with thin walled polygonal zooecia and angular mesozooecia, X32, and longitudinal section displaying diaphragms throughout and well developed mesozooecia, x 16, GSC 94741, GSC locality 96726, île du Fantôme.
Description: Colonies are multilaminate, thin encrustations with individual zoaria from 0.8 to 2.2 mm thick, to ramose with short stubby branches.

In tangential section, zoecia are oval to petaloid, ranging from 0.25 to 0.35 mm in diameter, 4 to 6 in 2 mm length, 4 to 5 whole zoecia in 1 mm square, walls thin. Large angular mesozooecia are numerous. Round acanthorods are clear, normally 0.02 to 0.04 mm in diameter but in some zones 0.07 to 0.10 mm in diameter with 3 to 4 usually surrounding a zooecium.

In longitudinal section, acanthorods vary in length, and diaphragms are common, ranging from 2 in 0.5 mm along zoecial length to 5 in 0.5 mm along mesozooecial length, flat to inclined at times and curving upward into acanthorod walls.

Discussion: In her original studies of the Chazyan Bryozoa of the New York state - Vermont Lake Champlain region, Ross (1963d) erected two species of Batostoma, B. chazyensis and B. campensis, with only subtle morphological differences. The name B. chazyensis was applied to ramose colonies with cylindrical branches up to 5 mm in diameter, characterized by large acanthorods (0.03 to 0.05 mm in diameter) “located at the outer edge of the distinctly laminate walls, by thick laminated diaphragms regularly spaced in the zoecia and mesopores so as to form a boxlike structure in the peripheral region, and by large mesopores.” (Ross 1963d, p. 860). B. campensis included “ramose, laminate or incrusting colonies that may have cylindrical branches 3 to 10 mm in diameter” (Ross 1963d, p. 863) and displayed considerable variation in their microstructures; the “thickness of the zoecial walls in the peripheral region, the diameter of the acanthoporferences and indentation of the walls by the diaphragms may be conspicuous features of some colonies and not of others” (Ross 1963d, p. 864).

Considerable morphological variability and overlap seems apparent. Moreover, both species appear very similar in numerical morphological characters. Subsequently, most laminar colonies were assigned to B. chazyensis (Pitcher 1964, 1971, Finks & Toomey 1969, Toomey & Nitecki 1979, Ross 1981) rather than to B. campensis.

Our study of the Mingan Islands material, and also obfistomial samples from the Laval Formation near Hawkesbury, Ontario (Bolton et al. 1991), shows that considerable intergrading and similarity exists both within and between individual Batostoma colonies, whether ramose or laminate, and that variation within one species is, therefore, the most logical interpretation. Accordingly, B. chazyensis Ross and B. campensis Ross are herein considered synonymous, with the former name having page priority. The larger zoecia and abundant mesozooecia present within some areas of the Mingan Islands colonies are features which might be interpreted as more suggestive of B. campensis if considered in isolation, but not within a larger population context.

In addition, exact distributions of these two species seem confused. In her original studies, Ross (1963d, p. 857) reported B. chazyensis as the oldest species of Batostoma, but reported it only from localities assigned to the middle and upper Chazy Formation (Ross 1963d, Text-fig. 6). Finks & Toomey (1969) and Toomey & Nitecki (1979) illustrated laminar colonies of B. chazyensis from the lower Chazyan Day Point Formation, and Ross (1981, p. 10) listed the species from all three members of the Day Point Formation (i.e., basal and lower Chazy).

Batostoma campensis according to Ross (1963d, p. 857) was widely distributed in the upper part of the Chazy Formation (Valcourian - Pitcher 1964, p. 674, Fig. 43), and in the Crown Point bioherms (Ross 1981, p. 20). However, elsewhere, Ross (1964, p. 929, Fig. 2; 1984, p. 145, Fig. 2) recognized B. campensis throughout the Chazyan sequence.

By considering the different forms as belonging to one species, the variation in colonial characteristics appears to explain the variously stated ranges of the two forms originally denoted as B. chazyensis and B. campensis.

According to Pitcher (1964, p. 674, Fig. 43), B. chazyensis ranged throughout the lower (Dayan) and middle (Crownian) Chazyan, and specified (ibid., p. 672) that in B. chazyensis colonies from the younger Chazyan Crown Point (and Valcour) reefs, acanthoroids were more abundant than in conspecific forms in the older Chazyan Day Point reefs. Such variation of acanthorod abundance over time within a species can be interpreted as an example of nonstasis within species evolution, that is, a species does not necessarily remain precisely constant in morphology throughout its geologic lifespan.

Separation of B. chazyensis from B. lanensis Ross also is difficult, especially in encrusting representatives. The latter differs from B. chazyensis “in having a laminate growth form that has larger zoecial openings, larger acanthoporferences [0.01 to 0.07 mm compared to 0.03 to 0.05 mm], and narrower zoecial walls” (Ross 1963d, p. 861). One Mingan Formation specimen encrusting a sponge, hypotype GSC 94373, from GSC locality 95877 (Île du Fantôme), has abundant clear acanthoroids with slender, laminate walls, 0.04 to 0.08 mm in diameter, predominantly 0.06 mm, and zooecia 0.20 to 0.32 mm in diameter, characteristics seemingly more typical of B. lanensis than B. chazyensis when viewed individually, but again not in a population context.

Finally, Bork & Perry (1967, p. 1390) had suspicions that B. chazyensis and B. varium (Ulrich, 1893) from the Black Riveran Stage of Iowa and Minnesota also might be conspecific, but hesitated to place them in synonymy without further study.
**Material and occurrence:** Multilaminate colonies, GSC 94735 and 94735a, Mingan Formation; GSC locality 96701, biohermal beds, île Saint-Charles. GSC 94736; GSC locality 96716, île Quarry. GSC 94737; GSC locality 95877, île du Fantôme. Branching colony, GSC 94738; GSC locality 96732, île à Calculot.

Other encrusting multilaminate colonies were identified in biohermal beds at Desrochers’ (1985) localities 477B (île de la Fausse Passe), and branching forms at 399B (île du Fantôme) and 440D (île Saint-Charles); branching colonies were also found in interbiohermal beds at locality 398A (île du Fantôme).

### Stenopora adhaerens

**Description:** The supposed holotype (Twenhofel 1938) forms a 2.6 to 4.6 mm thick multilaminate colony encrusting a fragment of the colonial coral *Eofletcheria incerta* (Billings). In tangential section, zooecia are oval, rarely polygonal, thin walled, generally 0.20 mm in diameter (ranging from 0.16 to 0.22 mm), 6 to 7 in 2 mm length, 9 to 11 whole zooecia in 1 mm square. Round solid acanthorods are rare in the walls, 0.04 mm in diameter. Large angular mesozoecia are abundant. In longitudinal section, zooecia are inclined to attachment surface for some 0.10 mm before straightening, and diaphragms are abundant, complete, flat to slightly sagging, ranging from 10 to 13 in 1 mm along zooecial length, closely spaced in the mesozoecia and more widely spaced in mature regions of the zooecia.

Specimen GSC 94739 is an expansion some 45 mm wide and 7 to 10 mm thick. In tangential section, zooecia are oval, rarely polygonal in maculae areas, 0.24 to 0.28 mm in diameter, 6 to 7 in 2 mm length, 9 to 13 whole zooecia in 1 mm square, with walls thin and occasionally indented by a small acanthorod, 0.04 to 0.06 mm in diameter. In longitudinal section, diaphragms are very abundant, flat and complete to convex but incomplete in zooecia, 9 to 12 in 1 mm along zooecial length, and flat and complete in mesozoecia, 16 to 19 in 1 mm along mesozoecial length.

**Discussion:** The small zooecia, abundant diaphragms and few acanthorods distinguish this species from other Chazyan species of *Batostoma*.

### Crepipora adherens

**Description:** The supposed holotype (Billings, 1859) forms a 2.6 to 4.6 mm thick multilaminate colony encrusting a fragment of the colonial coral *Eofletcheria incerta* (Billings). In tangential section, zooecia are oval, rarely polygonal, thin walled, 0.20 to 0.28 mm in diameter, 6 to 7 in 2 mm length, 9 to 11 whole zooecia in 1 mm square. Round solid acanthorods are rare in the walls, 0.04 mm in diameter. Large angular mesozoecia are abundant. In longitudinal section, zooecia are oval, rarely polygonal, thin walled, 0.20 to 0.30 mm in diameter, rarely up to 0.50 mm, with abundant angular mesozoecia surrounding each opening.

In transverse section, zooecia are polygonal, and 6 flat diaphragms are present in 2 mm along zooecial length whereas 14 diaphragms are present in 2 mm along mesozoecial length. In longitudinal section, zooecial walls are thin, undulate, exozone is narrow up to 0.6 mm wide; zooecial diaphragms are thin, flat, sparse throughout, slightly more abundant in the exozone.

### Discussion

The Mingan Formation specimens of *J. heroensis* are larger zoaria with larger zooecia at depth than the type material from the Chazyan of Vermont - New York state. The species was not recognized in the Laval Formation of Ontario.

### Material and occurrence

**Type species:** *Jordanopora heroensis* Ross, 1962 (by monotypy).

*Jordanopora heroensis* Ross 1962 Fig. 3 (6, 8); Fig. 4 (1-9)

*Jordanopora heroensis* Ross 1962, p. 732, PI. 105, figs. 1-8; PI. 106, figs. 1\(^{a}\), 6, 7.

**Description:** Colonies are ramose with overgrowths, 10 to 12 mm in diameter. In tangential section, peripheral zooecia are round to oval with thick amalgamate walls in which are scattered tiny clear pores or granules (0.012 to 0.015 mm in diameter), 4.5 zooecia in 2 mm length and 13 to 16 whole zooecia in 1 mm square; in deep tangential sections, zooecia are polygonal and thin walled, 0.20 to 0.30 mm in diameter, rarely up to 0.50 mm, with abundant angular mesozoecia surrounding each opening.

In transverse section, zooecia are polygonal, and 6 flat diaphragms are present in 2 mm along zooecial length whereas 14 diaphragms are present in 2 mm along mesozoecial length. In longitudinal section, zooecial walls are thin, undulate, exozone is narrow up to 0.6 mm wide; zooecial diaphragms are thin, flat, sparse throughout, slightly more abundant in the exozone.

*J. heroensis* also was identified in Desrochers’ biohermal localities 440A, C (île Saint-Charles), 477A (île de la Fausse Passe) and 399C (île du Fantôme), and interbiohermal locality 398A (île du Fantôme).

### Genus Champlainopora Ross, 1970

**Type species:** *Atactotoechus chazyensis* Ross, 1962 (Ross, 1970, p. 374).

*Champlainopora chazyensis* (Ross, 1962)

**Description:** Colonies are ramose with overgrowths, 10 to 12 mm in diameter. In tangential section, peripheral zooecia are round to oval with thick amalgamate walls in which are scattered tiny clear pores or granules (0.012 to 0.015 mm in diameter), 4.5 zooecia in 2 mm length and 13 to 16 whole zooecia in 1 mm square; in deep tangential sections, zooecia are polygonal and thin walled, 0.20 to 0.30 mm in diameter, rarely up to 0.50 mm, with abundant angular mesozoecia surrounding each opening.

In transverse section, zooecia are polygonal, and 6 flat diaphragms are present in 2 mm along zooecial length whereas 14 diaphragms are present in 2 mm along mesozoecial length. In longitudinal section, zooecial walls are thin, undulate, exozone is narrow up to 0.6 mm wide; zooecial diaphragms are thin, flat, sparse throughout, slightly more abundant in the exozone.

*J. heroensis* also was identified in Desrochers’ biohermal localities 440A, C (île Saint-Charles), 477A (île de la Fausse Passe) and 399C (île du Fantôme), and interbiohermal locality 398A (île du Fantôme).
Figure 4. Bryozoa, Mingan Formation. 1-9: *Jordanopora heroensis* Ross. 1: Longitudinal section displaying abundant mesozooecia in a thin exozone; specimen GSC 94744, X32; GSC locality 95877, île du Fantôme. 2: Tangential section displaying a few angular mesozooecia; GSC 94740, X 16; GSC locality 96726, île du Fantôme. 3: Longitudinal section with only a few widely spaced diaphragms in endozone; GSC 94742, X 16; same locality as fig. 2. 4, 7: Shallow tangential section displaying pores in thick amalgamate walls, X32, and longitudinal section with few diaphragms, xl6, GSC 94744a, same locality as Fig. 1. 5, 9: Shallow tangential section displaying pores, X 32, and transverse section with abundant mesozooecia, X 16, GSC 94743, GSC locality 95873, île du Fantôme. 6: Oblique tangential section displaying few pores, GSC 94746, X16, GSC locality 96701, île Saint-Charles. 8: Longitudinal section with diaphragms few in the endozone, becoming more abundant in the exozone, GSC 94745, X16, same locality as Fig. 1.
Figure 5. Bryozoa, Romaine (4, 5) and Mingan (1-3, 6-9) Formations. 1, 2: *Champlainopora chazyensis* Ross. Deep tangential section displaying only rare mesozooecia, and transverse section displaying variation in diaphragm spacing; specimens GSC 94750 and 94750a, X32; GSC locality 96700, île Saint-Charles. 3, 9: *LamioUopora duncanae* Ross. Oblique tangential peel and deep tangential section displaying large acanthorods and oval zooecia with thick walls, GSC 94752, 94751, X16; Desrochers' localities 440D, A, île Saint-Charles. 4, 5. *Nicholsonelia* aff. *acanthobscura* McKinney. Tangential section with widely spaced zooecia and abundant acanthorods, X32, and longitudinal section with only rare diaphragms in the exozone, X 16, GSC 94753, Romaine Formation; GSC locality 96722, île du Havre. 6. *Nicholsonela* aff. *irregularis* Loeblich. Tangential section displaying suboval zooecia and abundant large clear acanthorods; GSC 94754, X 16; GSC locality 96716, île Quarry. 7, 8. *Nicholsonella* aff. *parafrondifera* McKinney. Longitudinal section displaying wide exozone and widely spaced diaphragms, and tangential section displaying small oval zooecia, thick walls and abundant clear acanthorods; GSC 94755, X16; Desrochers' locality 309C, île Nue de Mingan.
**Alactotoechus chazyensis** Ross 1962, p. 734, PI. 107, figs 6-10; PI. 108, figs 1-11.

**Champlainopora chazyensis** Key 1990, p. 713, figs 9.6-9.9, 10.1-10.3

**Champlainopora chazyensis** Bolton, Steele-Petrovich & Munro 1991, p. 9, PI. 1.3, fig. 2; PI. 2.1, figs 1-7; PI. 1.6, figs 1-4, 8, 9.

**Champlainopora chazyensis** Mehrtens & Cuffey 2003, fig. 6A.

**Description:** Colony ramose, 4 to 5 mm in diameter. In transverse section, zooecia in the axial region are pentagonal to hexagonal in shape with walls varying from very thin to up to 0.04 mm thick, 0.22 to 0.36 mm in diameter. Angular mesozooecia are sparse. In the peripheral region, zooecia are oval with walls up to 0.04 mm thick, 0.16 to 0.20 mm in diameter. In longitudinal section, zooecial diaphragms in the peripheral region are flat to concave and curving upward into the walls, variably spaced.

**Description:** This species is rare. The two Mingan Formation colonies which are imbedded in a Billingsaria coral colony have larger branches with fewer pores and diaphragms than the type specimens of *C. chazyensis*, and statistically are close to the less common *C. kayi* Ross, which has even fewer diaphragms.

**Material and occurrence:** GSC 94750 and 94750a, Mingan Formation, biothermal beds; GSC locality 96700, île Saint-Charles.

**Nicholsonella aff. acanthobscura** McKinney 2002a, p. 206, fig. 4D.

**Description:** Zoarium is ramose with a branch diameter of 3 to 4 mm. In tangential section, zooecia are petaloid to suboval, 0.08 to 0.14 mm in diameter, rarely 0.18 mm; walls are very thick in exozone with abundant dense acanthorods, 0.02 to 0.04 mm in diameter. In longitudinal section, zooecia curve gently to the periphery, are thin walled in endozone and thick walled in the exozone (which is 0.6 mm wide); diaphragms absent in endozone, but suggestion of such in exozone; no mesozooecia evident.

**Discussion:** Virtual absence of diaphragms and mesozoecia (specifically lack of monilae-like hollows); and thickness of peripheral zooecial walls (resulting in very wide spacing of zooecial apertures) distinguish this species, recorded here for the first time from the Lower Ordovician.

**Identification** of this (and the other) Mingan *Nicholsonella* species is extremely difficult, and so best stated only as affinities, due to their skeletal microstructure being thoroughly recrystallized. In contrast to the low-magnesium calcite original mineralogy of most Paleozoic Bryozoa, *Nicholsonella* in life was either high-magnesium calcite (J.E. Utgaard 1995, personal communication; Taylor & Wilson 1999, p. 42-45) or aragonite (McKinney 1971, p. 290-292; Johnson and Walker 1986), both unstable over geologic time.

**Material and occurrence:** GSC 94753, Romaine Formation; GSC locality 96722, île du Havre.

**Nicholsonella irregularis** Loeblich 1942, p. 428, PI. 64, figs 5-7.

**Description:** Large sheet-like to ramose zoarium with branches from 8 to 14 mm in diameter. In tangential section, zooecia are suboval, ranging from 0.20 to 0.45 mm in diameter, 5 to 6 in 2 mm length, 1 to 2 in 1 mm square; walls are thick in exozone with abundant dense acanthorods or granules, 0.04 to 0.06 mm in diameter, located in polygonal mesozooecia.
Figure 6. Bryozoa, Mingan Formation. 1-3, 5: *Constellaria islensis* Ross. 1, 2: Tangential section displaying stellate-arranged mesozooecia, and longitudinal section with wide mesozooecial zones; specimen GSC 94763, X16, GSC locality 96726, île du Fantôme. 3: Oblique tangential section with rare small acanthorods; GSC 94759, X12, GSC locality 95776, île de la Maison. 5: Longitudinal section displaying mainly zooecia and acanthorods; GSC 94760, X32; GSC locality 96700, île Saint Charles. 4: *Ceramoporella adamarhombica* sp. nov. Tangential section displaying diamond-shaped zooecia; holotype, GSC 94757, X32; Desrochers’ locality 369B, île du Fantôme; (also see Fig. 3 (2)). 6-8. *Phylloporina incepta* (Hall). Surfaces of reticulate branches sufficiently weathered in places to display both aligned oval zooecial openings and long zooecial tubes; GSC 94765, 94766, X4 and x8; GSC locality 95785, île Nue'de Mingan; and GSC 94767, X4; GSC locality 96732, île à Calculot.
Figure 7. Bryozoa, Mingan Formation. 1, 4, 7: *Chazydictya rossae* sp. nov. 1, 7: Large zoaria; holotype, specimen GSC 94774, X1.6; GSC locality 96732, île à Calculot; paratype, GSC 94777, X4; GSC locality 95785, île Nue de Mingan. 4: Oblique transverse section displaying local development of tabulate interspaces between tubes as in *Pachydictya*; paratype, GSC 94773, x 16; GSC locality 96716, île Quarry. 2, 3: *Stictopora cf. fenestrata* Hall. Transverse and longitudinal sections; GSC 94780, 94779, X32 and xl6; GSC locality 96735, île du Fantôme. 5, 8, 9: *Phylloporina incepta* (Hall). 5: Small zoarium displaying oval zooecia aligned in 2 or 3 rows; GSC 94770, X2.4; GSC locality 96726, île du Fantôme. 8: Weathered surface of a reticulate branching zoarium displaying both oval zooecial openings and long zooecial tubes; GSC 94768, X8; same locality as Fig. 1. 9: Tangential peel displaying 3 to 4 rows of oval zooecia on reticulate branches and long zooecial tubes; GSC 94772, X16; Desrochers’ locality 399A, île du Fantôme. 6: *Eopachydictya aff. gregaria* Ross. Oblique tangential peel displaying alignment of oval zooecia; GSC 94778, X16; Desrochers’ locality 309B, île Nue de Mingan.
In longitudinal section, walls are thin where not recrystallized, gently curving to the periphery where thickened; one or two diaphragms are preserved near surface of the zoarium.

**Discussion:** Nicholsonella aff. acanthobscura and *N.* aff. *irregularis* are similar in longitudinal section in the scarcity of diaphragms but differ in tangential section in thickness of zooecial walls, size of zooecia and acanthorods. Neither taxon relates to *Nicholsonella* spp. A or B identified by Ross (1963b) in the type Chazyan. *N.* aff. *irregularis* is especially characterized by clear acanthorods with a central dark spot, as visible in the upper right corner of the Mingan specimens figured here (Fig. 5 (6)). and evident in the holotype (Loeblich 1942, Pl. 64, figs 6, 7).

**Material and occurrence:** GSC 94754, Mingan Formation; GSC locality 96716, île Quarry.

*Nicholsonella aff. parafrondifera* McKinney, 1971 Fig. 5(7, 8)


**Description:** Zoarium is usually ramose with branches 8 to 10 mm in diameter, but rarely encrusting. In tangential section, zooecia are oval, 0.12 to 0.16 mm in diameter, 4 to 5 in 2 mm length; walls are thick with abundant tiny clear granules (possibly acanthorods); faint traces of polygonal mesozooecia. In longitudinal section, thin walls of endozone curve gently into the thick exozone (up to 2.0 mm); diaphragms are rare and widely spaced within the axial region, increasing in number and more closely spaced as near the exozone, with up to 7 in 1 mm length in exozone mesozooecia.

**Discussion:** The wide, thick-walled exozone separates Nicholsonella aff. *parafrondifera* from its nearest relative *Nicholsonella* sp. B of Ross (1963b). Among Mingan relatives, *N.* aff. *parafrondifera* is distinguished by moderately wide spacing between zooecial apertures, sparse diaphragms, and relatively few monilae-like mesozooecia.

**Material and occurrence:** GSC 94755, Mingan Formation, interbiohermal beds; Desrochers’ locality 309C, île Nue de Mingan.

Order CYSTOPORIDA Astrová, 1964

Suborder CERAMOPORINA Bassler, 1913

Genus Ceramoporella Ulrich, 1882

**Type species:** *Ceramoporella distincta* Ulrich, 1890, p. 464.

*Ceramoporella adamarhombica* sp. nov. Fig. 3 (2); Fig. 6 (4)

*Cheiloporella* sp. Pitcher 1964, p. 645, Pl. 3, figs 1, 2; Text-fig. 14.

*Ceramoporella* n. sp. Bolton, Steele-Petrovich & Munro 1991, p. 10, Pl. 1.3, figs 3, 10; Pl. 1.4, fig. 1.

**Diagnosis and Description:** Zoaria are unlaminar to multilaminate encrustations. Zooecia are short tubes, straight to slightly curved, rising steeply (in longitudinal section, vertically in transverse section) from a thin basal lamina; they are thin-walled throughout, 0.40 to 0.60 mm in diameter, mostly without diaphragms (although a few zooecia may contain one thin diaphragm). In well-oriented tangential sections, zooecial apertures tend toward diamond-shaped, with their walls locally arranged in a distinctly rhombic grid. In many zooecia, proximal walls are slightly thickened (lunarium, which does not project much above the colony surface), and in a few the proximal zooecial angle is somewhat rounded. Local small interruptions in a few zooecial walls may represent occasional interzooecial or communication pores (but could instead be diagenetic defects). Neither exilazooecia nor acanthorods are developed.

**Discussion:** This combination of morphologic characters, particularly the diamond-shaped or rhombic apertures, subduded lunaria, near lack of diaphragms, and lack of exilazooecia, does not match any of the eleven *Ceramoporella* (including *Cheiloporella* and *Acanthoceramoporella*) species described in the North American and Baltic Ordovician literature available to us. The Upper Ordovician *Ceramoporella ohiensis* (Nicholson) (Cumings 1908, Pl. 11, figs. 4-4g) is the most similar in zooecial arrangement but possesses small exilazooecia between the adjacent zooecial angles. The other described species possess exilazooecia (often numerous; *C. distincta*, *C. flabel­lata*, *C. interporosa*, *C. minor*), acanthorods (*C. gran­ulosa*), prominently projecting or sharply curved lunaria (*C. grandis*, *C. inclusa*, *C. uxnormensis*), or irregular, triangular, or petaloid apertures (*C. ingenus*, *C. distincta*, *C. triloba*).

**Paleoecologic associations:** *Ceramoporella adamarhombica* sp. nov. occurs sparsely intermingled with layers of *Batostoma chazyensis* Ross and within *Billingsaria parva* (Billings) (especially as on île de la Maison). Similar intergrowth assemblages are more abundant in the biostratigraphy of the Laval Formation in the Hawkesbury area, Ontario, and also throughout the type Chazyan bryozoan bioherms in Vermont - New York state.

**Types and occurrence:** Holotype, GSC 94757, Mingan Formation, biohermal beds; Desrochers’ locality 369B, île du Fantôme. Paratypes, GSC 94756, GSC locality 96701, biohermal beds, île Saint-Charles, and GSC 94758 and 94758a, Desrochers’ locality 315C, île Nue de Mingan.
**Etymology:** The name chosen for this new species reflects the diamond shape of the apertures (from Latin *adamas* = diamond) and the overall rhombic-grid pattern (from Latin *rhombicus*— rhombic).

Suborder FISTULIPORINA Astrová, 1964  
Genus *Constellaria* Dana, 1846  
*Type species:* *Constellaria florida* Ulrich, 1882 (by Ulrich, 1883)  
*Constellaria islensis* Ross, 1963  
Fig. 6 (1-3, 5)

**Description:** Zoaria generally thin expansions located within *Billingsaria* colonies. In tangential section, zooecia are round to polygonal, dominantly 0.20 to 0.24 mm in diameter, some up to 0.36 mm, 5 to 7 in 2 mm length, 1 to 2 whole zooecia in 1 mm square, with walls thin. Angular mesozooecia of various sizes and shapes are abundant, sometimes stellate in arrangement. Minute acanthorods are located in zooecial walls or at zooecia-mesozooecia junctions.

In longitudinal section, zooecial diaphragms are flat, inclined complete to incomplete, or sagging, at least 3 to 5 in 1 mm along zooecial length; mesozooecia are arranged in one to four longitudinal rows with diaphragms flat, complete to irregular, 9 to 10 in 1 mm along mesozooecial length.

Specimen GSC 94763 (Fig. 6 (1, 2)) is a massive form up to 20 mm thick with zooecia ranging from 0.28 to 0.44 mm in diameter, 3 to 3.5 in 2 mm length, 1 whole zooecium in 1 mm square, with diaphragms 2 to 3 in 1 mm or 4 to 8 in 2 mm along zooecial length, 6 in 1 mm or 11 to 15 in 2 mm along mesozooecial length, and few small acanthorods.

**Discussion:** The majority of *C. islensis* identified in the Mingan Formation have slightly larger zooecia but in overall characteristics are close to the type specimens from the Chazy Group. All features of GSC 94763 are somewhat larger sized than *C. islensis* types, but otherwise fit into the concept of this species.

**Material and occurrence:** GSC 94765, 94766, Mingan Formation; GSC locality 95785, île Nue de Mingan. GSC 94767-94769; GSC locality 96732, île à Calculot. GSC 94770, 94771; GSC locality 96726, île du Fantôme. GSC 94772; Desrochers’ locality 399A, île du Fantôme.

**Phylloporina incepta** Ross 1963c, p. 597, PI. 10, figs 4, 5.

**Description:** Colonies are undulating reticulate expansions with some forms exhibiting a regularity in their meshwork; branches are 0.25-0.35 mm wide and cross-bars (dissepiments) are 0.20-0.30 mm wide; oval to elongate fenestrules ranges from 0.88 mm in diameter to 0.80 X 0.40 mm to 1.00 X 0.60 mm, 2 to 3 in 2 mm laterally and 1 to 5 in 2 mm longitudinally. Zooecia are circular to oval, small, arranged in 4 rows with lateral rows opening into fenestrules and extending onto cross-bars, 4 to 6 zooecia in 1 mm longitudinally. Reverse surface is marked by 3 to 6 longitudinal lines (striaions) and abundant tiny pustules.

**Material and occurrence:** GSC 94770, 94771, with branches 0.44 to 0.50 mm wide and very reticulate, display more elongate, narrow fenestrules, 0.64 X 0.20 mm in diameter, 2.5 to 3 in 2 mm laterally and 1.5 to 2 in 2 mm longitudinally, features more suggestive of “Phylloporina” sp. A.

Suborder PTILODICTYINA Astrová & Morozova, 1956  
Genus *Chazydictya* Ross, 1963  
*Type species:* *Chazydictya chazyensis* Ross, 1963c, (by monotypy).
**Chazydictya rossae** sp. nov.

*Fig. 7 (1, 4, 7)*

**Diagnosis and Description:** Zoaria are bifoliate, bifurcating branches, composed of longitudinally aligned zooecia, arranged in 6 to 8 central rows of oval openings varying in diameter from 0.26 x 0.20 to 0.22 x 0.16 mm, 6 in 2 mm longitudinally. These central zooecia are bounded on each side by 6 to 7 rows of more elongate openings inclined to the surface, varying in diameter from 0.26 x 0.10 to 0.22 x 0.12 mm, up to 10 in 2 mm laterally, 18 to 23 ranges in all; zooecial walls are thin to thickened, laminate, no pustules observed. Simple mesotheca in transverse section; in longitudinal section, zooecia are thin walled, long, with widely spaced flat diafragms, and lack hemisepta.

**Discussion:** In comparison with the type species, *C. chazyensis* Ross, this *Chazydictya* new species from the Mingan Formation has more ranges on a branch (31 to 34 compared to 8 to 10) and its zooecial openings are larger (0.26 x 0.20 mm compared to 0.16 x 0.12 mm).

**Types and occurrence:** Holotype, GSC 94774, Mingan Formation; GSC locality 96732, île à Calculot. Paratypes, GSC 94773; GSC locality 96716, île Quarry. GSC 94775, 94776; same locality as holotype. GSC 94777; GSC locality 95785, île Nue de Mingan.

**Etymology:** The species is named in honour of June Phillips Ross, in recognition of her long-term excellent studies of Chazyan Bryozoa.

**Genus Eopachydictya** Ross, 1963

**Type species:** *Eopachydictya gregaria* Ross, 1963c.

*Eopachydictya aff. gregaria* Ross, 1963, *Fig. 7 (6)*

**Eopachydictya gregaria** Ross 1963c, p. 591, PI. 4, figs 1-5, 7, 9-11.

**Discussion:** One small bifoliate branching thin zoarium displays oval zooecia aligned in 6 ranges, with thick walls, suggestive of *E. gregaria*.

**Material and occurrence:** GSC 94778, 94780, Mingan Formation; GSC locality 96735, île du Fantôme.

The species is abundant, occurring in the biothermal beds at Desrochers’ localities 398D, F and 399C (île du Fantôme), 477A (île de la Fausse Passe), 440A (île Saint-Charles), and interbiothermal beds at localities 398A (île du Fantôme) and 398A, B (île Nue de Mingan).

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**Stictopora fenestrata** Phillips 1960, p. 7-9, PI. 1, figs 3, 5, 9, 11.

**Stictopora fenestrata** Ross 1963c, p. 591, PI. 7, figs 1, 2, 4-8, 11.

**Stictopora fenestrata** Arens & Cuffey 1989, p. 114, figs 4L-Q.

**Stictopora fenestrata** Cuffey et al. 2002a, p. 206, fig. 4F.

**Description**—Zoaria are bifoliate bifurcating branches 1.6 to 2.0 mm across, with narrow marginal bands lacking zooecia. Zooecia are oval or elliptical, 0.16 to 0.20 mm in diameter, opening obliquely to surface, walls thick, aligned in distinct ranges 7 to 11 per branch; mesothecae straight to slightly curved with closely spaced median tubuli.

**Discussion:** These specimens differ sufficiently from the holotype (Phillips 1960) to justify comparison only.

**Material and occurrence**—GSC 94779, 94780, Mingan Formation; GSC locality 96735, île du Fantôme.

The species is abundant, occurring in the biothermal beds at Desrochers’ localities 398D, F and 399C (île du Fantôme), 477A (île de la Fausse Passe), 440A (île Saint-Charles), and interbiothermal beds at localities 398A (île du Fantôme) and 398A, B (île Nue de Mingan).


Collecting locality in the Romaine Formation

île du Havre (Eskimo Island, but could be confused with elongate “Harbour Island” immediately along mainland shore 11 km northeast of île Nue de Mingan; Fig. 1) —
GSC 96722: Center of north shore - *Nicholsonella* aff. *acanthobscura*.

Collecting localities in the Mingan Formation

île Saint-Charles (St. Charles Island) - 
GSC 95981: Southeast shore - *Constellaria islensis*.
GSC 96700: Southwestern point area - *Champlainopora chazyensis*, *Constellaria islensis*.
GSC 96701: Southwestern point itself - *Batostoma chazyensis*, *Jordanopora heroensis*, *Ceramoporella adamarhombica*, *Constellaria islensis*.
GSC 96703: Southwest shore - *Batostoma adhaerens*.

île de la Fausse Passe -
Desrochers’ 477A, B: Southeast shore - *Batostoma chazyensis*, *Batostoma adhaerens*, *Jordanopora heroensis*, *Constellaria islensis*, *Stictopora* cf. *fenestrata*.

île à Calculot (Gull Island) -
GSC 96732: Very small island - *Batostoma chazyensis*, *Phylloporina incepta*, *Chazydictya rossae*.

île du Fantôme (Quin Island) -
GSC 95873: West shore, latitude 50°13.6'N, longitude 63° 4L3'W - *Jordanopora heroensis*.
GSC 95877: Southeast comer - *Batostoma chazyensis*, *Jordanopora heroensis*.
GSC 96726: First bay south of northwest point, on west shore - *Jordanopora heroensis*, *Constellaria islensis*, *Phylloporina incepta*.
GSC 96735: West shore - *Stictopora* cf. *fenestrata*.
Desrochers’ 369A-C: Southwest comer - *Jordanopora heroensis*, *Ceramoporella adamarhombica*, *Phylloporina incepta*.
Desrochers’ 399A-C: Southwest comer - *Batostoma chazyensis*, *Jordanopora heroensis*, *Phylloporina incepta*, *Stictopora* cf. *fenestrata*.

île Quarry (Quarry Island, the middle of the three large islands 9 km west of île du Fantôme; Fig. 1) -
GSC 96716: Southeast tip - *Batostoma chazyensis*, *Nicholsonella* aff. *irregularis*, *Chazydictya rossae*.

île Nue de Mingan (Mingan Island) -
GSC 95785: Central-west shore - *Phylloporina incepta*. *Chazydictya rossae*.
Desrochers 315C: Northwest shore - *Ceramoporella adamarhombica*.

île de la Maison (southeastern island of the îles aux Parroquets (Parroquet Islands) group, the three small islands 4 km west of île Nue de Mingan; Fig. 1) -
GSC 95776: Very small island - *Ceramoporella adamarhombica*, *Constellaria islensis*. 
Bryozoan species and roles in small ‘Waulsortian-like’ mud-mound bioherms in the Mississippian of the American Mid-West

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ABSTRACT: Earlier Mississippian (Lower Carboniferous) strata in the Mid-Western United States preserve small mud-mound bryozoan-bearing bioherms, similar but not identical to the western European Waulsortian facies. In total, 62 bryozoan species occur in those mounds investigated, mostly fenestrates but including some bifoliate fistuliporoids and occasional tiny rhabdomesids. Two delicate fenestrates, *Exfenestella exigua* and *Banastella regalis*, are the most ubiquitous and common species encountered; the other species are all rarer and more widely scattered. A few fenestrates preserved intact and upright are consistent with possibly having played baffling or stabilizing roles in the formation of these bioherms.

1 INTRODUCTION

Bryozoan reefs have a lengthy geological history, from the Ordovician to the present, during which their importance fluctuated greatly (Cuffey 1977, 1985).

The earlier Mississippian (earlier Lower Carboniferous; “earlier” means Kinderhookian, Osagean, and early Meramecian, or Toumaisian and basal Viséan, in contrast to “later” for late Meramecian and Chesterian, or middle Viséan into early Namurian) was one time when bryozoan-bearing bioherms were conspicuous, in the form of mud-mounds in part possibly baffled or stabilized by fenestrate bryozoans (Cuffey 1985). Larger, more complex, contemporaneous, mud-mound structures have long been known in western Europe as the Waulsortian facies (Lees 1961, Bolton et al. 1982, Lees & Miller 1985, Webb 2002). That interval saw very few cnidarian- or coelenterate-dominated reefs, because the mid-Paleozoic coral-stromatoporoid reef community had been severely diminished by the mid-Late Devonian mass extinction.

Similar bioherms, but not identical (hence instead often termed “Waulsortian-like”), occur in the American Mid-West. In contrast to the European Waulsortian build-ups, these Mid-Western mounds are smaller-sized (on the order of a metre or two high by several metres across), and tend to occur in shallower (cratonic) palaeoenvironments. They are coarser-grained (calcisiltites rather than calcilutites; Lasemi et al., 2003). Some of them include, in addition to the usual carbonates, argillaceous greenshale cores (Ausch & Meyer 1990), which locally constitute the entire mound (Stapor & Knox 1995).

The Mid-Western mounds additionally differ from similar-age, larger, muddy build-ups in the Rocky Mountains by lacking sizeable masses of fibrous calcite cement (apparently of submarine origin; Cotter 1965, 1966, Bolton et al. 1982), and by not having crinoidal-limestone halos surrounding their lower parts (Laudon 1957).

Bryozoans, though sparse, are the most numerous fossils in these Mid-Western mounds, and therefore have been investigated as the subject of this present report. Identification of the species present, analysis of their recurrences and distributions, and consideration of their biogeographic and sedimentologic implications are the objectives herein.

2 MATERIALS AND METHODS

2.1 Localities and geological setting


Locally, in Illinois, fenestrates were sufficiently abundant on top of some mud-mounds to form frame-thicket caps, whose crushed, compacted remnants form a distinctive type of rudstone termed “wheat-chex” because of its similar appearance to a particular

In addition to the Mid-Western mud-mounds examined herein, other larger Mississippian mud-mounds are located in the Rocky Mountains, but these have not yet been investigated for their bryozoan species. Particularly noteworthy are those in New Mexico and Montana (Pray 1958, Cotter 1965, 1966, Stone 1972, Bolton et al. 1982).

Although the great majority of fenestrate-containing mud-mounds grew during the earlier Mississippian, a few came afterwards in the later Mississippian (Gibson 1986), and on into the Permian (Cuffey & Simonson 1980, Simonsen & Cuffey 1980). However, most later bryozoan-built structures contained progressively less mud, culminating in the more open frame-thickets of the Pennsylvanian (Upper Carboniferous) and Permian (Smith 1981, Zimmerman & Cuffey 1987, Ozhgibesov & Cuffey 1995, Cuffey & Babcock 1996).

The Mid-Western mud-mounds may have begun to develop as early as Kinderhookian time (early Tournaigain, earliest Mississippian), but flourished from middle Osagian through earliest Meramecian time (latest Tournaigain through early Viséan). They range from near-shore shallows (Brown & Dodd 1990) down ramps (King 1986) into intracratonic basins (Lasemi et al. 1994, 2003; still relatively shal-low compared to the deeper basins in Europe in which the larger type-Waulsortian mounds formed). Paleogeographically, North America and Europe were joined already in a small supercontinent (Laurussia) as plate tectonics moved toward the large supercontinent (Pangaea) by the end of the Early Palaeozoic (Frazier & Schwimmer 1987).

2.2 Taphonomy
Bryozoan fossils are sparse to common throughout the mud-mounds examined. The colonies are mostly broken or fragmentary, fallen over, lying aperturoc frontal-surface downward and horizontally parallel to bedding, but locally are preserved intact and still standing upright within the muddy sediment around them. The erect stance would be consistent with rapid deposition of mud trapped or baffled from suspension in the turbid waters flowing past (Simonsen & Cuffey 1980, Cuffey 1985, 1997).

3 IDENTIFICATIONS AND DISTRIBUTIONS
Within a major biohermal phylum or class, only a few among its many constituent species play dominant constructional or sedimentologic roles in bioherm-building. The roughly hundred, modem, western Atlantic coral species (Walton Smith 1971) provide excellent examples, with Acropora palmata (Lamarck, 1816), Acropora cervicornis (Lamarck, 1816), and Montastrea annularis (Ellis & Solander, 1786) dominating the shallow, middle, and deep fore-reefs there. The question naturally arises as to whether a similar pattern developed among bioherm-dwelling bryozoan species in the distant past, specifically motivating this and related investigations for many years. The most practical way to answer this question is to attempt species-level identifications for all the bryozoans preserved in these mounds, and to compare and contrast their distributions.

Bryozoans were identified from comparison of external shapes, sizes, proportions, and ornamentations as illustrated in the available literature. Because those references are readily accessible and because no new species were encountered, documentation herein is by citing the most representative figures for each species mentioned herein. The morphologic characteristics illustrated, though in some cases subtle, did permit consistent recognition of these species and discrimination of them from closely similar forms, a procedural finding which parallels recent work on fenestrates elsewhere (Hageman 1991).

In total, 62 bryozoan species were identified in the small Mid-Western mud-mounds, out of the several hundred so far described from Mississippian strata in that region. Most (43) are fenestrates, many delicate (38) and some slightly more robust (5), accompanied by a few (3) similar-appearing pinnates. In places, originally erect bifoliates (4 species, but fistuliporoids rather than ptilodictyoids) are prominent. Tiny (hence very inconspicuous) branching or encrusting fragments include rhabdomesids (8 species), trepostomes (2), and other fistuliporoids (2).

Two delicate fenestrate species occur commonly in all (Exifenestella exigua (Ulrich, 1890); Utgaard & Perry 1960 pi. 2, fig. 4; Snyder 1991 pi. 16, fig. 2) or most (Banastella regalis (Ulrich, 1890); Ulrich 1890 pi. 50, figs 1, la) of the Mid-Western mud-mounds, both carbonate and argillaceous, examined in the course of this study.

Several more are rare but found in the majority of these bioherms, both limestone and green-shale:

Banastella limitans (Ulrich, 1890) (Ulrich 1890 pi. 49, figs 4, 4a),
Hemitrypa hemitupa (Prout, 1859) (Snyder 1991 pi. 41, fig. 7, pi. 42, fig. 1),
Hemitrypa perstria (Ulrich, 1890) (Snyder 1991 pi. 39, figs 7, 11),
Laxifenestella coniunctisty (Snyder, 1991 (Snyder 1991 pi. 5, figs 6, 8),
Laxifenestella maculasimilis (Snyder, 1991 (Snyder 1991 pi. 7, figs 3, 4),
as well as the bifoliate fistuliporoid Cystodictya lineata (Ulrich, 1884 (Butts 1941 pi. 129, fig. 12; Duncan 1969 pi. 58, fig. 12).
The remaining species are rare and found in only a few of the mounds examined.

Many occur only in mounds which are entirely carbonate:

_Apertostella crassata_ Snyder, 1991 (Snyder 1991 pi. 36, figs 5, 8),
_Apertostella foramenmajor_ Snyder, 1991 (Snyder 1991 pi. 35, figs 1, 6),
_Archipedes negligeas_ Ulrich, 1890 (Snyder 1991 pi. 50, figs 1, 5),
_Archipedes wortheni_ (Hall, 1857) (Snyder 1991 pi. 57, figs 1, 5, 7),
_Banastella biseriata_ (Ulrich, 1890) (Snyder 1991 pi. 26, figs 1, 2),
_Banastella mediocreforma_ Snyder, 1991 (Snyder 1991 pi. 22, figs 2, 3),
_Cubifenestella multinodosa_ (Tavener-Smith, 1973) (Tavener-Smith 1973 pi. 6, figs 2, 3),
_Cubifenestella rudis_ (Ulrich, 1890) (Snyder 1991 pi. 29, figs 5, 6),
_Cubifenestella usitata_ Snyder, 1991 (Snyder 1991 pi. 31, figs 3, 4),
_Fenestella frutex_ M'Coy, 1844 (Tavener-Smith 1973 pi. 1, figs 1, 8),
_Fenestella hemispherica_ M'Coy, 1844 (Tavener-Smith 1973 pi. 4, figs 7, 8),
_Fenestella rotundata_ Koenig, 1958 (Koenig 1958 figs 1k, 1),
_Laxifenestella fluctuata_ Snyder, 1991 (Snyder 1991 pi. 11, figs 3, 5),
_Lyroporella divergeas_ (Ulrich, 1890) (Utgaard & Perry 1960 pi. 3, figs 5, 7),
_Ptiloporella varicosas_ (M'Coy, 1844) (Tavener-Smith 1973 pi. 21, figs 6, 8),
as well as the bifoliate fistuliporoid:
_Sulcoretepora parallela_ (Phillips, 1836) (Utgaard 1983 fig. 210-lc).

A number of species extend from carbonate mounds into argillaceous ones as well:

_Apertostella venusta_ Snyder, 1991 (Snyder 1991 pi. 38, figs 1, 2),
_Banastella guensburgi_ Snyder, 1991 (Snyder 1991 pi. 18, figs 2, 3),
_Fenestella inaequalis_ Ulrich, 1890 (Ulrich 1890 pi. 52, figs 9, 9a),
_Fenestralia sanctiludovici_ Prout, 1858 (Snyder 1991 pi. 63, figs 1, 4),
_Hemitrypa aprilae_ Snyder, 1991 (Snyder 1991 pi. 44, figs 1, 2),
_Hemitrypa aspera_ Ulrich, 1890 (Snyder 1991 pi. 46, figs 1, 4),
_Hemitrypa proutana_ Ulrich, 1890 (Ulrich 1890 pi. 57, figs 1, 1a),
_Hemitrypa vermicera_ Ulrich, 1890 (Snyder 1991 pi. 48, figs 1, 2),
_Laxifenestella serratula_ (Ulrich, 1890) (Snyder 1991 pi. 9, figs 4, 5),
_Minilyla paratriserialis_ Snyder, 1991 (Snyder 1991 pi. 14, figs 6, 7),
_Minilyla sivenella_ Snyder, 1991 (Snyder 1991 pi. 13, figs 2, 3),
_Polypora cestriensis_ Ulrich, 1890 (Ulrich 1890 pi. 60, figs 7a, c),
_Polypora spininodata_ Ulrich, 1890 (Cumings et al. 1906 pi. 39, fig. 3; Snyder 1991 pi. 68, fig. 2),
_Rectifinenestella multispinosa_ (Ulrich, 1890) (Tavener-Smith 1973 pi. 3, fig. 7; Snyder 1991 pi. 4, fig. 2),
as well as the bifoliate fistuliporoid:
_Cystodictya ocel lata_ Ulrich, 1882 (Cumings et al. 1906 pi. 35, fig. 2),
and the rhabdomesid:
_Saffordotaxis incrassata_ (Ulrich, 1888) (Ulrich 1890 pi. 70, fig. 12b).

Certain species are seen only in the argillaceous mounds:

_Fenestella compressa_ Ulrich, 1890 (Duncan 1969 pi. 53, figs 2, 3),
_Fenestella filistriata_ Ulrich, 1890 (Tavener-Smith 1973 pi. 10, figs 5, 6),
_Fenestella triserialis_ Ulrich, 1890 (Ulrich 1890 pi. 50, figs 4, 4a),
_Hemitrypa pateriformis_ Ulrich, 1890 (Ulrich 1890 pi. 57, figs 7a, b),
_Polypora varsoviensis_ Prout, 1858 (Ulrich 1890 pi. 60,'figs 2, 2b),
_Pylloporella vodoresovi_ Nekhoroshev, 1953 (Sarycheva 1960 figs 132a, b),
_Rectifinenestella tenax_ (Ulrich, 1888) (Snyder 1991 pl.l, figs 3, 4),
as well as the pinnates:
_Penniretepora flexuosa_ Ulrich, 1890 (Ulrich 1890 pi. 66, figs 4, 4a),
_Penniretepora vinei_ Ulrich, 1888 (Ulrich 1890 pi. 66, figs 5a, b),
_Pinnatopora subangulata_ Ulrich, 1888 (Ulrich 1888 pi. 14, fig. 2),
and the bifoliate fistuliporoid:
_Cystodictya pustulosa_ Ulrich, 1890 (Ulrich 1890 pi. 76, fig. 2a),
and the tiny rhabdomesids:
_Klaucena immortalis_ Trizna, 1958 (Blake 1983 fig. 286-la),
_Mediapora injaensis_ Trizna, 1958 (Blake 1983 fig. 283-2c),
_Rhombopora bedfordensis_ Cumings, 1906 (Cumings et al. 1906 pi. 35, fig. 5),
_Rhombopora exigua_ Ulrich, 1890 (Ulrich 1890 pi. 70, fig. 10a),
that shown by the trepostome mounds seems only moderate, less pronounced than exhibited by the Caribbean corals previously mentioned. The delicate fenestrates *Exfenestella exigua* (Ulrich, 1890) and *Banastella regalis* (Ulrich, 1890) dominated the Mississippian Mid-Western mud-mounds seems only moderate, less pronounced than that shown by the trepostome *Batostoma chazyensis* Ross, 1963 in Mid-Ordovician crust mound bryozoan reefs (Cuffey et al. 2002, Cuffey 2003); and much less than exhibited by the Caribbean corals previously mentioned. Instead, that extent appears intermediate, in contrast to the situation seen in Pennsylvanian-Permian frame-thicket bryozoan reefs, where a number of fenestrates, pinnates, and trepostomes share such dominance ecologically (Zimmerman & Cuffey 1987).

Bryozoan species biodiversity in Palaeozoic bryozoan bioherms during the three intervals when such structures were most numerous is roughly comparable. Approximately 70 bryozoan species are known in Mid-Ordovician crust-mounts (Cuffey 2003), 62 in Mississippian mud-mounts (as documented here), and over 80 in Permian frame-thickets (Zimmerman & Cuffey 1987).

Three sedimentologic or constructional roles can be envisioned as possible for the bryozoans in the Mid-Western mud-mounts (Cuffey 1977, Monty et al. 1995), and as compared with modern mud-mounts in Florida Bay (Cuffey & Simonsen 1980). Erect bryozoan colonies projecting upward into turbid water flowing past would have baffled or trapped mud from suspension, causing that sediment to have settled out and accumulate around the zoaria. Colonies growing close together could have stabilized, anchored, or bound the unconsolidated sediment forming the bottom and prevented its erosion or removal, as McKinney & Jaklin (2001) have documented in the modern Adriatic Sea. Colony fragments would have formed skeletal debris contributing at least locally to the accumulating carbonate sediment. Feeding activities may have increased sedimentation rates around the bryozoan colonies (McKinney et al. 1987). However, all of these possibilities remain difficult to document definitively, because none resulted in a preservable rigid reefal framework here, and because the relative sparseness of the preserved bryozoans might imply nothing more than that the mounds were a reasonable habitat in which to settle.

Finally, particularly in Ireland, certain Viséan deposits have been examined taxonomically, and some of their species also occur in the Mid-Western bioherms. Such commonality would be expected from the paleogeographic proximity of the two regions during Mississippian time. British-Isles species (Miller 1962, Owen 1969, Tavener-Smith 1973, Wyse Jackson 1996) also in the American mud-mounts include *Cubifenestella multinodosa* (Tavener-Smith, 1973), *Cubifenestella rudis* (Ulrich, 1890), *Fenestella filistriata* Ulrich, 1890, *Fenestella frutex* M'Coy, 1844, *Fenestella hemispherica* M'Coy, 1844, *Ptiloporella varicosa* (M'Coy, 1844), *Rectifenestella midtispinosa* (Ulrich, 1890), and *Sulcoretpora parallela* (Phillips, 1836), all previously listed. Moreover, three more species occur in both America and Russia (Blake 1983, Sarycheva 1960), further east on ancient Laurussia: *Klaucena immortalis* Trizna, 1958, *Mediapora injaensis* Trizna, 1958, and *Ptyloporella vodoresovii* Nekhoroshev, 1953.

5 CONCLUSION

The delicate fenestrates *Exfenestella exigua* (Ulrich, 1890) and *Banastella regalis* (Ulrich, 1890) were the most ubiquitous and common among the bryozoan species scattered through the small ‘Waulsortian-like’ mud-mounts examined in the earlier Mississippian in Indiana, Illinois, Kentucky, Tennessee, and Missouri. Sixty other species, also mostly delicate fenestrates but including some bifoliate fistuliporoids and occasional rhabdomesids, were also encountered in these bioherms, but more rarely and less widely distributed. A few fenestrates are preserved in place upright, consistent with the possibility that they may have played baffling or stabilizing roles in the deposition of these structures.
ACKNOWLEDGEMENTS

I thank Z. Lasemi, M. Hynes, J. Krothe, G. Grantz, D. Kogovsek, L. Knox, A. Heasley, and N. Longo for their substantial help in carrying out the investigations on which this present report is based, F. McKinney, P.N. Wyse Jackson and H. Moyano for constructive reviews, and D. Lambert for preparing this manuscript for publication.

REFERENCES


Lower Carboniferous Bryozoa from some localities in Sauerland, Germany

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ABSTRACT: Thirteen bryozoan species were determined from the Lower Carboniferous (Viséan) rocks of two localities in Sauerland, Germany. Eight species are previously known from the Lower Carboniferous of British Isles. One species *Rhabdoneson reguläre* Nekhoroshev 1932, was described initially from German localities, and was later also reported from the Lower Carboniferous of Russia. The genera *Evactinopora*, *Meekopora* and *Hinaclema* are reported for the first time from the Lower Carboniferous of the Western European region.

1 INTRODUCTION

Lower Carboniferous bryozoans in Germany are poorly investigated. The most comprehensive study is that by Nekhoroshev (1932), who described 18 fenestellid, 3 rhabdomesid and 2 trepostomid species from a museum collection. Another, more recent study, is that by Wyse Jackson & Weber (this volume). The German Lower Carboniferous is represented mostly by different kinds of shales, often silicified, containing pelagic faunas (ammonites, radiolarians), as well as plate carbonates (Kulmplattenkalk). Carbonate sediments appear usually in form of separate beds, few centimeters up to 2m in thickness. They consist of a crinoid-coral packstone, partly silicified, and are extremely rich on fossils (Korn, 2002). However, these are usually poorly preserved.

2 MATERIALS AND METHODS

The investigated material was collected by Dieter Weyer (Berlin) from active quarries Westenfeld, Hellefeld, and Frenkhausen in the Rheinisches Schiefegebirge (Sauerland, Germany). The material from Westenfeld and Hellefeld comes from the 2m thick carbonate bed just below the *Goniattites crenistria*–bed of Viséan stage, whereas the material from Frenkhausen is a bit younger, probably *Arnsbergites gracilis*–zone (Dieter Korn, Berlin, pers. comm.). A few samples from Hellefeld contain mostly indeterminable bryozoan fragments. The sampled material reveals an excellent preservation, only insignificantly disturbed by silicification. From this material 50 thin sections were prepared. The rock contains fragments of crinoids, corals, calcareous algae, bryozoans, foraminifers, and brachiopods. Besides the taxa described below some fragments of undeterminable fenestellids, the bifoliolate cystoporid *Sulcoretepora* sp., and phylloporinid *Rhomboacladia* sp. were found in the investigated thin sections.

The type collection of Nekhoroshev (1932) is housed at the Federal Institute for Geosciences and Natural Research in Berlin. The studied material for the present publication is housed at Senckenberg Forschungsmuseum, Frankfurt am Main, numbers SMF 1694-1709. The occurrence and geological range is given for each taxon under the section “Material” and additional occurrences and ranges given where applicable under the section “Additional occurrences and geological range”.

3 SYSTEMATIC PALAEONTOLOGY

Order Cystoporida Astrová, 1964
Suborder Fistuliporina Astrová, 1964
Family Fistuliporidae Ulrich, 1882

Genus *Fistulipora* M'Coy 1849

*Fistulipora incrustons* (Phillips, 1836)

Figure 1, A-B


Material: 10 colony fragments. SMF 1694. *Goniattites crenistria*–zone (Viséan, Lower Carboniferous), Westenfeld, Germany. SMF 1695. *Arnsbergites gracilis*–zone (Viséan, Lower Carboniferous), Frenkhausen, Germany.
Figure 1. AH specimens from the Viséan, Lower Carboniferous, Westenfeld, Germany. A - *Fistulipora incrustons* (Phillips, 1836). SMF 1694. Longitudinal section. Scale bar = 1 mm. B - *Fistulipora incrustons* (Phillips, 1836). SMF 1694. Tangential section. Scale bar = 0.5 mm. C - *Evactinopora* sp. SMF 1696. Cross section. Scale bar = 2 mm. D - *Goniocladia cellulifera* (Etheridge, 1873). SMF 1697. Scale bar = 1 mm. E - *Evactinopora* sp. SMF 1696. Cross section of the branch. Arrow - median rods of the mesotheca. Scale bar = 0.2 mm. F - *Evactinopora* sp. SMF 1696. Cross section of the branch, axial area. Scale bar = 0.5 mm. G - *Evactinopora* sp. SMF 1696. Longitudinal section of the branch. Arrow - autozooidal diaphragms. Scale bar = 0.5 mm. H - *Meekopora* sp. SMF 1698. Scale bar = 1 mm. I - *Meekopora* sp. SMF 1698. Scale bar = 0.5 mm.
**Description:** Encrusting colony, multilayering encrustings common. Single sheets reaching 0.5 to 3.5 mm and multilayering encrustings more than 10 mm in thickness. Autozooecial apertures rounded to oval, spaced 5 in 1 mm of the colony surface in the growth direction, separated usually by 1-2, rarely by 3 rows of vesicles. Lunaria prominent, 0.16-0.22 mm wide and 0.07-0.1 mm long. Basal diaphragms in the autozooecia thin, horizontal or slightly inclined, up to 7 in 1 mm autozooecial length. Vesicles polygonal in cross-section, having rounded roof in the longitudinal section, spaced 9-10 in 1 mm colony thickness.

**Comparison:** There are a couple of species from the Lower and Upper Carboniferous which are very close to the present material (see also discussion by Bancroft & Wyse Jackson (1995)). Some of these species may be conspecific with *F. incrustons* (Phillips, 1836). *Fistulipora micidolamina* McKinney, 1972 from the Upper Carboniferous of USA is very close to the present material. However, it differs in having smaller (in average 0.26 mm vs. 0.28 mm in present material) and more closely spaced (6 vs. 5) apertures. *F. taydonensis* Trizna, 1958 from the Lower Carboniferous of Kuznetzk Basin possess smaller apertures (0.26-0.28 mm vs. 0.24-0.34 mm in present material) and weakly developed lunaria.

**Additional occurrence and geological range:** In the Lower Carboniferous of British Isles this species occurs in rocks of age from Toumaisian to Namurian. Elsewhere *F. incrustons* has been reported from the Carboniferous of Kazakhstan and North America.

**Remark:** A comprehensive description of the species *F. incrustons* (Phillips, 1836) and a full synonymy list is given in Bancroft & Wyse Jackson (1995).

**Family Hexagonellidae Crockford, 1947**

*Evactinopora* Meek and Worthen, 1865

*Evactinopora* sp.

**Material:** SMF 1696 (four cross-sections of a single colony). *Goniatites crenistria-zone* (Viséan, Lower Carboniferous), Westenfeld, Germany.

**Description:** Erect colony comprising five bifoliate rays, 6 mm in diameter (incomplete). Rays narrowed near their bases, 4.2-4.6 mm wide, reaching 1.5-1.6 mm in thickness. Autozoocia budding at first parallel to the mesotheca for a long distance, then bending towards the colony surface at angles of 35-57° (50.5° in average), semicircular in cross-section at their basis, bearing thin complete diaphragms, separated widely by vesicular skeleton. Autozoocia apertures rounded, with thick peristom, 0.16-0.184 mm in diameter (0.176 mm in average). Vesicles relatively large, with gently curved roofs, near the colony surface flattened, spaced in number 11-13 in 1 mm of the longitudinal section. Mesotheca three-layered, containing numerous median rods. Extrazooidal skeleton strongly developed on the colony surface.

**Comparison:** The present material can not easily be compared with known *Evactinopora* species because no exact tangential section exists. Externally, it differs from Australian species by its smaller dimensions and greater number of rays: *E. irregularis* Crockford, 1947 possesses four rays, and *E. trifoliata* Crockford, 1947 three rays respectively. *E. l. incerta* Morozova, 1981 has comparable colony dimensions. However, it differs in having a larger apertural diameter (0.2-0.27 mm vs. 0.16-0.184 mm in present specimen). *E. radiata*. Meek & Worthen, 1865 is regarded as the closest species to the present material having 4 to 8 rays and very close external dimensions.

**Remark:** Morozova (1981) mentioned the specific name "tribifurcata" for the species *E. trifoliata* Crockford, 1947. This is obviously a typographical error.

**Family Goniocladiidae Waagen & Pichl, 1885**

*Genus Goniocladia* Etheridge, 1876

*Goniocladia cellulifera* (Etheridge, 1873)

**Material:** SMF 1697 (two thin sections of a single colony fragment). *Goniatites crenistria-zone* (Viséan, Lower Carboniferous), Westenfeld, Germany.

**Description:** Bifoliate branches, 0.9 mm thick and 1.7-2.6 mm wide. Autozoocia tubular, semicircular in cross-section at their basis, relatively short, budding

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Table 1. Measurements of *Fistulipora incrustons* (Phillips 1836) (4 colonies).

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<tr>
<td>Aperture width</td>
<td>31</td>
<td>0.28</td>
<td>0.031</td>
<td>10.968</td>
<td>0.24</td>
<td>0.34</td>
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<tr>
<td>Lunarium width</td>
<td>7</td>
<td>0.20</td>
<td>0.027</td>
<td>13.697</td>
<td>0.16</td>
<td>0.24</td>
</tr>
<tr>
<td>Lunarium length</td>
<td>7</td>
<td>0.10</td>
<td>0.019</td>
<td>18.903</td>
<td>0.072</td>
<td>0.13</td>
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from thin mesotheca, opening on both sides of the median carina. Autozooecial apertures arranged regularly in 4 rows on both side of median carina, rounded, with moderately developed lunaria, 0.14-0.16 mm in diameter, spaced 2.5 on 2 mm along the branch. Small styles in lunaria present. Autozooecial walls 0.02-0.04 mm thick, granular-prismatic. Extrazooecial skeleton consisting of columnar calcite crystals oriented perpendicularly to the colony surface. Vesicular skeleton weakly developed, consisting of low vesicles with flattened roofs.

Comparison: The only present fragments reveal enough features for recognition of the species *Goniocladia cellulifera* (Etheridge, 1873). However, it is difficult to make a comprehensive comparison because of the absence of external parameters as colony dimensions. Generally, the present material differs from other species, known from the Carboniferous, by having relatively thick and broad branches. *Goniocladia stepanovi* Nikiforova, 1927 from the Lower Carboniferous of Ukraine has smaller and more closely spaced apertures. Additional occurrences and geological range: Lower Carboniferous of British Isles.

Genus *Meekopora* Ulrich in Miller, 1889

*Meekopora* sp.

Figure 1, H-I, Figure 2, A-B

Material: SMF 1698. *Goniatites crenistria*-zone (Viséan, Lower Carboniferous), Westenfeld, Germany.

Description: Bifoliate colony, 1.8-2.06 mm in thickness. Autozoecia short, semicircular in cross section on their basis, completely separated by vesicular skeleton. Apertures 0.13-0.18 mm in diameter (0.16 mm in average), spaced 4—4.5 in 2 mm of the colony surface. Lunaria well-developed, 0.08-0.12 mm long and 0.08-0.12 mm wide. Autozoecial diaphragms rare, thin, planar. Skeletal vesicles relatively large, with rounded roofs, covered at the colony surface by thick layer of a dense calcitic material, arranged in 2-3 rows between autozoecia.

Comparison: The present material is very close to the species *Meekopora approximata* Ulrich 1890, described by Nekhoroshev (1956) and Trizna (1958) from the Lower Carboniferous of Siberia. The present material has a thicker colony and smaller apertures (0.13-0.18 mm as against vs. 0.2 mm in Nekhoroshev’s material, and 0.2-0.22 in Trizna’s material).

Order Trepostomida Ulrich, 1882
Suborder Amplexoprina Astrová, 1965
Family Stenoporidæ Waagen & Wentzel, 1886

Genus *Stenopora* Lonsdale, 1844

*Stenopora* sp.

Figure 2, H-K

Material. SMF 1699 (single colony, one tangential and two longitudinal sections). *Arnsbergites gracilis*-zone (Viséan, Lower Carboniferous), Frenkhausen, Germany.

Description: Encrusting colony, 0.7-1.2 mm in thickness. Autozoecia budding only for short distance parallel to the substrate, then bending sharply and intersecting the colony surface at the right angle. Autozoecial apertures rounded to polygonal, spaced 5 in 2 mm in each direction, 10 in 1 mm² of the colony surface. Maculae consisting of larger autozoecia apparently present. Acanthostyles large, with distinct cores, originating from the basis of the exozone, spaced 8 in 1 mm² of the colony surface. Autozoecial walls in the endozone granular-prismatic, 0.02 mm in thickness; in the exozone regularly thickened, 0.076-0.14 mm in thickness; in the deeper tangential section displaying central zone of lighter material.

Comparison: *Stenopora* sp. is very close to the species *S. confitioensis* Karklins, 1986 from the Chester (Late Mississippian) of Utah, USA. The two species are particular similar in the wall structure with rare monilae thickenings, large acanthostyles, rare exilazoecia and autozoecial budding pattern. *S. confitioensis* develops ramose solid stems with a narrow endozone and secondary overgrowths, and has smaller autozoecia (in average 0.21 vs. 0.26 in the present material).

Genus *Stenodiscus* Crockford, 1945

*Stenodiscus tumida* (Phillips, 1836)

Figure 3, A-C

1912 *Stenopora redesdalensis* Lee: 153-157, PI. 14, Figure 5A-D, PI. 15, Figures 1, 2.

Table 2. Measurements of *Stenopora* sp. (Abbreviations as in Table 1 ).

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<tr>
<td>Aperture width</td>
<td>20</td>
<td>0.26</td>
<td>0.0348</td>
<td>13.4123</td>
<td>0.22</td>
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<tr>
<td>Acanthostyle width</td>
<td>16</td>
<td>0.09</td>
<td>0.0109</td>
<td>11.6779</td>
<td>0.08</td>
<td>0.11</td>
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Figure 2. A-G All from the Viséan, Lower Carboniferous, Westenfeld, Germany; H-K all from the Viséan, Lower Carboniferous, Frenkhausen, Germany. A - *Meekopora* sp. SMF 1698. Tangential section displaying apertures with styles (arrow). Scale bar = 0.5 mm. B - *Meekopora* sp. SMF 1698. Tangential section displaying apertures with styles (arrow). Scale bar = 0.5 mm. C - *Stenophragmidium* sp. SMF 1702. Tangential section. Scale bar = 0.25 mm. D - *Hinaclema* sp. SMF 1703. Tangential section. Scale bar = 0.2 mm. E - *Hinaclema* sp. SMF 1703. Scale bar = 1 mm. F - *Stenophragmidium* sp. SMF 1702. Longitudinal section displaying hemiphragms (arrow). Scale bar = 0.2 mm. G - *Hinaclema* sp. SMF 1703. Longitudinal section. Scale bar = 0.2 mm. H - *Stenopora* sp. SMF 1699. Cross section of the autozoocelial chambers. Scale bar = 0.5 mm. I - *Stenopora* sp. SMF 1699. Longitudinal section. Scale bar = 1 mm. J - *Stenopora* sp. SMF 1699. Tangential section displaying acanthostyles. Scale bar = 0.25 mm. K - *Stenopora* sp. SMF 1699. Longitudinal section displaying acanthostyle cores. Scale bar = 0.5 mm.
Figure 3. All specimens from the Viséan, Lower Carboniferous, Westenfeld, Germany. A - Stenodiscus tumida (Phillips, 1836). SMF 1700. Cross section of the branch. Scale bar = 0.5 mm. B - Stenodiscus tumida (Phillips, 1836). SMF 1700. Tangential section. Scale bar = 0.5 mm. C - Stenodiscus tumida (Phillips, 1836). SMF 1700. Tangential section. Scale bar = 0.25 mm. D - Rhabdomeson progracile Wyse Jackson & Bancroft, 1995. SMF 1706. Tangential section. Scale bar = 0.5 mm. E - Rhabdomeson progracile Wyse Jackson & Bancroft, 1995. SMF 1706. Cross section. Scale bar = 0.5 mm. F - Streblotrypa (Streblotrypa) pectinata Owen, 1966. SMF 1704. Oblique section of the branch. Scale bar = 1 mm. G - Streblotrypa (Streblotrypa) pectinata Owen, 1966. SMF 1704. Longitudinal section (peel). Scale bar = 0.5 mm. H - Streblotrypa (Streblotrypa) pectinata Owen, 1966. SMF 1704. Tangential section. Scale bar = 0.5 mm. 1 - Stenophragmidium incrustans Owen, 1973. SMF 1701. Oblique section displaying hemiphragms (arrows). Scale bar = 0.5 mm. J - Stenophragmidium incrustans Owen, 1973. SMF 1701. Tangential section. Scale bar = 0.5 mm.


Description: Ramose colony, 2.3 mm in diameter. Endozone 1.14 mm wide; exozone 0.6 mm wide. Autozooidal apertures rounded to slightly polygonal, 4-6 in 2 mm (5 in average) of any direction, 4-8.5 in 1 mm² of the colony surface (7 in average). Diaphragms in autozooids common, usually positioned in transitional area from the endozone to the exozone. Acanthostyles small, numerous, 7-12 surrounding each aperture, variable in size. Exilazooecia small, rare, often 3-4 clustered together. Autozooidal walls in the endozone thin, granular-prismatic, in the exozone regularly thickened, laminated.

Comparison: The species Stenodiscus tumida (Phillips, 1836) is very close to the species St. haddingtonensis (Lee, 1912). The latter differs from the present material by more closely spaced apertures (7 vs. 4-6 in present material). The species Stenopora (= Stenodiscus) redesdalensis Lee, 1912 is a synonym of Stenodiscus tumida (Phillips, 1836) (P.N. Wyse Jackson, pers. comm.).

Additional occurrences and geological range: Lower Carboniferous of British Isles.

Genus Stenophragmidium Bassler, 1952

Stenophragmidium incrustons Owen, 1973

Figure 3, 1-J

1973 Stenophragmidium incrustons Owen: 301-302, PI. 9, Figures f, g.

Material: SMF 1701 (single fragment displaying tangential and part of a longitudinal section). Goniatites crenistria-zone (Viséan, Lower Carboniferous), Westenfeld, Germany.

Description: Thin encrusting colony (about 0.5-0.6 mm in thickness; no exact longitudinal section exists). Apertures polygonal in the deep tangential section; rounded to roughly polygonal in the exozone, spaced 4-5.5 in 2 mm and 5.5-6.5 in 1 square mm of the colony surface. Hemiphragms rare, apparently 1-2 in autozooids, restricting two-thirds of the zoooidal chamber. Exilazooecia rounded to roughly polygonal in their cross section, spaced 1-2 in 1 square mm of the colony surface. Acanthostyles of two types. Large acanthostyles having distinct, dark coloured cores and wide laminated sheathes spaced 8-10 in 1 square mm and 2-4 around each aperture. Small, dark coloured microacanthostyles abundant, 0.012-0.03 mm in diameter, irregularly spaced on the colony surface. Walls granular prismatic, 0.02-0.025 mm thick in the endozone; U-shaped reversely laminated, with dark medial line, 0.078-0.1 mm thick in exozone.

Comparison: Stenophagmidium incrustons Owen, 1973 differs from the species St. mirandum Dunaeva, 1964 by larger and more widely spaced apertures, from the species St. obscurum Perry and Gutschick, 1959 by more abundant exilazooecia, and from the species St. megistum Perry and Gutschick, 1959 by smaller acanthostyles.

Additional occurrences and geological range: Upper Viséan, Tullaghoge, County Tyrone, Ireland.

Stenophagmidium sp.

Figure 2, C, F

Material: SMF 1702. (single fragment displaying tangential and part of a longitudinal section). Goniatites crenistria-zone (Viséan, Lower Carboniferous), Westenfeld, Germany.

Description: Encrusting colony, 0.4-0.6mm in thickness. Autozooidal apertures rounded to strictly polygonal, spaced 6-6.5 in 2 mm in any direction and

Table 3. Measurements of Stenodiscus tumida (Phillips, 1836). (Abbreviations as in Table 1).

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<td>Aperture width</td>
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<td>0.048</td>
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<td>0.36</td>
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<tr>
<td>Acanthostyle diameter</td>
<td>30</td>
<td>0.04</td>
<td>0.008</td>
<td>19.81</td>
<td>0.02</td>
<td>0.06</td>
</tr>
<tr>
<td>Exilazooecia diameter</td>
<td>15</td>
<td>0.08</td>
<td>0.029</td>
<td>38.33</td>
<td>0.03</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Table 4. Measurements of Stenophagmidium incrustons Owen, 1973. (Abbreviations as in Table 1).

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>X</th>
<th>SD</th>
<th>CV</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aperture width</td>
<td>20</td>
<td>0.29</td>
<td>0.022</td>
<td>7.301</td>
<td>0.245</td>
<td>0.348</td>
</tr>
<tr>
<td>Exilazooecia diameter</td>
<td>10</td>
<td>0.13</td>
<td>0.042</td>
<td>32.51</td>
<td>0.064</td>
<td>0.181</td>
</tr>
<tr>
<td>Acanthostyle diameter</td>
<td>10</td>
<td>0.06</td>
<td>0.013</td>
<td>20.84</td>
<td>0.048</td>
<td>0.096</td>
</tr>
<tr>
<td>Acanthostyles per aperture</td>
<td>10</td>
<td>3</td>
<td>0.66</td>
<td>22.22</td>
<td>2</td>
<td>4</td>
</tr>
</tbody>
</table>
12 in 1 mm² of the colony surface in non-macular area, 4-5 in 2 mm in any direction and 7 in 1 mm² of the colony surface in maculae. Hemiphragms present in the autozooecia. Maculae consisting of larger apertures and exilazooecia between them. Exilazooecia polygonal, numerous in maculae, partly separating autozooecia, and rare in non-macular area. Acanthostyles of one type, small, indistinct because of re-crystallisation, restricted to the outer exozone, reaching 0.026-0.04 mm in diameter. Autozooecial walls thin in the exozone, slightly thickened in the exozone, reaching 0.02-0.023 mm in thickness. Monilae-shaped thickenings indistinct.

**Comparison:** Present material is strongly recrystallized. However, it reveals typical features of the genus *Stenophragmidium*. The present example differs from the species *Stenophragmidium incrustons* Owen, 1973 by smaller apertures, more abundant exilazooecia and rare macroacanthostyles.

Family Crustoporididae Dunaeva & Morozova, 1967

**Genus Hinaclema** Sakagami & Sugimura, 1987

**Hinaclema** sp.

Figure 2, D-E, G

**Material:** SMF 1703. *Goniatites crenistria*-zone (Viséan, Lower Carboniferous), Westenfeld, Germany.

**Description:** Encrusting colony, 0.3 mm in thickness, with an indistinct division between exo- and endozone. Autozooecia tubular, short, circular in their cross section. Autozooecial apertures rounded to oval, 0.13-0.18 mm in diameter (0.16 mm in average), spaced 13 in 2 mm of the colony surface. Exilazooecia abundant, but not completely separating autozooecia, rounded to slightly polygonal in their cross section, 0.26 mm in diameter, restricted to the exozone. Acanthostyles abundant, spaced 5 around each aperture, restricted to the exozone, 0.026-0.039 mm in diameter. Walls irregularly thickened, 0.02-0.04 mm thick in endozone, 0.02-0.04 mm thick in exozone.

**Comparison:** *Hinaclema* sp. has clear differences to the known species of *Hinaclema*, especially in having thin colony with small and closely spaced apertures. However, the present material is too scarce to allow erection of a new species.

Order Rhabdomesida Astrová & Morozova, 1956

**Family Streblotrypeidae Ulrich, 1890**

**Genus Streblotrypa** (Ulrich MS) Vine, 1884b

**Sub-genus Streblotrypa** (Streblotrypa) (Ulrich MS) Vine, 1884b

**Streblotrypa** (Streblotrypa) *pectinata* Owen, 1966

Figure 3, F-H

1966 *Streblotrypa pectinata* Owen: 144, Pl. 10A, B, C.


**Holotype:** LL. 2995, Manchester Museum, England; Upper Viséan, Treak Cliff, Castleton, Derbyshire, England.

**Material:** SMF 1704. *Goniatites crenistria*-zone (Viséan, Lower Carboniferous), Westenfeld, Germany. SMF 1705. *Arnsbergites gracilis*-zone (Viséan, Lower Carboniferous), Frenkhausen, Germany.

| Table 5. Measurements of *Stenophragmidium* sp. (Abbreviations as in Table 1) |
|-----------------------------------|-----|-----|-----|-----|-----|
| Aperture length                   | 15  | 0.31| 0.038| 12.48| 0.2 | 0.36 |
| Aperture width                    | 15  | 0.24| 0.021| 8.58 | 0.22| 0.28 |
| Exilazooecia diameter             | 15  | 0.07| 0.02 | 31.04| 0.04| 0.1  |

| Table 6. Measurements of *Streblotrypa* (*Streblotrypa*) *pectinata* Owen, 1973. ADB - Distance between aperture centres along the branch. AAB - Distance between aperture centres across the branch. (Other abbreviations as in Table 1) |
|---------------------------------|-----|-----|-----|-----|-----|-----|
| Aperture width                  | 11  | 0.09| 0.016| 18.48| 0.07| 0.12 |
| Metazooecia diameter            | 20  | 0.03| 0.006| 22.20| 0.01| 0.04 |
| ADB                             | 6   | 0.44| 0.043| 9.666| 0.38| 0.48 |
| AAB                             | 10  | 0.31| 0.020| 6.509| 0.27| 0.34 |
| Acanthostyle diameter           | 10  | 0.03| 0.002| 9.11 | 0.02| 0.03 |
Description: Ramose colonies, 0.6-1.4 mm in diameter. Exozone distinct, 0.15-0.54 mm wide. Autozooecia budding from a middle axis in a distinct spiral order, initially parallel to the axis, then bending outwards gently; in the exozone bending sharply and intersecting the surface at the right angle. Autozooecial apertures oval, arranged in diagonal rows on the colony surface, spaced 5.5-5.5 longitudinally and 6.5-8 diagonally. Metazooecia numerous, arranged in two rows between apertures, ovaly or irregularly shaped. Each aperture surrounded usually by 9-12 metazooecia. Acanthostyles numerous, quite large, budding from the basis of the exozone. Autozooecial walls granular-prismatic, quite thick in the endozone; fine laminated, considerably thickened in the exozone. Superior and inferior hemisepta absent.

Comparison: Streblotrypa (Streblotrypa) pectinata Owen, 1973 is very close to the species S. (Streblotrypa) cortacea Owen, 1966 from the Lower Carboniferous of Scotland, but differs in having thinner exozone and more abundant metazooecia.

Additional occurrences and geological range: Lower Carboniferous (Viséan) of British Isles, Belgium and Russia.

Rhabdomeson reguläre Nekhoroshev, 1932

Additional occurrences and geological range: Lower Carboniferous of British Isles (Courceyan-Pendleian), Belgium and Russia.
hemisepta well developed; inferior hemisepta absent. Autozooecial apertures ovally shaped, quite narrow, arranged in regular diagonal rows. Single large macroacanthostyle situated in interspaces between apertures. Microacanthostyles small, arranged by 1-2 between macroacanthostyles. Autozooecial walls in the endzone 0.01-0.013 mm in thickness, granular-prismatic, in the exozone thick and laminated.

**Comparison:** The species *Rhabdomeson reguläre* is very close to the species *Rh. progracile* Wyse Jackson & Bancroft, 1995. However, *Rh. reguläre* differs in having smaller apertures (averaged 0.076 vs. 0.10 mm.) as well as by weakly developed superior hemisepta.

**Additional occurrences and geological range:** Lower Carboniferous, Viséan, Germany; Lower Carboniferous, Tulskii Horizont, Russia (Middle Don); Lower Carboniferous, Ukraine.

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**Family Arthrostylidae Ulrich, 1882**

**Genus Pseudonematopora Balakin, 1974**

*Pseudonematopora planatus* Wyse Jackson, 1996

1996 *Pseudonematopora planatus* Wyse Jackson: 126-127, Figure 3c, 10-15.

**Holotype:** BMNH PD9450, The Natural History Museum, London. Upper part of the Glencar Limestone (Viséan, Asbian), Carrick Lough, County Fermanagh, Ireland.

**Material:** Four colonies SMF 1708. *Goniattites crenistria-zone* (Viséan, Lower Carboniferous), Westenfeld, Germany.

**Description:** Ramose colony, circular or slightly angular in cross-section, 0.68-0.72 mm in diameter (0.7 mm in average). Short autozoecia budding in spiral order from the central axis. Hemisepta absent; terminal diaphragms common. Autozoecial apertures ovally shaped, 0.145-0.16mm wide, arranged in regular diagonal rows. Autozoecia displaying two types of walls - the inner bright granular-prismatic and the outer dark laminated. The inner granular-prismatic- walls building three-layered endozone walls consisting of two bright outer layers and the dark inner one. No heterozooecia and styles present.

**Comparison:** The species *Pseudonematopora planatus* differs from other species of the genus in having smaller apertures, thinner colonies and absence of skeletal cysts (named by Goijunova (1985) tektitozooecia). The species *Ps. balakini* Gotjunova, 1988 from the Middle Carboniferous of Mongolia has rare to vanishing heterozooecia, as well as thicker branches and larger apertures.

**Additional occurrences and geological range:** The type locality: Viséan, Lower Carboniferous.

- Family Hyphasmoporididae Vine, 1885
- Genus *Clausotrypa* Bassler, 1929

1973 *Sulcoretepora ramosa* Owen: 304, Plate 9a-c.


**Holotype:** BELUM Kl 830. Ulster Museum. Rossmore Mudstone (Upper Viséan); Tullaghoge, County Tyrone, Ireland.

**Material:** Two oblique thin sections of a single colony. SMF 1709. *Goniattites crenistria-zone* (Viséan, Lower Carboniferous), Westenfeld, Germany.

**Description:** Ramose colony with secondary overgrowth, 1.04—1.5 mm in diameter. Autozoecia budding from the indistinct central axis, bending sharply outwards, having oval, 0.1-0.12 mm wide apertures. Acanthostyles very abundant, at least eight surrounding each aperture, 0.04-0.05 mm in diameter, having distinct 0.01-0.013 mm wide hyaline cores. Autozoecial diaphragms rare, thin, slightly curved proximally. Zooecial walls granular prismatic, 0.02 mm thick in the endzone; coarsely laminated, thickened in the exozone. Heterozooecia (tektitozooecia after Gotjunova 1985) budding from the base of the exozone, irregularly shaped in cross section, 0.06-0.08 mm in diameter, bearing frequent planar diaphragms.

**Comparison:** The species *Clausotrypa ramosa* (Owen, 1973) differs from the species *C. limpida* Gotjunova,
1988 by smaller apertures (0.1-0.12 mm vs. 0.15-0.19mm) and abundant acanthostyles. C. moniicola (Eichwald, 1860) has thicker branches and larger apertures.

Additional occurrences and geological age: Viséan, Lower Carboniferous; Counties Tyrone and Fermanagh, Ireland.

4 CONCLUSIONS

The investigation demonstrated a close similarity between the Lower Carboniferous bryozoan faunas of Germany and British Isles. Eight of eleven species occur in both basins. The species Fistulipora incrustons (Phillips, 1836) is cosmopolitan, occurring in the Lower Carboniferous of Europe, Russia and North America. Another species with a wide distribution is Rhabdomeson progracile Wyse Jackson & Bancroft, 1995, which was also reported from the Lower Carboniferous of Russia (Gotjunova, 1985). Rhabdomeson regulare Nekhoroshev, 1932 was originally described from Germany, and reported later in Lower Carboniferous of Russia (Morozova, 1955). Six species are apparently restricted to the Lower Carboniferous of British Isles and Germany.

The genera Evactinopora, Meekopora and Hinaclema were found for the first time in the Lower Carboniferous of Europe. The genus Evactinopora is quite widespread in the Lower Carboniferous of North America and Australia. One questionable species was described by Morozova (1981) from the Middle Carboniferous of south-eastern Russia. The genus Meekopora is common in the Lower Carboniferous rocks nearly worldwide. Two previously known species of the genus Hinaclema were reported from the Lower Carboniferous of Japan and Uzbekistan (Sakagami & Sugimura, 1987, Schastlivtzeva, 1991).

ACKNOWLEDGEMENTS

I am greatly thankful to Dieter Weyer, Berlin for providing of the material for study. Dieter Korn, Berlin is thanked for information regarding the position and stratigraphy of the Lower Carboniferous localities in Sauerland.

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Bryozoans from the Artinskian (Lower Permian) Great Bear Cape Formation, Ellesmere Island (Canadian Arctic)

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ABSTRACT: Samples containing bryozoans collected during the 1898-1902 expedition of the ‘Fram’ to the Canadian Arctic islands have been reinvestigated. A small amount of calcareous rock derived from the Artinskian Great Bear Cape Formation has yielded a very rich bryozoan fauna comprising 37 taxa (four of the Order Cystoporida, six of the Order Trepostomida, seven of the Order Rhabdomesonida, one of the Order Cryptostomida, one of the Order Phylloporinida and eighteen of the Order Fenestrida). The faunal composition when compared with contemporaneous units of adjacent Arctic areas shows most similarity to Spitsbergen and Timan-Pechora. The bryozoans support the ages previously known from conodont occurrences.

1 INTRODUCTION

The investigated material was collected during the 1898-1902 ‘Second Expedition in the Fram’ to the Canadian Arctic islands (Figure 1). The collection is now housed in the Geological Museum (former Palaeontological Museum) (prefix PMO), University of Oslo, Norway, and the figured bryozoans herein are kept in the collection of type and illustrated material. The expedition was under Captain Otto Sverdrup’s (1854-1930) leadership, and undertook botanical, geographical, geological and zoological investigations in the unmapped Arctic area. Per Schei (1875-1905) was the expedition geologist, and he was responsible for collecting the samples investigated here.

The plan of the expedition was to return home in 1900, but they were unable to get out of the ice in Gaasefjorden [Goose Fjord] until the following year. The fourth and unintended 1902 season of the expedition was also utilized for maximum exploration. The men travelled as far as to the northern tip of Ellesmere Island (a distance of 635 kilometres) with dogs and sleds, and collected thousands of geological samples. Material was sent to experts worldwide after the expedition, and 38 scientific reports were published.

The Colin Archer constructed vessel Fram was used, prior to the Canadian expedition, by Fridtjof Nansen (1861-1930) during his 1893-1896 North Pole expedition (Polar Sea), but he had to head back to Norway without reaching the Pole. Roald Amundsen (1872-1928) later used Fram for his successful South Pole expedition in 1910-1912. The vessel is now on display in the Fram Museum in Oslo, Norway.

Bryozoan samples have previously been published from the Fram collection, but identifications were primarily based on external features - only a few thin sections were made (Tschemyschew & Stepanov, 1916).

2 METHODS

The current investigation is based on material from the same locality, Great Bear Cape [Store Bjornekap] on the Bjorne Peninsula, SW Ellesmere Island, and from the same stratigraphic unit, the Great Bear Cape (GBC) Formation. The museum collection contains both specific samples with visible bryozoans, mainly fenestrates, and also larger bioclastic limestone samples which were cut to obtain bryozoans in different internal orientations. 140 thin sections and 70 acetate peels were prepared for this study.

3 GEOLOGICAL SETTING

When Tschemyschew & Stepanov (1916) published their paper on brachiopods and bryozoans, the investigated unit was believed to be of Late Carboniferous age (see also Schei in Sverdrup, 1904). Since then.
comprehensive work has been carried out on the
gEOLOGY of the Canadian Arctic islands - the Sverdrup
Basin - by P. Harker, R. Thorsteinsson, E.T. Tozer,
B. Beauchamp and C.M. Henderson, and the modern
stratigraphic definitions are presented in detail in
Beauchamp & Henderson (1994).

It is uncertain whether P. Schei collected the bryo-
zoan samples from talus or from bedrock. It is, how­
ever, certain that his samples are from the ‘Great Bear
Cape Limestone’, which Thorsteinsson (1974) corre­
lated with the Late Permian Degerböl Formation. The
rocks below the ‘Great Bear Cape Limestone’ were
in the same work correlated with the Assistance
Formation (Ufimian) elsewhere in the Canadian Arctic.
Prior to Thorsteinsson’s work Nassichuk et al. (1965)
reported Artinskian ammonoids in the ‘Assistance
Formation’ here, causing more stratigraphic confusion,
and work began to re-investigate the rocks. The ‘Great
Bear Cape Limestone’ continued as the ‘Unnamed
Formation’ in subsequent publications (e.g. Beauchamp
et al., 1989), until new fieldwork by B. Beauchamp and
C. M. Henderson (1984-1992) revealed what is now
the accepted modern stratigraphic scheme.

The lower part of the ‘Unnamed Formation’, i.e.
the succession correlated as Assistance Formation by
Thorsteinsson (1974), is now included in the Raanes
Formation; the upper part of the ‘Unnamed Formation’,
i.e. the succession correlated as Degerböl Formation
by Thorsteinsson (1974), is now included in the Great
Bear Cape Formation (Figure 2).
The Great Bear Cape Formation is defined by Beauchamp & Henderson (1994) as 'a unit of resistant, yellowish-weathering, pure to locally sandy, variably cherty, highly fossiliferous limestone that overlies either the Raanes or the Trappers Cove formations' (Figure 2). The top of the unit is stripped off at the Björne Peninsula locality. Rich conodont faunas contain species of *Adetognathus*, *Sweetognathus*, *Neostreptognathodus* and *Mesogondolella*, placing the unit in the P6b, P7 and P8 (Artinskian) and the top in the P9 (Artinskian-Kungurian) conodont zones of Beauchamp et al. (1989). As the top is stripped off where the current material derives from, the age of the investigated bryozoan fauna is most probably Artinskian. For further discussion of the stratigraphic problem see Beauchamp & Henderson (1994).

4 BRYOZOAN FAUNA

70 acetate peels and 140 thin sections have been prepared from selected samples from the Great Bear Cape Formation. These samples have revealed a high diversity bryozoan fauna.

The following species of non-fenestellid orders have been identified:

- Cystoporidida: *Fistulipora volongensis* (Nikiforova, 1938);
- *Fistulipora* sp.; *Cyclotrypa distincta* (Morozova, 1986);
- *Ramiporida variolata* (Shul'ga-Nesterenko, 1933);
- *Tabulipora* sp.; *Stenophragmidium* sp.; *Rhombotrypella cf. amdrupensis* (Ross & Ross, 1962);
- *Dyscritella vulgata* (Gorjunova, 1972);
- *Dyscritella tenuis* (Kruchinina, 1973);
- *Ulrichotrypa ramulosa* (Bassler, 1929);
- *Rhabdomesonia: Pseudonematopora sp.; Streblascopora vera* (Morozova, 1986);
- *Streblascopora germana* (Bassler, 1929);
- *Claustrophyra monticola* (Eichwald, 1860);
- *Primorella superba* (Morozova, 1981);
- *Primorella tundrica* (Kruchinina, 1986);

Selected taxa are illustrated in Figure 3.

The following species of the Order Fenestrida have been identified:

- *Alternifenestella bifida* (Eichwald, 1860);
- *Alternifenestella crassiseptata* (Shul'ga-Nesterenko, 1941);
- *Alternifenestella cyclotriangulata* (Eichwald, 1860);
- *Alternifenestella cf. invisita* (Kruchinina, 1986);
- *Fabifenestella cf. subvirgosa* (Shul'ga-Nesterenko, 1952);
- *Fabifenestella cf. virgosa* (Eichwald, 1860);
- *Fabifenestella tortuosa* (Trizna & Klautsan, 1961);
- *Fenestella akselensis* (N akrem, 1995);
- *Rectifenestella microporata* (Shul'ga-Nesterenko, 1939);
- *Rectifenestella robusta* (Shul'ga-Nesterenko, 1936);
- *Polypora confirmata* (Kruchinina, 1986);
- *Polypora kossjensis* (Ravikovich, 1948);
- *Polypora kutorgae* (Stuckenberg, 1895);
- *Polypora martis* (Fischer, 1837);
- *Polypora voluminosa* (Trizna & Klautsan, 1961);
- *Penniretepora invisa* (Trizna, 1939); *Acanthocladiad sf. sparsifurcata* (Shul'ga-Nesterenko, 1939) and *Acanthocladiad sf. rhombicellata* (Shul'ga-Nesterenko 1955). Selected taxa are illustrated in Figure 4.

The majority of these species have an Early Permian Sakmarian-Artinskian distribution in the Urals and the Timan-Pechora region of Russia, but a stratigraphical Artinskian-Kungurian range in Svalbard, Arctic Norway. The genus *Phragmophera* (Gorjunova, 1969), was originally described from the Upper Carboniferous of the Urals. The new species from the Great Bear Cape Formation is the second known species of this genus. The genus *Pseudonematopora* (Balakin, 1974), is quite exotic in Permian rocks; it is more commonly found in the Lower to Middle Carboniferous of Europe, Middle Asia, and Mongolia.

5 CONCLUSIONS

The Great Bear Cape Formation (Artinskian) ranges from the upper Irginian through most of the Sarginian Horizons as correlated with Western Siberian units (Morozova & Kruchinina, 1986), and is contemporary with most of the Artinskian Gipshuken Formation of Spitsbergen and the Hambergjellet Formation of Bjornoya (Nakrem et al., 1992). Presence/absence analysis of bryozoan species through different Early Permian units of the current Arctic regions is depicted in Figure 5. From this analysis it is evident that the faunal composition of the Great Bear Cape Formation is most similar to the Kungurian faunas of Spitsbergen (Svalbard), and that they form a group together with Kungurian faunas of Timan-Pechora (western Siberia), as well as with those of the Artinskian of Bjornoya (Svalbard). Faunal migrations through time from the Sverdrup Basin to the Svalbard and Timan-Pechora Basins may explain this discrepancy in stratigraphic position. The Great Bear Cape Formation fauna is quite different from the Sakmarian and Artinskian faunas of Timan-Pechora.

As noted above, the Great Bear Cape Formation is well dated by conodonts, and the bryozoans support the correlations provided by conodonts when compared with adjacent Arctic regions, although many bryozoan species also range up into the Kungurian. The current investigation also clarifies questions raised in Morozova & Kruchinina (1986, p. 25) about their reported occurrence of the Artinskian species *Rhombo­trypella invulgata* in the Belcher Channel (Sakmarian) and Assistance (Ufimian) Formations. The material described by Morozova & Kruchinina (1986) was collected from rocks at the time assigned to the Belcher Channel Formation and the Assistance Formation, but should be placed within the Great Bear Cape Formation according to the revised stratigraphical scheme by Beauchamp & Henderson (1994, pp. 564-565).
Figure 3. Non-fenestellid bryozoans. All are thin sections. Scale bars: 0.5 mm A-B, F, N; 1.0 mm C-E, G-M, O.

Figure 5. Cluster diagram (UPGMA, Unweighted Pair Group Method with Arithmetic Mean, M VSP, Kovach 2002) showing similarities between Lower Permian units of the Arctic region, analysis based on presence/absence of species from Great Bear Cape Formation, fauna lists in Morozova & Kruchinina (1986), and Nakrem (1994, 1995).

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ABSTRACT: Biofilms found epizoic on shell-encrusting laminar Bryozoa from various sites in Japan and New Zealand have been compared within the respective latitudinal gradients (cool-temperate - subtropical/marginal tropical). We observed a decrease of biofilm fouling of bryozoans from cool-temperate towards warm temperatures. On the other hand, abundance of laminar bryozoans with high morphological potential in overgrowth competition increases with lower latitudes. Accordingly, there are morphological signals of competitive rather than symbiotic interactive dynamics of bryozoans and epizoic microorganisms especially in warm waters. For all latitudes sampled, morphological taxonomy of bacteria revealed that the association of certain microorganisms and bryozoans is colony-specific rather than species-specific. Alpha-Proteobacteria and gram positive bacteria were predominant among the bryozoan-associated biofilms sampled.

1 INTRODUCTION

Living substrates such as bryozoans represent one of the common settling grounds for biofilms in which bacteria, diatoms, cyanobacteria, green algae and/or fungi are abundant (Voigt 1973, Winston 1988, Winston & Håkansson 1989, Schmaljohann 1993). This may result in competitive interactions between the living bryozoan substrate and its microbial biofilms (Soule and Soule 1977). The response of the respective bryozoan species becomes evident either in a chemical, or in a morphological pathway of defense.

The rise of marine biotechnology has resulted in an increase of funding for the molecular study of bryozoans and their associated microorganisms. Due to the presence of alkaloids (e.g. antibiotics, antmyotics), many species have been the subject of intensive investigations since the 1980s (Prinsep and Morris 1996). Many of those pharmaceutically relevant compounds found in bryozoans are actually not produced by bryozoans alone. For Bugula neritina it has been suggested that Bryostatin - an anti-cancer drug - is synthesised by endozoic microorganisms (Davidson et al. 2001).

Nowadays, modern tools of molecular taxonomy tend to overshadow aspects of morphological studies of bryozoan-associated microorganisms such as distribution patterns of microbial morphologies. Yet, environmental conditions may appear more convincingly in terms of relative dominance of microbial morphotypes per unit of habitat space. Particularly phototrophic bacteria such as cyanobacteria, microbenthic algae, such as diatoms, and fungi represent taxon groups of remarkable morphological heterogeneity and thus can be characterized by morphological and morphometric properties using combined field and microscopic assessments (Golubic et al. 1999). Cyanobacteria are able to organise themselves into chains, squares, spots, mats, and other morphologically distinct growth structures representing a kind of
true formany diatom species which form colonies in the shape of mats and chains (Paterson et al. 1986, Krumbein 1987, Wuchter et al. 2003). Aside from the morphology and colonial behaviour of dominant species or taxon groups, their way of interaction both with the living host and external factors such as bathymetry, sedimentation, pH, nutrient concentrations etc. influences the phenotype of a biofilm. Thus, the local dominance of morphologically distinct species provides biofacies, or in terms of paleoecology, environmental expression.

Modifications of bryozoan colonial growth structure as a response to microbial fouling may provide additional information about the nature of the microbial biofilms on or adjacent to them. This has been documented in previous parts of our studies of the bryozoans and microbial communities of shallow marine waters in cool-temperate and subtropical areas of Japan and New Zealand, and tropical areas in the Philippines and Red Sea (Scholz & Krumbein 1996, Scholz 2000). Advancing existing classifications (Jackson 1979, Lidgard 1985), we have subdivided the encrusting bryozoan morphotypes into different growth types that largely reflect the biological potentials of bryozoans to overgrow biomats (biofilms and microbial mats) for space on substrate surfaces. Characteristics and frequency distribution patterns of these types (s-/c-/m-/z-laminae, runners, spots, bryostromatolites) (Kaselowsky et al. 2002, 2004; Kaselowsky 2003) have thus documented their paleoecological and paleoclimatological relevance. In the present study, we shift our attention from bryozoan morphology to structure and taxonomy of bryozoan-associated biofilms and microbial mats. As a point of departure, we address two basic questions:

1) Since the growth of bryozoan laminae proceeds in interaction with biofilms, is there a latitudinal gradient in microorganisms colonising bryozoans as a living sediment, from cold-temperate to subtropical/marginally tropical?

2) Are the biofilms occurring on bryozoans species-specific, or colony-specific?

The first opens an additional pathway to paleoclimatological interpretations as we have attempted in the past (Lee et al. 1997), whereas answering the second goal might turn out to be useful for utilization of bryozoans in biotechnology.

2 MATERIAL

To outline whether different latitudinal settings may be reflected in bryozoan-associated biofilms and microbial mats, six bryozoan collection sites with different water temperatures were selected in Japan, and three stations in New Zealand, ranging from cool temperate to subtropical climate (Fig. la, lb).
Four settings were sampled both in May/June 2000 and October 2002 to estimate seasonal changes. Bryozoan specimens were collected either by dredging or by hand at several sites around Japan and New Zealand between May and June 2000 and in October 2002. Water depths ranged from the intertidal zone to 17 metres (Table 1).

2.1 Hand collected samples

We base our study exclusively on bryozoans that were found encrusting bivalve shells in order to compare similar microhabitats. From each of the stations, 300 colonies of encrusting laminar bryozoans were examined and categorised in terms of their growth forms (Kaselowsky et al. 2004, in press). Species record per station is presented in Tables 2a, b. 69 bryozoan colonies sampled in May/June 2000 and 23 in October 2002 were selected for the study presented here. Microbial fouling was studied using light and scanning electron microscopy (SEM), thin section preparation, microbiological and molecular biological methods.

2.2 Light microscopy and SEM

Microbial fouling was studied using photomicroscopes (Zeiss). Image processing was carried out using Analysis Pro software (SIS). For SEM, bryozoan colonies were placed in a series transfer from formalin-seawater to freshwater, washed, and afterwards transferred through an alcohol series (25%, 50%, 75%; 1 hour in each) to 100% ethanol, and finally critical point-dried. SEM was performed both at the Research Institute und Museum Senckenberg, Frankfurt/Main and the Institute for Chemistry and Biology of the Marine Environment (ICBM) of the University of Oldenburg. In this contribution, SEM images were used for both a qualitative approach to characterise the type of microbial fouling and organisms involved and a semi-quantitative approach to estimate the degree of fouling (Table 3). Morphological criteria were used for taxon identification of biofilms. Dr. Crawford and F. Hinz (Alfred Wegener Institute Bremerhaven) aided the identification of diatoms.

2.3 Microbiological and molecular analyses

Enrichment cultures: Parts of bryozoan samples (illustrated in Fig. 3) were used to enrich different fluid media (incubation: 2 weeks at room temperature). DNA extraction: Genomic DNA from isolates was obtained by using several freeze-thaw cycles (—85°C, 65°C) and additional ultrasonication, if necessary. DNA extraction of bacterial enrichment cultures followed the protocol of Zhou et al. (1996).

Table 1. Sampling sites at Japan and New Zealand following the latitudinal climate gradient.

<table>
<thead>
<tr>
<th>Locality</th>
<th>Sampling period</th>
<th>Mean annual water temperatures °C</th>
<th>Measured water temperatures °C</th>
<th>Water depth (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Japan</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hokkaido</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Akkeshi Bay, 43°N, 144.5°E</td>
<td>May 2000 9.1</td>
<td>15.6</td>
<td>3-6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>October 2002 12-13</td>
<td>11.2</td>
<td>3-6</td>
<td></td>
</tr>
<tr>
<td>2. Oshoro Bay, 43.24°N, 141.02°E</td>
<td>May 2000 12.3</td>
<td>11.2</td>
<td>Tidal area</td>
<td></td>
</tr>
<tr>
<td><strong>Honshu</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>October 2002 24.1</td>
<td>17-18</td>
<td>1-6</td>
<td></td>
</tr>
<tr>
<td>5. Sakkushima, 34.43°N, 137.02°E</td>
<td>June/July 2002 15-17</td>
<td>17-18</td>
<td>1-2</td>
<td></td>
</tr>
<tr>
<td><strong>Ryukyu, Sesoko Islands</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6. Okinawa, 26.3°N, 127.52°E</td>
<td>May 2000 24.6</td>
<td>23.8</td>
<td>1-4</td>
<td></td>
</tr>
<tr>
<td><strong>New Zealand</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7. Leigh, 36.17°S, 174.49°E</td>
<td>May 2000 17.1</td>
<td>18</td>
<td>1-8</td>
<td></td>
</tr>
<tr>
<td>8. Wellington, 41.28°S, 174.51°E</td>
<td>May/June 2000 14.9</td>
<td>16</td>
<td>1-3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>October 2002 13</td>
<td>16</td>
<td>1-3</td>
<td></td>
</tr>
<tr>
<td><strong>South Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. Dunedin/Portobello, 45.52°S, 170.30°E</td>
<td>May/June 2000 9.6</td>
<td>15</td>
<td>9-16</td>
<td></td>
</tr>
<tr>
<td></td>
<td>October 2002 11</td>
<td>15</td>
<td>9-16</td>
<td></td>
</tr>
</tbody>
</table>
**Table 2a, b.** Species record of those shell encrusting bryozoans from Japan and New Zealand (sampling periods 2000/2002) studied for taxonomy of their associated microorganisms.

<table>
<thead>
<tr>
<th>Japan</th>
<th>Species</th>
<th>Akkeshi</th>
<th>Sakkushima</th>
<th>Shimoda</th>
<th>Seto</th>
<th>Okinawa</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Buffonellodes sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>2</td>
<td>Bugula dentata (Lamouroux, 1816)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Cauloranthus spinifer (Johnston, 1832)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>4</td>
<td>Cellepora hyalina (Linnaeus, 1767)</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Cribrilina annulata (Fabricius, 1780)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>Electro angulata (Levinsen, 1909)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Fenestrulina malusii (Audouin, 1826)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Membranipora membranacea (Linnaeus, 1767)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Membranipora tuberculata (Ortmann, 1890)</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Parasmittina parasevalii (Audouin, 1826)</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>11</td>
<td>Pleurocodonellina signala (Ryland &amp; Hayward, 1992)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Porella acutirostris (Smit, 1873)</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>13</td>
<td>Schizomavella pimiliger (MacGillivray, 1883)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>Schizoporella unicorns (Johnston, 1847)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>Smithoidea levis (Kirkpatrick, 1890)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>Stylopoma viride (Thornely, 1905)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>Trypostega venusta (Norman, 1864)</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>Watersipora subovoidea (d’Orbigny, 1852)</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td>XX</td>
</tr>
<tr>
<td>19</td>
<td>Watersipora subtorquata (d’Orbigny, 1842)</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>New Zealand</th>
<th>Species</th>
<th>Dunedin</th>
<th>Wellington</th>
<th>Leigh</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Arachnopusia unicorns (Hutton, 1873)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Calloporina angustipora (Hincks, 1885)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Celleporaria agglatinos (Hutton, 1873)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Celleporaria tridenticulata (Busk, 1881)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Chaperiopsis cervicornis (Busk, 1854)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>6</td>
<td>Chaperiopsis rubida (Hincks, 1881)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>Crassimarginatella pyrula (Hincks, 1881)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Euryostomella foraminigera (Hincks, 1883)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>9</td>
<td>Fenestrulina disjuncta (Hincks, 1885)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>Hippomenella velicata (Hutton, 1873)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>Rhychozoon paa (Uttley &amp; Bullivant, 1972)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>Rhychozoon larreyi (Audouin, 1826)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>13</td>
<td>Schizomavellapunctigera (MacGillivray, 1883)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>Smithoidea maunganuensis (Waters, 1906)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>Watersipora subtorquata (d’Orbigny, 1842)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

Genomic DNA from bryozoa and associated biofilms was extracted by ultrasonication of the sample (~ 1 cm³), followed by the procedure of Bemtson et al. (2000), and purified using the QIAquick DNA purification kit (Qiagen, Hilden, Germany).

**PCR:** The variable V3 region of bacterial 16S rDNA (corresponding to positions 341-534 in the E. coli sequence) was amplified with primers P2 + GC-clamp and P3 (Muyzer et al., 1993).

With primer pair (Plf (eubacteria): 5’-GGTTGATCCGTTCGCTCAG-3’ and P2r (Gram⁺, primarily Bacillaceae): 5’-GATGTCAAGACCTG-GTAAG-3’) a fragment of 1,091 bp was amplified. PCR amplification was performed in a 251 reaction using 1.25 U of Taq polymerase (Eppendorf, Germany), 11 of each primer (10 pm/μl), 0.2 mM of each dNTP, 5.1 mM of sterile water in a 251 reaction. The PCR protocol was performed as follows: 94°C for 2 min, 65-57°C for 30 sec (8 cycles, touchdown), and 72°C for 30 sec, followed by another 20 cycles at 56°C (annealing) under the same conditions. The amplification products were analysed on ethidium bromide stained agarose gels (1%, w/v). For DGGE analyses the amplificables of 1,091 bp were used as templates for a second amplification with the primer pair P2 + GC-clamp and P3 (Muyzer et al., 1993).

Dénaturant Gradient Gel Electrophoresis (DGGE): DGGE was performed with a D-Code system (Bio-Rad Laboratories) according to the manufacturer’s instructions. Gels consist of a 6-8% (w/v) polyacrylamide gradient, superimposed with a 50-80%
### Table 3. Relative abundance (%) of visible taxon groups in bryozoan-associated biofilms (selected examples, estimated from SEM).

<table>
<thead>
<tr>
<th>Locality, sample no. (I)</th>
<th>Bryozoan species</th>
<th>Diatoms</th>
<th>Cyanobacteria</th>
<th>Other bacteria</th>
<th>Fungal structures N.d. (2)</th>
<th>Peritricha Sum% (3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sampling period 2000:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>akk 01</td>
<td><em>Fenestrulina malusii</em></td>
<td>10</td>
<td>10</td>
<td>5</td>
<td>5</td>
<td>30</td>
</tr>
<tr>
<td>akk 02</td>
<td><em>Porella acutirostris</em></td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>5</td>
<td>40</td>
</tr>
<tr>
<td>akk 04</td>
<td><em>Celleporaria</em> sp.</td>
<td>10</td>
<td>15</td>
<td>5</td>
<td>5</td>
<td>30</td>
</tr>
<tr>
<td>akk 08</td>
<td><em>P. acutirostris</em></td>
<td>30</td>
<td>5</td>
<td>5</td>
<td>10</td>
<td>45</td>
</tr>
<tr>
<td>shi 01</td>
<td><em>Tubulipora concinna</em></td>
<td>80</td>
<td>10</td>
<td>5</td>
<td>5</td>
<td>80</td>
</tr>
<tr>
<td>shi 02</td>
<td><em>Callopora</em> sp.</td>
<td>5</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>35</td>
</tr>
<tr>
<td>shi 03</td>
<td><em>T. pulcherrima</em></td>
<td>30</td>
<td>15</td>
<td>5</td>
<td>5</td>
<td>45</td>
</tr>
<tr>
<td>shi 07</td>
<td><em>Callopora</em> sp.</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td></td>
<td>20</td>
</tr>
<tr>
<td>oki 01</td>
<td><em>Parasmittina parsevalii</em></td>
<td>5</td>
<td>5</td>
<td>5</td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>oki 04</td>
<td><em>P. parsevalii</em></td>
<td>5</td>
<td>10</td>
<td>5</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>oki 06</td>
<td><em>P. parsevalii</em></td>
<td>5</td>
<td>10</td>
<td>5</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>oki 10</td>
<td><em>P. parsevalii</em></td>
<td>5</td>
<td>10</td>
<td>5</td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>wel 01</td>
<td><em>Arachnopusia unicornis</em></td>
<td>5</td>
<td>80</td>
<td>5</td>
<td></td>
<td>.85</td>
</tr>
<tr>
<td>wel 02</td>
<td><em>A. unicornis</em></td>
<td>5</td>
<td>65</td>
<td>5</td>
<td></td>
<td>75</td>
</tr>
<tr>
<td>wel 04</td>
<td><em>A. unicornis</em></td>
<td>10</td>
<td>5</td>
<td>5</td>
<td></td>
<td>30</td>
</tr>
<tr>
<td>wel 05</td>
<td><em>Watersipora subtorquata</em></td>
<td>20</td>
<td>10</td>
<td>10</td>
<td></td>
<td>40</td>
</tr>
</tbody>
</table>

| Sampling period 2002:    |                  |         |               |               |                            |                     |
| shi 12                   | *T. concinna*     | 85      |               | 95            |                            | 85                  |
| shi 14                   | *T. concinna*     | 3       | 2             | 5             |                            | 5                   |
| shi 15                   | *Celleporaria triacantha* | 15    | 10            | 5             |                            | 20                  |
| sak 01                   | *Tellyella tuberculata* | 15    | 10            | 5             |                            | 20                  |
| sak 04                   | *Schizoporella unicornis* | 55    | 5             | 5             |                            | 30                  |
| sak 05                   | *S. unicornis*     | 20      | 10            | 10            |                            | 30                  |
| sak 06                   | *E. angulata*      | 5       | 5             | 5             |                            | 10                  |
| wel 10                   | *Aimulosia marsupium* | 40    | 5             | 5             |                            | 50                  |
| wel 12                   | *Eurystomella foraminigera* | 20    | 10            | 5             |                            | 30                  |
| wel 13                   | *E. foraminigera*  | 15      | 10            | 10            |                            | 25                  |
| dun 10                   | *Chaperiopsis rubida* | 30    | 5             | 5             |                            | 35                  |
| dun 11                   | *Crassimarginatella pyrula* | 10 | 5             | 10            |                            | 15                  |
| dun 13                   | *C. pyrula*       | 20      | 5             | 10            |                            | 25                  |
| dun 14                   | *C. rubida*       | 10      | 5             | 10            |                            | 10                  |

Remarks: (1) localities: Japan: akk: Akkeshi Bay/Hokkaido, shi: Shimoda Bay/Hondshu, sak: Sakushima/Hondshu, oki: Okinawa Bay/Ryukyu. New Zealand: wel: Wellington/North Island, dun: Dunedin/South Island; (2) n.d.: not determinable organismic structures; (3) data indicate the estimated percentage of living compounds, not considered here the various mineral compounds, broken diatom frustules and floccose organics which also constitute the biofilm matrices.

dénaturant gradient (Muyzer et al., 1993), and electrophoresis was performed for 14 h at 100 V at 60°C. Subsequently, the gels were stained with ethidium bromide, and gel images were obtained using the Gel Doc 2000 system (Bio-Rad Laboratories).

Fatty acids were extracted from bacterial isolates, derivatized to fatty acid methyl ester and analysed using a gas chromatograph. For identification of the fatty acid patterns, the ‘Microbial Identification System’ (MIS) (Midi, Newark. DE) was used (Hoffmann, 2002).

### 3 RESULTS

#### 3.1 Taxonomic composition of bryozoan-associated biofilms

#### 3.1.1 Scanning electron microscopy

Diatoms, cyanobacteria, other bacteria, fungal structures and protozoans in changing frequency and abundance were visible in biofilms on the bryozoan zooids (Table 3; Fig. 2a-f). Benthic diatoms (Fig. 2a, c)
Figure 2 a-f. Taxon groups and types of biofilms found on bryozoans of the study areas:
a) Diatoms (dominant here *Cocconeis* sp.), broken diatom frustules, cluster of coccoid bacteria and floccose and amorphous organic material, probably from EPS, make the biofilm of Type I: agglutinated biofilm. Sample from Evans Bay, Wellington, New Zealand (SEM archive V/WEL 02-31).
b) Coccoid bacteria grow on zooids of the growth margin of *Parasmillina parsevalii*. To the right, the growth margin spreads over a microbial mat dominated by filamentous cyanobacteria (Type III) which occupy the substrate adjacent of the bryozoan colony. To the left, Type 1 biofilm agglutinating mineral compounds cover older zooids of the bryozoan colony. Sample from Okinawa Bay, Ryukyu, Japan (SEM archive No. II/OK.I 04-21).
c) Fungal mycelia showing characteristic branching filaments developed on a zooid of *Tuhulipora conchiima* associated with diatoms (*Cocconeis* sp.). Sample from Shimoda Bay, Honshu, Japan. (SEM archive No. I/SHI 01-14).
d) Filamentous cyanobacteria of the LPP group contribute to the biofilm of *Arachnopusia unicornis*. The filaments are draped upon organic lumps characteristic of biofilm Type I (agglutinated). Sample from Evans Bay, Wellington, New Zealand (SEM archive V/WEL 01-06).
e) Stalked Peritricha settling on a bryozoan colony (not determined) from Akkeshi Bay. The underlying biofilm represents Type I. (SEM archive III/AKX 24-06).
f) A ring of probably Protozoa immersed in threads (possibly EPS) rounds the operculum of a bryozoan zooid (not determined species). Associated are much smaller coccoid bacteria attached to the zooid surface by pili (bacterial threads of EPS). (SEM archive III/AKK 17-304).
and bacteria (Fig. 2b, f) were most frequent, whereas fungi (Fig. 2c) and cyanobacteria (Fig. 2b, d) were comparatively rarer. Among protozoans, particularly Peritricha were abundant (Fig. 2e, f).

Diatoms were attached to almost all samples collected at cool and warm water habitats. Species of *Cocconeis* (Fig. 2a, c) were particularly frequent. Preference sites of diatom attachment were the operculi, spaces between the zooids, and spinae. On several frontal surfaces, the diatoms occurred in weedy biofilms which also included bacteria, cyanobacteria, hyphae of fungi and actinomycetes. At other sites the diatoms formed discrete clusters embedded in gelatinous layers. *Chaperiopsis cervicornis* sampled at Evans Bay, Wellington, showed various aggregates of pennate diatoms settling along and in between the spinae (‘bryozoan microreef’; Scholz 1995). Only a few parts of the surfaces of the bryozoan colonies showed single cells which may suggest random patterns. The species composition of diatoms were variable even at the same sampling site.

3.1.2 Molecular studies

DGGE profiles of 16S rDNA obtained from bacteria and cyanobacteria colonizing bryozoans at different localities revealed a high geographic variation (Fig. 3a-c). However, even banding patterns of bacteria colonizing bryozoan colonies at the same locality and time were almost irregular viewing phylogenetically mixed communities.

Purified DNA extracts of bryozoan biofilms were used to amplify 16S rDNA fragments with a specific primer pair for *Bacillaceae*. Although some single bands showed conformities (Fig. 3c), the majority of bands was distributed at different positions in the lanes indicating changes in species composition. The diversity was high compared to DGGE patterns of enrichment cultures. Selected isolates of bacteria were also analysed by a fatty acid approach (Hoffmann 2002). Most were identified as ubiquitous species groups related to different Gram+ bacteria, mainly bacilli and the genus *Rhodobacter* (alpha-Proteobacteria).

Fatty acid analyses of non-cultured bacilli obtained from biofilms of the fouling bryozoa *Watersipora subtorquata* from two geographically different localities, Shimoda Bay and Shirahama Bay, both Honsyu, Japan, made a good match as revealed by cluster analysis using the unweighted pair group method (UPGM). The bacilli of both were closely related to alpha-Proteobacteria and Firmicutes (Fig. 4a-b). In the biofilm of *W. subtorquata* collected from Shimoda Bay, the neighbour-joining trees revealed one cluster of genomically similar bacilli (Fig. 4a), whereas in the biofilm from Shirahama Bay, the primers used amplified a wider range. At least two clusters of genomically similar cells were recognized (Fig. 4b).
Figure 4a-b. Cluster analysis of fatty acids extracted from isolates of bacteria present in biofilms of *Watersipora subtorquata* collected at (a) Shimoda Bay, (b) Shirahama Bay, both Honshu, Japan (collection from May 2000). Dendrograms performed by the unweighted pair group method (UPGM). Both localities show an array of alpha-Proteobacteria and Firmicutes, matches of genomically similar bacilli in one cluster in (a) and two clusters in (b). The range of alpha-Proteobacteria and Firmicutes suggests environment-specific rather than host-specific colonization of bacilli on both colonies of *W. subtorquata*.

3.2 **Structural records of bryozoan-associated biofilms**

Diatoms, cyanobacteria, other bacteria, fungi and protozoans by their distinct morphology, spatial order and excretion of extracellular polymeric substances (EPS) contributed to a diverse structural record of biofilms (Fig. 2). Organic polymers of microbial origin were frequently responsible for binding cells and
other particulate materials together and to the substrate (Characklis and Wilderer 1989), thereby providing the biofilms their plastic properties.

We found biofilms both on bryozoan surfaces and the adjacent substrate (Fig. 2b). Microbial cells settling on bryozoan zooids occurred as aggregates, thalli, mycelcs, or occurred dispersed spreading over the substrate in regular or random patterns.

3.2.1 Biofilm types

Based on scanning electron studies, we defined three types of biofilm fouling of bryozoans (Gerdes et al. 2004, in press):

Type I (Fig. 2a-e) was termed ‘agglutinated biofilm’: This type, compared to the next two, showed the relatively lowest degree of coherence. Various allogenic particles of various size and origin trapped by EPS were common (diatom debris, mineral grains, flocose amorphous organic matter). Type I was unstructured in comparison to microbial mats (Type II) and/or microbial bacterial colonies (Type III). Debris of diatom shells was abundant, perhaps representing undigestible skeleton remains excreted by bryozoans.

Type II was termed ‘microbial mat’. This type represents tangled layers of filamentous cyanobacteria or fungi and associated microorganisms (Fig. 2b).

Type III represents a ‘biofilm dominated by individual taxa in colonial order’, e.g., aggregates of rod-shaped or spherical bacterial cells (Fig. 2b, f), or diatoms of the Cocconeis genus (Fig. 2a).

All three types occurred closely together on a sample from Okinawa Bay, Ryukyu Island, Japan (Fig. 2b). Type I was realized on older zooids, Type III on zooids of the growth margin, while Type II occurred on the adjacent substrate (Fig. 2b).

3.2.2 Frequency and distribution of biofilm morphotypes

At all settings studied. Type I biofilms were most frequent. Various parallel samples collected at Akkeshi Bay (cool temperate) and Shimoda (warm temperate) were dominated by Type I. Likewise, also Okinawa samples (marginal tropical climate) were dominated by this type. The relative dominance was similar in both sampling periods (June 2000, October 2002).

Type II, the densely entangled meshworks of epi­zoic microbial mats, was rare on the bryozoan surfaces studied, yet predominant on surrounding substrates (Fig. 2b) and dead colonies. Particularly the samples from Shimoda (warm temperate) and Okinawa (marginal tropical climate) demonstrated that microbial mats were not able to colonize living laminar encrusting bryozoan colonies, although single cyanobacteria filaments were repeatedly observed (Fig. 2d). Both SEM studies and molecular studies (Fig. 3b) evidenced species diversity of cyanobacteria settling on bryozoan colonies.

In biofilms of Type III, diatoms, fungi and bacteria others than cyanobacteria were dominant. SEM studies revealed that cocci and rod-shaped bacteria were the dominant type on various zooids of living bryozoans. Bacteria-dominated biofilms have frequently been found on bryozoan growth margins (Fig. 2b).

3.2.3 Degree of total cover of zooid space by biofilms

The space of bryozoan colonies occupied by biofilms was estimated on the base of SEM images (Gerdes et al. 2004, in press). Biofilms of bryozoans collected from warm water habitats occupied the surface areas of zooids only 50% and less. Comparatively higher was the number of bryozoans from cool water habitats that have been occupied by biofilms to more than 50% (Fig. 5). Both sampling periods (2000, 2002) reconfirmed this trend.

3.3 Bryozoan-specific biofilms

Biofilms of colonies of the same bryozoan species were never completely identical in composition, dominance and density (Gerdes et al. 2004, in press). Biofilms documented from Celleporella hyalina from Oshoro and Shimoda Bay, and biofilms of Porella acutirostris from three parallel samples collected at Akkeshi Bay showed that in both cases, no selection for a specific biofilm type nor for a specific taxon or taxon group was evident. Comparing colonies of Tubulipora pulcherrima (two parallel samples from Shimoda Bay), Parasmittina parsevalii (seven parallel samples from Okinawa), and Chaperiopsis cervicomic (three parallel samples from Evans Bay, Wellington) showed the same. All these bryozoan specimen exhibited a complex pattern of agglutinating ‘microgardens’ composed of layers of unstructured EPS in which diatoms, bacteria, some filaments and cocci of cyanobacteria, and fungal hyphae were detectable similar to those described by Sterflinger & Scholz (1997). Two colonies of Watersipora subtorquata sampled at geographically different localities revealed genomically similar bacilli (Fig. 4a-b). Yet, it has to be kept in mind that bacilli make only a part in the complex biofilms.

3.4 Biofilms of locally adjoining bryozoans

The comparison of biofilms on Steginoporella sp. and W. subtorquata growing side by side on the same substrate revealed some variability. Bacterial diversity of Steginoporella sp. was much higher compared to a neighboring colony of W. subtorquata (Gerdes et al. 2004, in press). Other comparisons of locally adjoining bryozoans of different taxa showed higher conformity at least in the range of alpha-Proteobacteria and Firmicutes (Hoffmann 2002).
3.5 Gradation of fouling

3.5.1 Determination of fouling levels

Based on microscopic, microbiological and molecular taxonomic data we distinguished low, medium and high levels of bryozoan-associated microbial fouling. The following criteria were used (Gerdes et al. 2004, in press):

Low level fouling:
- zooid surface area covered by biofilms: low (<50%)
- biofilm composition: mainly Type 1: diffuse water-enriched slimes which agglutinate diatoms, broken diatom frustules, mineral compounds and floccose organic matter ('agglutinated biofilm'); some few individual organisms are dispersed rather than showing colonial organization
- biofilm consistency: low degree of cohesion
- biofilm distribution on the zooids: patchy, inhomogenous.

Medium level fouling:
- zooid space covered by biofilms: 50-75%
- biofilm composition: the 'agglutinated biofilm' (see above) is still dominant, although colonial aggregates of organisms (both coccoid and filamentous ones) become increasingly abundant
- biofilm consistency: increasingly coherent
- biofilm distribution on the zooids: increasingly homogenous, colonial aggregates of individuals of the same species occupy larger areas.

High level fouling:
- zooid space covered by biofilms: 75-100%
- biofilm composition: morphological heterogeneity due to the presence of filamentous and coccoid organisms
- biofilm consistency: highly tangled and cohesive due to EPS enrichment including slimes, capsules and sheathes
- biofilm distribution: larger areas homogeneously covered.

3.5.2 Distribution and frequency of fouling levels

At both sampling times, May/June 2000 and October 2002, medium fouling levels were frequent in cooler water habitats, while low level fouling predominated at warm water settings (Fig. 6). Only the samples collected at Sakkushima, being situated at almost the
Figure 6. Levels of microbial fouling on bryozoans in percentages of the total number (n) of samples. Sampling periods May 2000 (above) and October 2002 (below). The order of settings on the y-axis indicates geographic variation and changing water temperatures: May 2000 from top to bottom: Akkeshi and Wellington: cool temperate. Shimoda: warm temperate. Okinawa: marginal tropical. October 2002 from top to bottom: Dunedin and Wellington: cool temperate. Shimoda and Sakushima: warm temperate climate. For criteria defining the fouling levels see text. The diagrams view the decrease of microbial fouling towards lower latitudes (trend similar at both sampling periods).

same latitude as Shimoda, provided seemingly an exception. A reason could be the geographic position of Sakkushima which is more inland and only marginally influenced by the warm oceanic current which characterizes the Shimoda sampling sites.

The percentage of samples showing the high level type of fouling were relatively low. Two of these samples revealed dense biofilms covering dead bryozoans, thus clearly underlining the importance of lethal effects.

4 DISCUSSION

The study of epizoic microbial films attached to the surfaces of laminar encrusting bryozoans provided some surprising results. One was the general decrease of biofilm covering and fouling levels towards warm water habitats which apparently signaled competitive rather than symbiotic interaction of both lamina-forming systems, bryozoans and microbiota, especially in warm waters.

Probably substrate competition has flattened the levels of microbial fouling over the surfaces of bryozoan zooids. The latitudinal gradient was clearly expressed by the distribution pattern of lamina types (Kaselowsky et al. 2004, in press). The decrease of biofilm covering and increase of low level fouling in warm water habitats may be considered as response to the increasing abundance of bryozoan growth forms which are effective substrate competitors. They have been termed s-laminae, showing the biological potential to produce huge giant buds, and c-laminae, performing frontal budding in situations of overgrowth competition (Scholz 2000).

Additionally, chemical defence should be considered. Particularly the low levels of fouling observed at sampling sites of lower latitudes indicate some antibacterial activity. Shellenger and Ross (1998) showed that the presence of antibacterial compounds may allow bryozoans to manipulate the microbial film growing on them, and thus may influence the types of organisms that are able to settle near or on them. Walls et al. (1993) used the extracts of four species of bryozoans found in Tasmanian coastal waters to demonstrate selective antibacterial activity. Counts of bacteria over the surfaces of the four species revealed that the species which had the most active antibacterial extracts had the lowest numbers, while other species having no known secondary metabolites had weak antibacterial properties and, thus, higher numbers of bacteria on their surfaces.

The trends observed for (i) biofilms (gradations of fouling, decreasing covering; Gerdes et al. 2004, in press) and (ii) bryozoan lamina types (Kaselowsky et al. 2004, in press) may be valued as parallel signals of latitudinal gradients from cool to warm climate. The obvious changes observed at settings situated at lower latitudes may be interpreted in terms of a mutual ecological selection taking place under the control of external factors: (i) on the one hand there is the usual trend of biofilms and microbial mats to change to more complexity with increasing water temperatures, intensity and angles of incidence of light; (ii) stages advancing to the mat phenotype were outcompeted by bryozoans strong in defense, while (iii) bryozoan colonies weak in defense were outcompeted by the potentially efficient microbial productivity. This may account for both the dominance of low to medium grades of fouling, and agglutinated biofilm types.

Benthic phototrophs such as diatoms and cyanobacteria are important stabilizers of sedimentary surfaces. In protected environments they are able to produce thick and cohesive surface mats. Favourable light and nutrient conditions in shallow waters trigger their distribution and abundance. Both are important EPS
producers which trap sediments. While it is well documented that diatoms represent a food source of bryozoans (Winston 1977; Markham & Ryland 1987; McKinney 1990), less is known of relationships between bryozoans and cyanobacteria. Golubic et al. (1999) pointed out that the diversity of benthic cyanobacteria is apparently the highest in tropical oceans. Cyanobacteria are mainly involved in the highly entangled meshwork termed microbial mat. Several cyanobacterial species are able to take such a secondary morphology as a result of the aggregation or entanglement of many filaments (Reynolds & Walsby 1975, Whitton & Potts 2000, with review of literature). In their ability of mass production, benthic cyanobacteria-dominated microbial mats and bloom-forming planktonic cyanobacteria may be comparable. Results from this study, however, indicate that the mat-forming potential of cyanobacteria was obviously restricted on living bryozoan surfaces. It is widely accepted that microbial mats are weak in substrate competition with sessile encrusting fauna under normal marine salinity (Pratt 1983). Probably due to such weakness, microbial mats thrive best in environments under ecological stress such as hypersaline aquatic systems (Gerdes & Krumbein 1987), or hyperthermal springs. These environments are characterized by extraordinary thick, carpet-like mats in which filamentous cyanobacteria dominate associated by a wealth of other prokaryotic and eukaryotic organisms, often far exceeding 500 species. Mats of this consistency have the potential to form stromatolites, last but not least due to their mineral-precipitating ability (Krumbein 1983). The epizoic microbial films on bryozoan surfaces in this study, with few exceptions, was not comparable to this type of potentially stromatolitic mats. The term biofilm in its strict sense may comprise monobacterial layers or those made by only a very few dominant types (Christensen & Characklis 1990) so that only the dense bacterial colonies observed on some bryozoan surfaces would apply to this definition. However, microbial mats pass through various developmental stages along gradients of ecological determinants (Gerdes et al. 2000, Riding & Awramik 2000). Their pioneer stages comprising only a few species forming agglutinated layers may match the type of agglutinating micro-gardens formed by diatoms, bacteria, cyanobacteria and fungi observed on bryozoan surfaces in this study. The wide distribution of this type independent of both geographic variation, and variation of hosts suggests competitive interactive dynamics. Competitive mechanisms are also indicated by the fact that outside of the living substrate, microbial mats certainly can develop in these shallow euphotic environments of normal marine salinity. The observations in this study thus support the assumption of limitation of microbial mats due to effective substrate competition by

encrusting sessile colony formers in subtidal habitats (Pratt 1983).

Our SEM studies have shown a variety of motile and nonmotile coccoid and rod-shaped bacteria on various zooids of living bryozoans. According to molecular studies, alpha-Proteobacteria (mainly Rhodobacter group) and gram positive bacteria (Bacillaceae) were predominant among the bacteria isolated from the biofilms (Hoffmann 2002). According to Pukali et al. (2001), these groups are among the most widely isolated organisms from the marine environment and may have been transferred into these environments from terrestrial sites. The bryozoans apparently are able to tolerate biofilms composed of or dominated by these groups. Further indication for random local factors was the overall heterogeneity of the biofilms. None of these organisms seemed to live obligately on the bryozoans. The heterogeneity was also visible when comparing biofilms attached to the same bryozoan species, and to adjoining bryozoans of the same subpopulation. Likewise, DGGE banding patterns of adjoining species matched only few bacterial populations (Gerdes et al. 2004, in press).

5 CONCLUSIONS

a. The type of agglutinated biofilms in which diatoms, cyanobacteria, fungi and bacteria others than cyanobacteria are common was the main type tolerated by the bryozoans of the shallow subtidal environments studied.

b. Also bacteria of probably terrestrial origin enriched on zooids were tolerated by the bryozoans which may utilize them as food resource.

c. On the other hand, bryozoans control the active succession of cyanobacterial biofilms to mature microbial mats.

d. Biofilm structures on substrates not colonized by bryozoans clearly show a latitudinal gradient. While dominated by diatoms in cooler water, biofilms in warm water habitats are able to advance to highlevel microbial fouling.

e. Vital-lethal effects are reflected by the specific distribution patterns of microbial mats which are rare on bryozoan surfaces (vital effect), but common on dead colonies (lethal effect).

f. The decrease of biofilm covering and increase of low level fouling towards warm water habitats parallels the morphological signals of latitudinal gradients in bryozoans.

g. The effective substrate competition proceeding in the subtidal habitats studied suggest stable ecology conditions in terms of salinity and temperature.

h. The low significance of seasonal changes reflected by the samples may account for the predominance
of oceanographic factors overprinting the local climate of the sampling sites.

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The cheilostomatous genera of Alcide d'Orbigny - nomenclatural and taxonomic status

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ABSTRACT: Alcide Dessalines d’Orbigny was the author of 75 genera of Cheilostomata, 73 of which were introduced in his volume on Bryozoa in the Paléontologie française series Terrains crétacés. A recent SEM study of available type and other specimens pertaining to these genera has made possible the clarification of their nomenclatural and taxonomic status. Discarding those genera that are junior synonyms, have missing type specimens, or which may never be properly understood, we regard 37 as having current availability. These include 13 genera with d’Orbigny type species that were previously rejected, synonymized, or overlooked in Bassler’s (1953) Treatise on Invertebrate Paleontology, i.e. calloporids Prufilustrina, Reptoflustrella, Reptoporina, Semiflustrella, and Semiflustrina, antroporid Lateroflustrella, onychocellids Latereschara and Reptolumulites, cribrilinids (s.l.) Multescharipora, Reptescharella, Reptoporella, and Semiescharipora, and Filiflustrina (family uncertain). These genera are reinstated, based on identifiable type species that are illustrated herein. We give new diagnoses for each of the genera and classify them to family level according to current phylogenetic concepts of the order Cheilostomata. The status of the remaining 62 d’Orbigny genera is briefly summarized in tabular form.

1 INTRODUCTION

The scientific accomplishments of Alcide Dessalines d’Orbigny (1802-1857) were truly remarkable. He worked tirelessly, contributing to a number of disciplines, and it seems likely that stress from the pressure of work, travel, and rivalries contributed to a heart condition, implicated in his untimely death at the age of 54. His life’s work, reviewed in a volume published in the bicentennial year commemorating his birth (Taquet 2002), included compendious taxonomic descriptions and/or diagnoses and illustrations of fossil and living Bryozoa. d’Orbigny’s paleontological collection largely survives and is located in the Salle d’Orbigny, Laboratoire de Paléontologie du Muséum National d’Histoire Naturelle, Paris (Lauriat-Rage 2002). In the context of revising the bryozoan part of the Treatise on Invertebrate Paleontology, we examined the d’Orbigny Collection in 2001. All available nominal type specimens of d’Orbigny’s genera. Recent and fossil, were borrowed and imaged using environmental SEM by PDT before being returned to Paris. This Treatise-related work and the results of electron microscopy will be made available on a website that is under development (http://www.nhm.ac.uk/palaeontology/dorbigny/). Taylor & Gordon (2002) gave an overview of all of d’Orbigny’s publications dealing with Bryozoa, published in the 14-year period between 1841 and 1854. In these works, d’Orbigny introduced approximately 203 new genera and 1141 new species, predominantly Cretaceous (d’Orbigny 1851-54), but also including Recent taxa (d’Orbigny 1841-47).

Quite apart from the present-day difficulties inherent in obtaining d’Orbigny’s publications, some now quite rare, several authors (Pergens 1890, Gregory 1899, 1909, Canu 1900, Waters 1905, Buge 1957, Prud’homme 1968, Voigt 1972, Taylor & Gordon 2002) have pointed out serious challenges concerning the identity and status of many of d’Orbigny’s taxa. Collectively, these include: (1) frequent listing of new taxa without figures or adequate descriptions; (2) the use of stylized and/or composite drawings; (3) taxonomic oversplitting based on stratigraphy or slight differences in colony form; (4) dates of publication that do not coincide with those given on the title pages of the works or are simply unknown; (5) appending new taxa with the date that d’Orbigny wrote the description rather than the actual date of publication; (6) d’Orbigny’s confusing habit of attributing generically reassigned species of other authors to himself; (7) using the same species name repeatedly among different genera; (8) d’Orbigny’s tendency to create
confusingly similar generic and familial names (Taylor & Gordon 2002). Unfortunately, many identifications and taxonomic attributions of d’Orbigny’s species made by previous authors are incorrect.

Inter aliæ, d’Orbigny authored 75 genera of Cheilostomata, 73 of which were introduced in his volume on Bryozoa in the Terrains crétacés. Our recent SEM study of available type and other specimens pertaining to these genera has made possible the clarification of their nomenclatural and taxonomic status. Discarding those genera for which type species and specimens are lost and which may never be properly understood, we regard 37 as having validity. These include 13 genera, based on d’Orbigny type species, that were previously rejected, synonymized, or overlooked in Bassler’s (1953) Treatise. The goal of this paper is to illustrate, by scanning electron microscopy, the type species of these 13 genera, give new diagnoses for them, and suggest how they may be classified. The status of the other 62 cheilostome genera introduced by d’Orbigny is summarized in tabular form.

2 MORPHOLOGICAL EXAMINATION OF TYPE SPECIES OF SELECTED D’ORBIGNY GENERA

In the accounts below, we give annotated information on the opinions of some previous students of d’Orbigny’s material, in particular Canu (1900) and Voigt (1972). We also reproduce d’Orbigny’s species numbers—species that he described fully were allocated numbers, ranging from 1247 to 2094 for the Bryozoa.

2.1 Family Calloporidae

2.1.1 Pyriflustrina d’Orbigny, 1853, p. 580

Type species (Fig. 1, A-C): Pyriflustrina elegans d’Orbigny, 1853, p. 580, pl. 733, figs 9-11, by monotypy, Coniacian, Tours, France, d’Orbigny No 1726. Genus included in Pyripora d’Orbigny, 1849 by Canu (1900), Bassler (1935), and Bassler (1953).

Diagnosis: Colony encrusting, forming branching uniserial chains of zooids, new zooid rows being produced laterally (distolateral dichotomous branching of zooid rows not seen). Autozooids elongate-oval to subpyriform, narrower proximally, rarely with a short caudal portion. Opees sunken, rounded triangular with a broad granular cryptocyst proximally and the proximal third of the zooid a smooth gymnocyst. Articulated spines not evident; the proximal corners of the mural rim may appear as a rounded boss on each side. Avicularia not seen. Ovicell recumbent on distal gymnocyst. Small basal pore-chambers inferred to be present mid-laterally. Reparative/regenerative budding within an autozooidal chamber may produce a kenozooid. Ancestrula not known.

Remarks: d’Orbigny’s stylized drawings overemphasize the triangularity of the opesia and depict exaggerated tapering and flattening of distal and proximal ends of zooids. Lateral budding is well shown but the frontal bosses misleadingly appear as spine bases. The occurrence of an ovicell (unfortunately with a missing ooecial roof) in the type specimen negates Bassler’s (1953) synonymy of Pyriflustrina (Calloporidae) with Pyripora d’Orbigny, 1852 (Electridae). Among existing calloporid genera, Pyriflustrina appears closest to Recent Pyriporoides Hayward & Thorpe, 1989, which has articulated oral/mural spines and distolateral budding and the ovicell is not recumbent on a distal autozooid but may be associated with a kenozooid (Gordon 1989). Rosso & Taylor (2002) included Pyriflustrina in a key to uniserial calloporids.

2.1.2 Reptoflustrella d’Orbigny, 1853, p. 570

Type species (Fig. 1, D, E): Reptoflustrella cenomana d’Orbigny, 1853, p. 570, no figure, by subsequent designation (Bassler 1935, p. 185) of the first of 13 species included by d’Orbigny, Cenomanian, Le Mans, France. Considered a junior subjective synonym of Escharina confinis Reuss, 1846 (as Pyripora) by Canu (1900, p. 383).

Diagnosis: Colony encrusting, multiserial, sheetlike. Autozooids with extensive oval opesia surrounded by a narrow granular cryptocyst of equal width except distally where it is lacking; a smooth gymnocyst occupies the proximal third to quarter of the zooidal length. Bases of 4. possibly more, widely spaced articulated spines on distal opesial rim of many zooids. An interzooidal avicularium proximolateral to most autozooids, the rostral rim rounded, raised, the presence of a crossbar equivocal. Ovicell recumbent on distal zooid, concealing gymnocyst. Interzooidal communications and ancestrula not known.

Remarks: Bassler (1953) listed Reptoflustrella as “an unrecognized generic name” but the existence of a well-preserved type specimen with unequivocal skeletal characters requires its reinstatement. Among existing genera, it is reminiscent of Mystriopora Lang, 1915 which, although unio- to pluriordinal, has similar autozooids and interzooidal avicularia. Ovicells have not yet been reported in Mystriopora, however, and the genus was included in the Electridae by Bassler (1953), but the presence of neocheilostome-type avicularia shows that it cannot be an electid. The calloporid genus Dionella Medd, 1965 is similar but, in the type and other species, most avicularia occur mid-distally to autozooids and ovicells, there may be vicarious avicularia, and articulated spines are well developed, judging from the conspicuous spine bases. Marginaria Roemer, 1840 is closest, and could possibly be a senior subjective synonym of Reptoflustrella. The type species Cellepora elliptica von Hagenow, 1839, has.
Figure 1. A-C. *Pyritflustrina elegans*, Cretaceous, Senonian, Tours, MNHN R61766, d’Orbigny Collection: A. Portion of uniserial colony showing a chain of three zooids at left, from each of which is budded a row laterally to the right (scale bar 0.5 mm). B. Autozooids; notice the bosses at the proximal ends of the opesial rim in the zooids at upper left and the reparative budding of a kenozooid in the zooid at lower left (0.2 mm). C. Ovicelled zooid with frontal ooecial wall broken (0.1 mm).

Figure 1, D, E. *Reptoflustrella cenomana*, Cretaceous, Cenomanian, Le Mans, MNHN 6554, d’Orbigny Collection: D. Group of autozooids, one with a broken ovicell (0.1 mm). E. Close-up of zooids, showing oral spine bases and an adjacent interzooidal avicularium (0.1 mm).

Figure 1, F-G. *Reptoporina micropora*, Cretaceous, Senonian, Fécamp, MNHN R61707, d’Orbigny Collection: F. Autozooids near colony margin, one with a closure plate (0.5 mm). G, H. Close-up of zooids with and without closure plates (0.2 mm). (Scale bar sizes in parentheses throughout.)
however, articulated spines around the entire mural rim and even on the highly reduced gymnocyst in some zooids and interzooidal avicularia (Voigt 1989, pi. 3, figs 1-4). *Reptoflustrina cenomanana* also has proportionately more gymnocyst and one avicularium may have a crossbar. We consider it premature to include *Reptoflustrina* in *Marginaria*.

2.1.3 *Reptoporina* d’Orbigny, 1852, p. 441
*Type species* (Fig. 1, F-H): *Escharina micropora* d’Orbigny, 1850, p. 263 (1852, p. 444, pi. 605, figs 5-7), by subsequent designation (Bassler 1935, p. 186) of one of 20 species included by d’Orbigny, Senonian, Fécamp, France, d’Orbigny No 1602.

*Diagnosis:* Colony encrusting, multiserial, sheetlike. Autozooids rounded to elongate-oval, with an extensive opesia occupying virtually the entire frontal area, bordered by a narrow granular cryptocyst of equal width except distally where it is lacking; gymnocyst restricted to sides of zooids in interzooidal furrows, becoming more evident proximally in zooids at the colony margin in the zone of astogenetic repetition. Articulated spines absent. No avicularia or ovicells evident. Closure plates, resulting from calcification of the original operculum and frontal membrane, occlude many zooids, leaving longitudinal foramina in the midline on the plate and a crescentic indentation marking the position of the opercular sclere. Basal porechambers lacking. Ancestrula resembling ordinary zooids, lacking spines, surrounded by six daughter zooids, with a narrow kenozooid midproximally.

*Remarks:* Bassler (1953) treated *Reptoporina* as an “unrecognized generic name”, describing it merely as a “membraniporoid cheilostome”. The wellpreserved type specimen suggests that the absence of zooidal polymorphs may represent a genus-level character. Although *Pyriporopsis* Pohowsky, 1973 has closure plates (lacking median slits, however) (Taylor 1987), *Reptoporina* is not a malacostegan. Congeneric (possibly even conspecific) material from the British Chalk has ovicells (PDT, pers. observ.).

2.1.4 *Semiflustrina* d’Orbigny, 1853, p. 563
*Type species* (Fig. 2, A-C): *Semiflustrina rhomboidalis* d’Orbigny, 1853, p. 564, pi. 730, figs 5-8 by subsequent designation (Bassler 1935, p. 199) of one of eight species included by d’Orbigny, Senonian, Fécamp, France, d’Orbigny No 1707.

*Diagnosis:* Colony encrusting, multiserial. Autozooids rounded to elongate-oval, with an extensive opesia that occupies the entire frontal area, bordered by a narrow granular cryptocyst of equal width except distally where it is lacking; gymnocyst extremely reduced to lacking. Spine bases not in evidence. A small interzooidal avicularium distal to each autozooid, set transversely, evidently lacking a crossbar. Ovicells not seen. Strongly buttressed recesses present along the inner walls of zooids but basal pore-chambers not obvious. Ancestrula not known.

*Remarks:* Bassler (1953) did not recognize *Semiflustrina*. The genus is remarkably similar to *Cranosina*. The well-developed basal pore-chambers and the ovicell is endozooidal with vestigial ooecial calcification. As Chimonides & Cook (1994) pointed out in their discussion of the genus, *Cranosina* has been accorded a wide temporal range by several authors, from the Late Cretaceous to the present day. Living and fossil species have also been confused with *Ellisina* Norman, 1903, sometimes treated as a recent subjective synonym of *Cranosina*. *Ellisina*, however, has well-developed ovicells, which, when present, occur in intimate association with the avicularia in most species—differing, for example from some Cretaceous species attributed to *Cranosina*, with well-developed ovicells not associated with avicularia (e.g. Voigt 1962). It also appears that fertile zooids and orifices in *C. coronata* may be dimorphic, as illustrated by Hastings (1945) in a specimen from Sri Lanka—but not by Fransen (1986) from Curaçao.

According to Canu (1900, pp. 356, 364, 371), *S. rhomboidalis* includes the following species: *S. exca­vata* d’Orbigny, 1853, p. 567, pi. 731, figs 5-8, *Reptoflustrina ovalis* d’Orbigny, 1853, p. 572, pi. 731, figs 17, 18, and *Reptoflustrina simplex* d’Orbigny, p. 571, pi. 731, figs 15,16. Medd (1979) rejected the latter synonymy, including *R. simplex* in *Ellisina*. Like *Cranosina, Ellisina* has a Recent type species. We agree with Chimonides and Cook (1994) that the relationship of the fossil forms to the Recent taxa needs further investigation. Although the type specimen of *Semiflustrina rhomboidalis* is fragmentary, we believe that the skeletal characters illustrated here allow adequate characterization of the genus *Semiflustrina* for comparative studies.

2.1.5 *Semiflustrina* d’Orbigny, 1853, p. 576
*Type species* (Fig. 2, D, E): *Semiflustrina monilifera* d’Orbigny, 1853, p. 577, pi. 732, figs 6-9, by subsequent designation (Bassler 1935, p. 199) of the first of five species included by d’Orbigny, Senonian, Fécamp, France, d’Orbigny No 1721.

*Diagnosis:* Colony encrusting, multiserial. Autozooids with relatively large opesia, this becoming sunken relative to the development of a pair of swollen avicularian chambers proximally; these, and adjacent avicularia borne on other zooids, completely conceal any potential or actual gymnocyst and cryptocyst; the
avicularia with apparent mandibular pivots and slight development of a rostral palate. Distal autozooidal rim with two pairs of relatively small bases of articulated oral spines. Large vicarious avicularia present.

linguiform with a pair of pivots at the extreme proximal end and a small palatal shelf distally. Ovicells hooded, the ectoecium smooth, partly concealed distally by adjacent avicularia, the ovicellular opening...
above the level of the operculum in life. Interzoooidal communications and ancestrula unknown.

Remarks: *Semiflustrina* appears most closely related to callioporids such as *Amphibiestrum* Gray, 1848 and *Ramphonotos* Canu & Bassler, 1920, but differs particularly in lacking an exposed area of endoocium in the ovicell and in the presence of vicarious avicularia. The *Amphibiestrum* subgenus *Aviculamphibiestrum* Rosso, 1999 has very large subvicarious interzoooidal avicularia but the sole included species is otherwise a typical *Amphibiestrum*. Canu (1900, p. 364) included *Semiflustrina lateralis* d’Orbigny 1853, p. 577, pl. 732, figs 10-13 in the synonymy of *S. monilifera*.

2.2 Family Antroporidae

2.2.1 *Lateroflustrella* d’Orbigny, 1853, p. 568

Type species (Fig. 2, F-H): *Lateroflustrella complanata* d’Orbigny, 1853, p. 569, pl. 731, figs 11-14, by monotypy, Maastrichtian, Meudon, France, d’Orbigny N° 1714.

Diagnosis: Colony encrusting, multiserial. Autozooids somewhat diamond-shaped, i.e. roughly 4-sided and tapering proximally and distally with angular lateral margins. Opesia large, longitudinally elongate-oval, the cryptocyst granular, sloping inwards; no trace of gymnocyct. Articulated spines absent. A small mid-distal adventitious avicularium associated with each autozooid, of variable orientation, generally distal or obliquely so, with tapered rostrum. Fertile zooids indicated by a distal excavation within which is a smooth oral shelf; distal avicularium lacking. Pustular structures on the outer lateral walls of some zooids suggest the presence of small mural pore-chambers. Ancestrula unknown.

Remarks: *Lateroflustrella* resembles some species of *Antropora* Norman, 1903 in the predominance of the cryptocyst, endozooidal ovicell, and small adventitious avicularia, and is accordingly included in the Antroporidae. The status of this family was discussed by Tilbrook (1998). *Lateroflustrella* was not listed by Bassler (1953); Bassler (1935) did not recognize the genus and, probably alluding to a comment by Canu (1900, p. 384), asserted that the specimen and figures do not conform. We disagree with this opinion. It is clear from d’Orbigny’s figure 12 that, although reversed in orientation, the zooids do conform to the type specimen in general features, albeit somewhat stylized.

2.3 Family Onychocellidae

2.3.1 *Latereschara* d’Orbigny, 1852, p. 345

Type species (Fig. 3, A, B): *Eschara achates* d’Orbigny, 1852, pp. 114, 346, pi. 662, figs 7-9, by monotypy, Senonian, Fécamp, France.

Diagnosis: Colony erect, forming flattened bilamellar branches that divide dichotomously in one plane. Autozooids somewhat hexagonal, acutely angled distally and proximally. Cryptocyst sunken, broadest proximally, surrounding on all sides a circular to sub-circular opesia. No spines. Ovicells not known. Avicularia vicarious, confined to lateral margins of the branches from which the acute, elongate rostra angle outwards; avicularian cryptocyst well developed, granular, pivots small, crossbar lacking. Interzoooidal communications and ancestrula unknown.

Remarks: Bassler (1953) listed *Latereschara* among “unrecognized generic names” but Voigt (1959, p. 10; 1967, p. 43) regarded it as a valid genus that also includes *Eschara galeta* von Hagenow, 1839. The latter species has abundant large interzoooidal avicularia and well-developed ovicells, however.

2.3.2 *Reptolunulites* d’Orbigny, 1852, p.356

Type species (Fig. 3, C, D): *Reptolunulites angulosa* d’Orbigny, 1852, p. 357, pi. 707, figs 1, 2, by subsequent designation (Bassler 1935, p. 185) of the first two species included by d’Orbigny. Senonian, Sainte-Colombe, France, d’Orbigny N° 1546 [misprinted as 1646].

Diagnosis: Colony encrusting, multiserial. Autozooids with variably hexagonal outlines, with thick, raised the lateral rims bordering the granular, sunken cryptocyst; opesia suboval, occupying slightly more than half the zooidal length. No spines. Avicularia vicarious, narrower than autozooids, with practically no cryptocystal shelf. Ovicells subimmerced/recumbent. Ancestrula surrounded by six perianzooidal zooids. Nature of interzoooidal communications unknown.

Remarks: The type specimen of *R. angulosa* is worn and some morphological details (such as the morphology of the ancestrula and perianzooidal zooids) are indistinct. One apparent oivicellular cavity lacks an ovicell roof.

Bassler (1935) included as synonyms *Pavolunulites* d’Orbigny, 1853, *Oligotreisium* Gabb & Horn, 1862, *Lunularia Busk, 1884, and Dimiclausa Gregorio, 1890, but subsequently (Bassler 1953) synonymized *Reptolunulites* with *Lunulites* Lamarck, 1816. Without having examined a specimen, Bassler may have assumed that *R. angulosa* was free-living, when it is in fact encrusting. The genus may be among the morphologies ancestral to free-living forms but a detailed study would be required to demonstrate this. Voigt (1981) referred to *Reptolunulites* (Turanian) as “the first primitive Lunulitidae”, being somewhat intermediate between an encrusting onychocellid ancestor and *Pavolunulites*. Cook and Chimonides (1986) noted that *R. angulosa* was encrusting and thus “not, in fact, a highly organized lunulitiform species”, excluding it and the genera *Pavolunulites* d’Orbigny,
1852 and *Volviflostrellaria* Brydone, 1936 from the Lunulitidae as “a grouping where colony organization, autozooids and avicularia are intermediate in character between the Cretaceous *Onychocella*-like forms and the Lunulitidae proper”.

2.4 Family Cribrilinidae

2.4.1 *Multescharipora* d’Orbigny, 1853, p. 495

*Type species* (Fig. 3, E): *Multescharipora insignis* d’Orbigny, 1853, p. 496, pi. 720, figs 11-15, by subsequent designation (Lang, 1921, p. lxii) of one of
three species included by d’Orbigny, Maastrichtian, Meudon, France, "d’Orbigny N° 1639."

**Diagnosis:** Colony encrusting, multiserial, multilamellar. Autozooids with a frontal shield of about 12-18 simple (non-pinnate, imperforate) costae, radially disposed with gaps between them, their distal tips fused. The suborificial pair of costae enlarged, stout, their lumina confluent, mostly frontally open (unroofed) with a tongue-like extension of the combined basal costal wall extending proximally, covering the distal tips of most costae, i.e., the frontal surface of the extension is mostly interior-walled. An area of proximal gymnocyst present, up to a third or more of the zooidal length but frequently concealed by polymorphs and/or ovicells. No oral spines. The orificial rim defined by the adjacent walls of generally three avicularia—two lateral and one (occasionally two) middistal—that have pivots and no crossbar; the distal avicularium lacking if an ovicell is present. Ovicell recumbent on gymnocyst of distal autozooid, the ectooecium smooth, imperforate, flanked proximally by kenozooidal chambers or avicularia differentiated from them. Adventitious kenozooids occurring in interzooidal areas, their walls encroaching imolaterally by kenozooidal chambers or avicularia.

Ovicell recumbent on gymnocyst of distal autozooid, the ectooecium smooth, imperforate, flanked proximally by kenozooidal chambers or avicularia differentiated from them. Adventitious kenozooids occurring in interzooidal areas, their walls encroaching on adjacent zooids and ovicells. Basal pore-chambers apparently lacking. Ancestrula unknown.

**Remarks:** *Multescharipora* is most closely related to the group of genera included by Lang (1916, 1922) in his subfamily Tricephaloporinae, in particular *Coelopora* Lang, 1917, *Phractoporella* Lang, 1917, and *Polycephalopora* Lang, 1916 (see Bassler 1953), which share the character of a tonguelike extension of the suborificial bar along the fusion line of the costae. It is significant that Lang (1916) did not list *Multescharipora* among his list of "indeterminable described forms" of d’Orbigny species; in fact, he included *M. insignis*, without discussion, in *Polycephalopora*. Later, Lang (1921, p. 58) formally selected *M. insignis* as type species of *Multescharipora*, commenting: "It is best... to choose *M. insignis* as the genolectotype of *Multescharipora*, and if it can be certainly established that *M. insignis* is congeneric with *Polycephalopora hydra* [type species of *Polycephalopora*], the genus *Polycephalopora* must be abandoned, becoming synonymous with *Multescharipora". Lang (1922, p. 120) made the same comment, adding: "It is not likely, however, that the characters of *M. insignis*, and therefore the characters of the genus *Multescharipora* will ever be clearly established." It is distinctly possible that the two genera are congeneric—ironically, less is now known about the characters of *Polycephalopora* and indeed all the tricephaloporines need reexamining in relation to one another. In the event, the combination *Multescharipora insignis* does not qualify as a nomen oblitum according to Article 23.9.1 (ICZN 1999) and the status of *Multescharipora* as a valid genus may be taken as established whether or not it is congeneric with *Polycephalopora*.

2.4.2 **Reptescharella lorieri** d’Orbigny, 1853, p. 464

**Type species** (Fig. 4, A, B): *Escharina lorieri* d’Orbigny, 1852, pi. 604, figs 11-12, by subsequent designation (Lang, 1917, p. 172) of one of 21 species included by d’Orbigny, Cenomanian, Le Mans, France, "d’Orbigny N° 1611."

**Diagnosis:** Colony encrusting, multiserial. Autozooids with a costae shield of 5-6 pairs of simple spines, the suboral pair not different from the remainder, the area of proximal gymnocyst relatively small. Two pairs of stout oral spine bases present, the proximal pair broader than the distal pair and retained in ovicelled zooids. Large interzooidal (subvicarious) avicularia present, the rostrum, long, acutely arched with an extensive palate and palatal foramen, no crossbar. Ovicell recumbent on distal gymnocyst, the ectooecium smooth, imperforate. Basal pore-chambers present. Ancestrula unknown.

**Remarks:** *Reptescharella* resembles some Recent taxa but differs from them and from all other genera in the sum of its characters. Canu (1900, p. 444) included the genus in *Membraniporella* Smitt, 1873, influencing Bassler (1953) who indicated this synonymy in his Treatise entry. The genera are indeed similar but the type species of *Membraniporella* (*Lepralia nitida* Johnston, 1838) has only small interzooidal avicularia and the ovicellular skeletal surface is endooecial, the ectooecium being reduced to a narrow peripheral rim.

2.4.3 **Reptoporella** d’Orbigny, 1853, p. 474

**Type species** (Fig. 4, C, D): *Reptoporella regularis* d’Orbigny, 1853, p. 475, pi. 717, figs 6, 7, by monotypy, Senonian, Sainte-Colombe, France, "d’Orbigny N° 1620."

**Diagnosis:** Colony encrusting, multiserial. Autozooids with 7-8 pairs of simple costal spines, the suboral ones not different from the rest, the area of proximal gymnocyst relatively small. Articulated oral spines present, a proximal pair retained in ovicelled zooids. A small interzooidal avicularium distal to most zooids, or to ovicells, the rostrum rounded to subacute, the crossbar complete. Occasional vicarious avicularia also present, the rostrum broadly subspathulate, the palate extensive, with subjacent large foramen; no crossbar. Ovicell recumbent, the ectooecium smooth with a central endooecial exposure. Basal pore-chambers present. Ancestrula unknown.

**Remarks:** Lang (1916, p. 397, 1921, p. 71) doubtfully suggested that *R. regularis* might be congeneric with
his genus *Leptocheilopora*. In the event, the two genera are quite distinct—the type species of *Leptocheilopora, L. tenuilabrosa* Lang, 1916, has costate ovicells and the vicarious avicularia also have costae (Larwood, 1962, p. 111). An ancestrula occurs in the type specimen of *R. regularis*. It appears tetiform but is thin-walled and may have lacked mural spines. Both Gillard (1943) and Larwood (1962, p. 119) disagreed that *Membranipora crenulata* d’Orbigny, 1852 is synonymous with *R. regularis* as suggested by Canu (1900, p. 449).
2.4.4 *Semiescharipora* d’Orbigny, 1853, p.479  
_Type species* (Fig. 3, F): *Semiescharipora complanata* d’Orbigny, 1853, p. 484, pl. 718, figs 17-20, by subsequent designation (Lang, 1917, p. 172) of one of 14 species included by d’Orbigny, Conian, Vendôme, France, d’Orbigny N° 1627.

_Diagnosis:_ Colony possibly encrusting, multiserial. Autozooids elongate-oval with a frontal shield of 8-9 pairs of costae, probably laterally contiguous, the suboral pair not obviously different from the others; lumen pores (pelmata) not apparent. The presence of oral spine bases equivocal. Conspicuous interzooidal kenozooids occur, typically two pairs with a presumed small avicularium inserted between each lateral pair such that they appear to flank autozooidal orifices, one on each side, but not necessarily at the same level. Ovicells not seen. Basal pore-chambers probably lacking. Ancestrula unknown.

_Remarks:_ The sole specimen matches d’Orbigny’s illustration of the zooids but overgrowth of diagenetic calcite makes the interpretation of features somewhat equivocal, e.g. lumen pores and oral spine bases appear to be lacking. The status of the genus _Semiescharipora_ has been uncertain; Bassler (1935, 1953) suggested a similarity to _Membranipora_, which must be rejected. It appears closest to _Rhacheopora_ Lang, 1916, the species of which were encrusting or erect and unilamellar or cylindrical, with imperforate, laterally contiguous costae and interzooidal kenozooids and small avicularia. Interestingly, Lang (1921) did not describe or illustrate ovicells in the species that he personally named in this genus. It is highly likely that the two genera are congeneric but, until more and better specimens of _S. complanata_ are available for comparison, it is better to keep them separate.

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2.5 _Family_ Incertae Sedis

2.5.1 _Filiflustrina_ d’Orbigny, 1853, p. 575  
_Type species* (Fig. 4, E-G): _Filiflustrina cylindrica_ d’Orbigny, 1853, p. 575, pi. 732, figs 1-5, by monotypy, Maastrichtian, Meudon, France, d’Orbigny N° 1720; illustrated by Canu (1900, p. 367, pi. 6, fig. 20) as _Membranipora_ and listed by Bassler (1953, p. 235) as an “unrecognized generic name”.

_Diagnosis:_ Colony narrowly cylindrical, dichotomously branching, with zooids opening all around the stem. Autozooids alternating in quincunx, with extensive longitudinally oval opesiae. Opesiae flanked along each lateral margin by a raised broad tubular structure, half the width of an opesia, with a median longitudinal slit and distal frontally facing opening. Oral and opesial spines, avicularia, ovicells, interzooidal communications, and ancestrula not seen or unknown.

_Remarks:_ d’Orbigny’s illustrations of zooids are inverse to what we think may have been their orientation in life. The raised tubular structures are curious and the state of preservation of the specimen does not allow a precise interpretation. Of the several that are possible, two interpretations appear more probable. As viewed frontally, each zooid may conceivably comprise an opesia proximal to which is a pair of parallel tubular structures pertaining to that zooid. On this interpretation, the tubular structures would likely be supported by an underlying frontal wall, presumably a gymnocyct. If this is the case, how are the tubular structures to be interpreted? Are they hollow spines? If so, they could conceivably take their origin from the zooid proximal to them but why would they have a median longitudinal slit or furrow?

Alternatively, the tubular structures may not be proximal but lateral to each opesia. In this case they could represent the frontal expression of interzooidal kenozooids, i.e. their lateral walls arch across the frontal face of each kenozooid, not quite fusing but leaving a slit where they oppose and enclosing a space within. We prefer this interpretation but it is not without its difficulties—while elongate interzooidal kenozooids are known in Late Cretaceous (and later) bryozoans, these are all cribiformorphs and the kenozooids are single, not paired (Gordon & Voigt 1996). If these structures in _F. cylindrica_ are kenozooids, one must ask if they are budded from the autozooids proximal to them or lateral to them. In either case they might not descend to the substratum but be supported by an underlying gymnocyct. One of d’Orbigny’s illustrations shows reduced opesiae surrounded by what may be interzooidal calcification, which would support the interpretation of the tubular structures as being the frontal expression of kenozooids.

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3 d’ORBIGNY’S OTHER CHEILOSTOME GENERA

In addition to the 13 genera discussed above, d’Orbigny (1849, 1851-54) introduced 62 others. Some (e.g. _Conescharetlia, Discoporella, Porina, Pyripora_) are well known and in common use; most of the others are little-used, little-known, or forgotten and, despite Bassler’s (1953) _Treatise_ index, their status is not necessarily clear. We have examined all available putative type specimens in the d’Orbigny Collection (some were missing even at the time of Canu or have not yet been located) and provide here our conclusions on the current status of the balance of the genera in Table 1.

Several authors have introduced genera or subgenera based on d’Orbigny species. Based on available d’Orbigny types, the status of these genusrank taxa is given in Table 2.
Table 1. List of additional cheilostomc genera introduced by d’Orbigny and their current status.
Genus

Date, page

Type species

Status and affiliation of genus

Revisedbinominal

Biflustra
Cellarina
Celleporina
Conescharellina
Discoflustrella
Discoflustrellaria
Discoporella
Distansescharella
Distansescharellina
Disteginopora
Electrina
Escharella
Escharellina
Escharifora
Escharinella
Escharipora
Filiflustra
Filiflustrella
Filiflustrellaria
Flabellopora
Flustrella
Flustrellaria
Flustrina
FusiceUaria
Lanceopora
Lateroflustrellaria
Multescharellina
Multescharinella
Multiporina
Ornithopora
Ornithoporina
Pavolunulites
Planicellaria
Porellina
Poricellaria
Porina
Pyriflustrella
Pyripora
Quadricellaria

1851: 241
1851: 181
1851: 212
1852:446
1853: 561
1853: 507
1852:472
1852:463
1852:451
1852: 235,498
1851: 188
1852: 218
1852: 206,447
1852: 208
1852: 200
1852: 20
1852: 240
1853: 562
1853: 512
1851: 52
1852: 282
1853: 515
1852: 298
1851: 185
1851: 186 bis
1853: 571
1852: 457
1852: 430
1852: 445
1852: 321
1852: 32
1852: 538
1851: 36
1853:476
1854: 1106
1852: 432
1853: 569
1849: 499
1851: 32

B. ramosa d’Orbigny, 1852
C. clavala d’Orbigny, 1851
Cellepora incrassata Lamarck, 1816
C. angustata d’Orbigny, 1852
D. doma d’Orbigny, 1853
D. clypeiformis d’Orbigny, 1853
Lunulites umbellata Defiance, 1823
Cellepora familiaris Hagenow, 1839
Cellepora pteropora Reuss, 1848
D. horrida d’Orbigny, 1852
E. lamellosa d’Orbigny, 1851
Eschara edwardsiana Hagenow, 1851
Eschara macrocheila Reuss, 1848
E. argus d’Orbigny, 1852
E. lorieri d’Orbigny, 1852
E. inornata d’Orbigny, 1852
F. compressa d’Orbigny, 1852
F. lateralis d’Orbigny, 1853
F obliqi^eti' Orbigny, 1853
F elegans d’Orbigny, 1851
F. turonensis d’Orbigny, 1852
F.fragilis d’Orbigny, 1853
F. transversa d’Orbigny, 1852
Fpulchella d’Orbigny, 1851
L. elegans d’Orbigny, 1851
L. hexagona d’Orbigny, 1853
Cellepora accumulata Hagenow, 1839
Cellepora proliféra Reuss, 1848
M. ostracites d’Orbigny, 1852
Cellularia avicularia Linnaeus, 1758
CeUtdùria avicularia var. B
P. costata d’Orbigny, 1852
P oculata d’Orbigny, 1851
Eschara macrocheila Reuss, 1848
P alata d’Orbigny, 1854
Eschara gracilis Lamarck, 1816
Hippothoa tuberculum Lonsdale, 1845
Criserpia pyriformis Michelin, 1848
Q. elegans d’Orbigny, 1851

Accepted. Membraniporidae
Preoccupied. Now Cellarinidra
Junior homonym of Celleporina Gray
Accepted. Conescharellinidae
Junior subj. synonym of Discoporella
Accepted. Lunulitidae s.l.
Accepted. Cupuladriidae
Accepted. Cribrilinidae s.l.
Junior subj. synonym of Escharoides
Accepted. Cribrilinidae s.l.
Junior subj.? synonym of Electra
Junior homonym of Escharella Gray
Senior subj. synonym of Umbonula
Accepted. Coscinopleuridae
Indeterminate. Calloporidae?
Accepted. Microporidae
Indeterminate. Zooid row?
Senior subj. synonym of Bactrellaria
Indeterminate. Zooid row?
Accepted. Conescharellinidae
Preoccupied. Calloporidae
Accepted. Calloporidae
Preoccupied. Calloporidae
Accepted. Fusicellariida
Accepted. Lanceoporidae
Accepted. Lunulitidae s.l.
Accepted. Lepraliellidae
Indeterminate. Family?
Senior subj. synonym of Schiioporella
Junior subj. synonym of Bugula
Junior subj. synonym of Bugula
Accepted. Lunulitidae s.l.
Accepted. Calloporidae
Junior obj. synonym of Escharellina
Accepted. Poricellariidae
Accepted. Porinidae
Junior subj. synonym of Pyripora
Accepted. Electridae
Accepted. Quadricellariidae

Biflustra ramosa
Cellarinidra clavata
Unknown; type missing
Conescharellina angustata
Reussirella doma
Discoflustrellaria clypeiformis
Discoporella umbellata
Distansescharella familiaris
Escharoides coccinea
Disteginopora horrida
Electra pitosal
Needs new genus
N. obi.; Umbonula macrocheila
Escharifora argus
Unknown; type missing
Escharipora inornata
Type specimen incomplete
Norn, obi.; Bactrellaria lateralis
Type specimen incomplete?
Flabellopora elegans
Unknown; type missing
Flustrellaria fragilis
Needs new genus
FusiceUaria pulchella
Lanceopora elegans
Lateroßustrellaria hexagona
Multescharellina accumulata
Unknown; type missing
N. obi.; Schizoporella unicornis?
Bugula avicularia
Bugula flabellata
Pavolunulites costata
Planicellaria oculata
Umbonula macrocheila
Poricellaria alata
Porina gracilis
Pyripora tuberculum
Pyripora pyriformis
Quadricellaria elegans
(Continued)


<table>
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<tr>
<th>Genus</th>
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<td>Reptoflustrina arctica d'Orbigny, 1853</td>
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<td>Cellepora subgranulata Hagenow, 1851</td>
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Of the 75 cheilostome genera introduced by d’Orbigny, we regard 37 as having current availability and validity. In addition to the 13 genera discussed in the paper these include 24 that are already firmly established or based on valid species of other authors: Biflustra, Conescharellina, Discoflustrellaria, Discoporella, Distansescharella, Disteginporella, Escharifora, Escharipora, Flabelloporella, Flustrellaria, Fusicellaria, Lanceopora, Lateroflustraella, Multescharella, Pavolunulites, Planicellaria, Poricellaria, Porina, Pyriporella, Quadracellaria, Repetescharinella, Semieschara, Sparsioporina, and Steginopora.

Nineteen names cannot be used because they are objective (7) or subjective (12) synonyms of preexisting genera: Cellarina, Celleporina, Discoflustrella, Distansescharella, Electrina, Escharella, Flustrella, Flustra, Omithopora, Ornithoporina, Porellina, Pyriflustrella, Reptelectrina, Repolatereschara, Semicelleporaria, Semiescharinella, Temicellaria, Trochopora, and Tubucellaria. Of course, future studies may determine that some existing genera may need splitting, in which case some of the above subjective synonyms may become available for use as genera or subgenera.

Nine genera may remain forever indeterminable owing to the fact that type specimens are missing, viz: Escharinella, Multescharellina, Repetescharipora, Reptoflustrina, Semiescharinella, Semiflustra, Semiporina, and Vincularina. Presumably these are lost, or perhaps have not yet been identified and isolated from the d’Orbigny and other collections because of inadequate labelling, documentation, and/or the difficulty of matching specimens with figures.

Seven names are senior synonyms of later introduced genera but may be treated as nomina obita: Escharella (Umbonula), Filiflustrella (Bactrellaria), Multiporina (Schizoporella) (see Hayward & McKinney 2002, p. 66), Quadriflustra (Tegella), Repetescharipora (Balantiostoma), Repetoporellina (Reptadeonella), and Semiescharilla (Hipposleuraliera).

Two other genera (Filiflustra, Filiflustrellaria) have existing type specimens but these are so fragmentary (parts of zooid rows with few zooidal characters) as to be presently uninformative as to their taxonomic affinities and are effectively unusable. It is possible that future work on the French Cretaceous may yield more and complete material that will clarify their status.

Reptoflustra, uniquely, never had a designated type species. Of the ten species attributed to the genus by d’Orbigny, none was illustrated, and their status has not subsequently been ascertained. It is permissible for a reviser to select one of them as type species, thus validating the genus, if specimens still exist and do not belong to some other genus.
ACKNOWLEDGEMENTS

The Muséum National d’Histoire Naturelle is gratefully acknowledged for providing visiting professorships enabling the authors to study bryozoans in the d’Orbigny Collection. Professor Agnès Lauriat-Rage is warmly thanked for her generous help during visits to Paris.

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**Oshurkovia: a new genus of Umbonulidae (Bryozoa: Cheilostomata) from the northwest Pacific**

Andrei V Grischenko & Shunsuke F. Mawatari

*Laboratory of Systematics and Evolution, Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo, Japan*

**ABSTRACT:** A new umbonulomorph bryozoan *Oshurkovia kamtschatica* gen. et sp. nov. (Bryozoa: Cheilostomata) is described from two areas of the northwestern Pacific: Ptichii Island (western Kamchatka shelf of the Sea of Okhotsk) and Bering Island (Commander Islands, Bering Sea). The new genus is close to *Umbonula* Hincks, 1880 in having an umbonate frontal shield with marginal areolae separated by elongated ridges; however the new species differs from *U. ovicellata* Hastings, 1944 (the type species of *Umbonula*) in the cormidial nature of the secondary orifice and the absence of a suboral avicularium and ovicells. Discovery of the new genus and species justifies splitting the genus *Umbonula*. In a newly suggested classification, each segregated genus includes several species, avoiding monotypy. Accordingly, *U. littoralis* Hastings, 1944 and *U. inarmata* Kluge, 1962, together with the newly described species, are included in the new genus. The nominal genus is here taken to include *U. patens* (Smit, 1868), an undescribed species from the Commander Islands as well as the type species. Whereas *Arctonula* Gordon & Grischenko, 1994 was segregated from *Umbonula* and removed to the Romanchinidae, the new genus is accepted as a member of the family Umbonulidae even though it lacks ovicells. The new taxon occurs predominantly intertidally but ranges to 25 m, on hard substrata, and can be categorized as a Pacific High-Boreal species.

1 INTRODUCTION

The bryozoan genus *Umbonula* Hincks, 1880 is the type genus of the family Umbonulidae Canu, 1904. Harmer (1902) described the formation of the frontal shield in the type species, using the descriptor ‘umbonuloid’ for this mode of development. The term is now well known and describes frontal shields in a wide range of taxa that are collectively known as umbonulomorph. In these forms, the primary frontal membranous wall of the zooid is overarched by a complex fold that is outwardly interior-walled with a hypostegal coelom, while, on the underside, the surface is exterior wall with planar-spherulitic skeletal microstructure (Sandberg 1977).

Species exhibiting a wide range of morphological characters have been placed in the genus *Umbonula*. For example, Hayward and Ryland (1979) included three British species in *Umbonula*, two of which have characters differing significantly from the type species. The type species *U. ovicellata* Hastings, 1944 is ovcicled whereas the other two species (*U. littoralis* Hastings, 1944 and *U. arctica* (M. Sars, 1851)) are internal brooders. Of these two latter species, *U. arctica* has paired avivularia while *U. littoralis* has a single median avicularium. Around the world, various authors have ascribed other morphologies to *Umbonula* - e.g., Brown (1952) included *Mucronella bicuspis* Hincks, 1883 in *Umbonula*, but this species has ovicells that are typical of petraliellids. Gordon (1989) made this species the type of *Mobunula* and now includes it in the Petraliellidae (D.P. Gordon, pers. comm.). Similarly, Gordon and Grischenko (1994) segregated *U. arctica* from *Umbonula* as the type of a new genus, *Arctonula*, which they included in the umbonulomorph family Romanchinidae Jullien, 1888. Other species may be included in *Arctonula* (see below). This action still left *U. littoralis* as not fully conforming to a generic diagnosis based on *U. ovicellata*.

In this paper, we introduce a new genus, *Oshurkovia*, for two species of *Umbonula* and one new species, which is designated as a type, based on newly collected specimens from the northwest Pacific.

2 MATERIALS AND METHODS

Specimens of the new species were collected in two areas of the north-western Pacific: Bering Island (Commander Islands, Bering Sea) and Ptichii Island (western Kamchatka shelf, Sea of Okhotsk). In summer seasons of 1990-91, twenty six specimens were...
obtained by the First co-author (AVG) on expeditions to the Commander Islands with the Laboratory of Benthic Communities, Kamchatka Institute of Ecology and Nature Management (KIENM), Petropavlovsk-Kamchatsky, Russia. The material was collected intermittently and subtidally, at depths of 0-25 m, from three sites along the northwestern Pacific coast of Bering Island (Cape Vkhodny Reef, Cape Gaupta and Toporkov Rock). In September 1992, three additional specimens were collected by AVG from the lower rocky-boulder intertidal zone of Ptichii Island, a small volcanic island, located 11 km from the Cape Kharyryuzova.

Specimens were preserved by drying. Colonies were cleaned in sodium hypochlorite solution, rinsed with tap-water, and air dried prior to their measurement under a binocular microscope (NIKON: SNZ-10). The dried colonies were coated with Pd-Pt by an ion sputter coater (HITACHI: E-1030) and observed under a scanning electron microscope (HITACHI: S-2380N) at 15kV accelerating voltage.

The specimens described here are deposited in the Zoological Institute Russian Academy of Science (ZIRAS), Saint Petersburg; The Natural History Museum (NHM), London; and the National Institute of Water and Atmospheric Research (NIWA), Wellington.

Specimens of related taxa, including species of *Umbonula* and *Arctonula*, were examined for comparison with the new species. This material was collected by KIENM in the Kronotsky Gulf (coastal waters of the Kamchatka Peninsula, Bering Sea) and by the Institute of Marine Biology, Vladivostok, at Mednyy Island (Commander Islands, Bering Sea). Other material was borrowed from the Museo di Paleontologia, Catania, Italy.

### 3 SYSTEMATICS

Order Cheilostomata Busk, 1852  
Suborder Neocheilostomina d’Hondt, 1985  
Infraorder Ascophora Levinsen, 1909  
Superfamily Lepralielloidea Vigneaux, 1949  
Family Umbonulidae Canu, 1904

Genus *Oshurkovia* gen. nov.

**Description**: Colony encrusting, multiserial, sheet-like. Colonies were examined for comparison with the new species. This material was collected by KIENM in the Kronotsky Gulf (coastal waters of the Kamchatka Peninsula, Bering Sea) and by the Institute of Marine Biology, Vladivostok, at Mednyy Island (Commander Islands, Bering Sea). Other material was borrowed from the Museo di Paleontologia, Catania, Italy.

**Type species**: *Oshurkovia kamtschatica* sp. nov.

**Diagnosis**: Colony encrusting, multiserial, sheet-like. Colonies were examined for comparison with the new species. This material was collected by KIENM in the Kronotsky Gulf (coastal waters of the Kamchatka Peninsula, Bering Sea) and by the Institute of Marine Biology, Vladivostok, at Mednyy Island (Commander Islands, Bering Sea). Other material was borrowed from the Museo di Paleontologia, Catania, Italy.

**Type species**: *Oshurkovia kamtschatica* sp. nov.

**Etymology**: The new genus is named in memory of Dr Vladimir V Oshurkov (1946-94), Russian zoologist and hydrobiologist, an outstanding organizer of marine biological research in the coastal waters of the Kamchatka Peninsula, and former head of the Laboratory of Benthic Communities, Kamchatka Institute of Ecology and Nature Management (KIENM), Petropavlovsk-Kamchatsky, Russia.

*Oshurkovia kamtschatica* sp. nov.  
(Figures 1-2)

**Material examined**: Holotype: ZIRAS 1/50132 (large colony, about 15 X 20 mm, encrusting broken shell of bivalve mollusc *Mya (Mya) truncata* L., 1758), collected by A.V. Grischenko, 6 September 1992. Type locality: western Kamchatka shelf of the Sea of Okhotsk, Ptichii Island, 57°10’N, 156°35’E, lower horizon of rocky intertidal, biocones *Balanus* sp.  
Paratypes: ZIRAS 2/50328 (colony encrusting shell of bivalve mollusc), KIENM Collections, Stn 219, 31 July 1991, the Commander Islands, Pacific coastal water of Bering Island, Toporkov Rock, 55°12.0’N, 165°56.7’E, depth 25 m, silted rocky plateau with boulders and lenses of broken shells, by scuba, collector D.D. Danilin. NHM 2001.12.11.1 (colony on a small rock fragment), same locality data as for holotype. NIWA P-1385, (colony fragment detached from the shell of bivalve mollusc), KIENM Collections, Stn 216, 30 July 1991, the Commander Islands, Pacific coastal water of Bering Island, Toporkov Rock, 55°11.9’N, 165°56.9’E, depth 15 m, boulders and pebbles with mixed sand and broken shells, by scuba, collector D.D. Danilin.

**Additional material examined**: several colonies stored in AVG personal collection.

**Measured specimens**: ZIRAS 1/50132, 2/50328.

**Description**: Colony encrusting, multiserial, sheet-like. Colonies were examined for comparison with the new species. This material was collected by KIENM in the Kronotsky Gulf (coastal waters of the Kamchatka Peninsula, Bering Sea) and by the Institute of Marine Biology, Vladivostok, at Mednyy Island (Commander Islands, Bering Sea). Other material was borrowed from the Museo di Paleontologia, Catania, Italy.

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**Additional material examined**: several colonies stored in AVG personal collection.

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**Type species**: *Oshurkovia kamtschatica* sp. nov.
Figure 1. *Oshurkova kamtschatica* gen. et sp. nov. (ZIRAS 1/50132 for A, B, D-F; ZIRAS 2/50328 for C). A, growing edge of a colony with developing zooids at different stages of differentiation, x 66; B, zooids with broad uncalcified rim of bell-shaped secondary orifice, and prominent, sharp suboral umbo, x 87; C, zooids with reduced uncalcified rim of circular secondary orifice, and bulge-like, solid, thickened suboral umbo, x 87; D, lateral view of zooids with high umbones and openings of marginal areolae, x 109; E, distal view of zooids, showing proximal part of secondary orifice represented by uncalcified margin of umbo, x 136; F, hexagonal kenozooid, possibly as a consequence of damage and repair, with closed frontal of calcareous ribbing, surrounded by autozooids, x 87.
Figure 2. *Oshurkoviya kamtschatica* gen. et sp. nov. (ZIRAS 1/50132 for D, F; ZIRAS 2/50328 for A-C, E). A, lateral view of the secondary orifice comprising four lobes with distinct sutures between them, indicating its cormidial structure, x 437; B, longitudinal section through zooids, showing interior of lateral wall with multiporous septula, heavily calcified frontal shield with marginal areolar pore channels, and narrow extrazooidal coelomic cavities (kenozooids) located beneath the basal wall of zooids, x 164; C, interior of the lateral vertical wall with row of multiporous septula, x 437; D, interior of distal vertical wall of newly budded zooid, showing differentiation of multiporous septula, x 437; E, interior of the frontal shield, showing umbonuloid area, indiscrete ring scar, and openings of marginal areolar pore channels from the hypostegal coelom, x 273; F, ancestrulate region of the holotype colony, showing its complexity for recognition of ancestrula position, x 66.
Table 1. Measurements of *Oshurkova kamtschatica* gen. et sp. nov. (in mm. except for N and Nz). The following abbreviations are used for measurements: L: length; W: width; N: number; S.D.: standard deviation; Nz: number of zooids.

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<td>30</td>
<td>0.43</td>
</tr>
<tr>
<td>W</td>
<td>0.45</td>
<td>0.37-0.53</td>
<td>0.033</td>
<td>30</td>
<td>0.42</td>
</tr>
<tr>
<td>Orifice</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>0.21</td>
<td>0.18-0.25</td>
<td>0.017</td>
<td>30</td>
<td>0.17</td>
</tr>
<tr>
<td>W</td>
<td>0.19</td>
<td>0.16-0.23</td>
<td>0.015</td>
<td>30</td>
<td>0.17</td>
</tr>
<tr>
<td>Orifice rim</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>0.06</td>
<td>0.02-0.10</td>
<td>0.016</td>
<td>30</td>
<td>0.04</td>
</tr>
<tr>
<td>Marginal pores</td>
<td>N</td>
<td>9.63</td>
<td>7-12</td>
<td>1.217</td>
<td>30</td>
</tr>
<tr>
<td>Kenozooids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>0.53</td>
<td></td>
<td>-</td>
<td></td>
<td>0.39</td>
</tr>
<tr>
<td>W</td>
<td>0.47</td>
<td></td>
<td>-</td>
<td></td>
<td>0.37</td>
</tr>
</tbody>
</table>

exterior of proximal wall of daughter zooid; lateral parts are proximolateral walls of neighbouring left and right zooids; proximal lobe represented by lightly calcified margin of umbo.

Some zooids occurring only as kenozooids (Fig. 1F), possibly as a consequence of damage and repair; such zooids have a closed frontal wall of calcareous ribbing continuous with frontal shield of neighbouring zooids.

Interzooidal communications achieved via multiporous mural septula (Fig. 2B-D). Basal wall of zooids fully calcified, smooth and inflated. Operculum semi-circular, brown in colour. No oral spines. No avicularia. No ovicells. Ancestrula and early astogeny (Fig. 2F) not determined.

Remarks'. In spite of the general morphological similarity of specimens of the new species from both regions studied there are some minor differences. Colony size and mean zooid length of *O. kamtschatica* from the area of Bering Island are smaller compared to specimens from the type locality (Table 1), and calcification of the frontal walls is much greater. The suboral umbo is thickened and solid; orifices are nearly circular in outline (Fig. 1C); and the rim of the orifice is reduced. Additionally, a narrow extrazooidal coelomic cavity (kenozooid) is located beneath the basal wall of some zooids (Fig. 2B). This cavity possess its own basal and vertical walls, with multiporous mural septula in the latter.

The new genus most resembles *Umbonula* in having an unboneat frontal shield with marginal areolae separated by elongated ridges. However, the new species differs from *U. ovicellata* (the type species of *Umbonula* (Fig. 3A)) in the distinct cormidial nature of the secondary orifice and the absence of a suboral avicularium and ovicells.

Ecology and Distribution'. At the type locality, *O. kamtschatica* was found encrusting broken shells of *Mya* (*Mya* truncata), rock shingle, and barnacle fragments within the lower horizon of the rocky intertidal (biocenosis *Balanus* sp.). In the region of Bering Island, the new species was found encrusting shingles and barnacles in the middle and lower horizons of the rocky and rocky-boulder intertidal zone within the belt of brown algae: biocenoses *Fucus evanescens*, *Thalasiophyllum clathrus* + *Ulva fenestrata*, *F evanescens* + *U. fenestrata*; and *Laminaria dentigera* + *Alaria fistulosa*. In addition *O. kamtschatica* was also collected at depths of 15 and 25 m in the upper subtidal zone at Bering Island, on a silted rocky plateau with lenses of sand, where it was found encrusting broken shell fragments. In both regions studied, *O. kamtschatica* occurred predominantly intertidally (93% of specimens collected) and colonised only hard substrata including shingles (79%), boulders (7%), barnacles (7%), and broken bivalvian shells (7%) at depths of 0-25 m.

According to the presently known range of the new species - Bering Island (Commander Islands, Bering Sea), and Ptichii Island (western Kamchatka shelf, Sea of Okhotsk) - it can be categorized as a Pacific High-Boreal littoral-upper sublittoral species, possibly endemic to the western Pacific.

4 DISCUSSION

4.1 Systematic relationships

Hincks (1880) established the genus *Umbonula* on the basis of *Cellepora verrucosa* Esper, 1790, from British waters. He mentioned that this species exhibits a great variation in morphology under different conditions: whereas zooids from intertidal populations possess a very slightly calcified, thin and smooth wall, frequently lack an avicularium, and lack ovicells (as indicated in his plate 39), zooids of subtidal colonies always have suboral avicularia and well-developed perforated ovicells.

Hastings (1944) restudied Hincks' specimens of *U. verrucosa* (Esper, 1790) and demonstrated that two morphologically different forms, described by Hincks as variations of *U. verrucosa*, represent two clearly different species. Recognizing *Cellepora verrucosa*
Esper, 1790 to be a junior homonym of *C. verrucosa* Linnaeus, 1767, she described these as new species. One of them, *U. littoralis*, has a comparatively inflated and thin frontal shield, suboral avicularia (often absent), and no ovicells. The other, *U. ovicellata* (which was designated as the type species for the genus), has a convex frontal wall, always with a symmetrical suboral avicularium, and spherical, perforated ovicells. Ecologically these species are also different: whereas *U. littoralis* is restricted to the intertidal and upper subtidal zones only, *U. ovicellata* is primarily subtidal.

Historically and in recent years, several other authors attributed some additional species from cool-temperate to Boreal-Arctic regions to the genus *Umbonula*. Osbum (1952) included *U. patens* (Smitt, 1868) and *U. arctica* from the Beaufort Sea in this genus. Kluge (1962) included *Umbonula littoralis* (* verrucosa* in his text and text-fig. 315), *U. patens*, *U. arctica*, and his *U. inarmata* sp. nov. from the Nordenskjold Islands (Laptev Sea). Hayward and Ryland (1979) included *U. ovicellata*, *U. littoralis*, *U. arctica* in the genus. Shortly afterwards, Gontar (1982) described *Umbonula*...
Revised diagnosis. Colony incrusting, multiserial, with umbonuloid frontal shield. Orifice simple, with symmetrically placed suboral avicularium. Ovicells well-developed, spherical, perforated. Uniporous or multiporous septula present in distal and lateral walls.

Genus *Oshurkovia* gen. nov.

Diagnosis. Given above.

*Oshurkovia kamtschatica* sp. nov. (type species) *Oshurkovia littoralis* (Hastings, 1944) comb. nov. *Oshurkovia inarmata* (Kluge, 1962) comb. nov.

4.3 Ecology and distribution for genera *Umbonula* and *Oshurkovia*

We regard *Umbonula* and *Oshurkovia* as cool-temperate to Boreal-Arctic genera. The genus *Umbonula* contains predominantly to strictly subtidal species with cool-temperate to Boreal-Arctic distributions. *U. patens* occurs at depths 9-112 m in Arctic and High-Boreal regions (Kluge 1962) and was found at 125 m in Kronotskyi Gulf, eastern Kamchatka shelf of the Bering Sea (present data). Although *U. ovicellata* lives in the Mediterranean at depths of 0-50 m, it is strictly subtidal in British waters (Hayward & Ryland 1979). The undescribed species of *Umbonula* from the region of the Commander Islands (Bering Sea) has been collected at depths of 30-40 m.

Species of the newly described genus *Oshurkovia* are predominantly intertidal to upper subtidal elements with a Boreal-Arctic distribution. Hayward and Ryland (1979, p. 74) have pointed out concerning Boreal-Atlantic *O. littoralis* that this is “a common and characteristic intertidal species extending into the shallow sublittoral, but probably no further than the Laminaria zone”. *O. inarmata* is known only from the Arctic region of the Nordenskjold Islands and the New Siberian shoals (Laptev Sea), from the upper sublittoral zone at 20 m depth (Kluge 1962, Gontar 1990). *O. kamtschatica* described herein occurs in the High- Boreal western Pacific regions, at depths of 0-25 m, but predominantly intertidally.

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Benthic Communities, Kamchatka Institute of Ecology and Nature Management (KIENM), Petropavlovsk-Kamchatsky, Russia, for their assistance in collecting the material from which bryozoans were sorted. This research was supported by a 21st Century COE Program on “Neo-Science of Natural History” (Program Leader: Hisatake Okada) financed by the Ministry of Education, Culture, Sports, Science and Technology, Japan.

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Diversity, evolution and palaeoecology of the Tertiary bryozoan assemblages of western Kachchh, Gujarat, India

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Department of Geology & Geophysics, Indian Institute of Technology, Kharagpur, India

ABSTRACT: Ninety-nine bryozoan taxa have been retrieved from the Tertiary (early Middle Eocene - late Early Miocene) sequences of western Kachchh, Gujarat, India. The diversity and richness of colonies are highly variable within and between formations, reaching their maximum during the deposition of the Khari Nadi Formation (Early Miocene). Fifteen fossil species of *Thalamoporella* Hincks, 1887, recognised in these sequences, have doubled the number of fossil taxa known in this genus from fifteen to thirty, and have enriched our knowledge about the Tertiary evolutionary history of this common extant genus. The presence of three steginoporellid genera makes Kachchh one of the main centres of radiation in the evolution of this family. *Therenia indica* takes a conspicuous place in the phylogeny of the genus. Study of bryozoan growth forms indicates two episodes of deepening in the shallow pericratonic rift basin of Kachchh. The environment that supported a moderately diverse assemblage was restricted during the early Middle Eocene but gradually opened up and reached its zenith during the Early Miocene stage.

1 INTRODUCTION

The Kachchh Basin, a pericratonic rift basin in the western margin of India, represents one of the classical areas of Indian geology, which has preserved a condensed section (about 900 metres thick) of the Tertiary rock sequences (Figure 1) ranging from Paleocene to Pliocene. These sequences (Table 1) have been classified on chrono-, litho- and biostratigraphic basis, the boundaries of which are somewhat parallel and seldom mutually transgressive (Biswas & Raju 1973, Biswas 1992, Raju 1993, 1997).

The Tertiary rock sequences of the Kachchh Basin are fossiliferous with rich and diverse assemblages of molluscs, gastropods, bivalves, echinoderms, corals, foraminiferans, ostracodes, algae and bryozoans. A varied vertebrate fauna has also been reported. Among the microbiota large benthic Foraminifera form the major group, and have been successfully used for biostratigraphical classification.


In connection with a Council of Scientific and Industrial Research sponsored project AKG studied different Tertiary lithologies of Kachchh for twelve weeks in three sessions from December 1995 to December 1998. 191 samples were collected of which 87 yielded 6675 bryozoan colonies. Field data and observation on type-sections, litho-boundaries and taphonomic aspects obtained during the above project (Guha 1999) have been used in the present study. Standard methods of disintegration, ultrasonic cleaning and development of specimens have been followed. Taxonomic classification and identification of bryozoans up to species level have been checked and vetted by eminent bryozoologists in different repositories of New Zealand, U.S.A., England and Australia.

The bryozoans, though restricted in spatial distribution, form an important group of microfossils among the Kachchh microbiota. The diversity and density of taxa in this group vary widely within and among lithologic units. The updated taxonomic information on this colonial group from this area provides significant clues for deciphering the evolutionary history of many taxa. The overall changes in abundance, diversity and distribution of these bryozoans may provide important information regarding the changes in the microenvironment in which they were deposited.
2 DIVERSITY OF KACHCHH BRYOZOA

The Kachchh bryozoan assemblage is quite diverse (see Appendix) with 99 species contained in 62 genera and 38 families (Gopikrishna 2003). This study has resulted in an increase in the number of species compared to that reported by Tewari et al. (1960) and Tewari & Srivastava (1967). Table 2 shows the summary of distribution of families, genera and species of Cyclostomata and Cheilostomata in different formations.

Bryozoans of the order Cyclostomata are restricted to the early Middle Eocene (Harudi Formation) and make up only around 4% of the Kachchh bryozoan colonies collected. The order is represented by seven species in seven genera in five families expressing unique taxonomic diversity and equitability. The order Cheilostomata is represented by 92 species in 55 genera in 33 families.

Of the 99 species, only 16 occur in more than one Formation (Appendix). The family Calloporidae is
Table 1. Tertiary stratigraphy of the Kachchh Basin (after Biswas 1992).

<table>
<thead>
<tr>
<th>AGE</th>
<th>FORMATION</th>
<th>LITHOLOGY</th>
</tr>
</thead>
<tbody>
<tr>
<td>MIDDLE MIOCENE-PLIOCENE</td>
<td>SANDHAN</td>
<td>Sandstones, limestones and shale. (NO BRYOZOA)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>—Unconformity—</td>
</tr>
<tr>
<td>LATE EARLY MIOCENE (BURDIGALIAN)</td>
<td>CHHASRA</td>
<td>Shale limestone and silty shale</td>
</tr>
<tr>
<td>EARLY MIOCENE (AQUITANIAN)</td>
<td>KHARI NADI</td>
<td>Variegated siltstone and sandstone</td>
</tr>
<tr>
<td></td>
<td></td>
<td>—Unconformity—</td>
</tr>
<tr>
<td>OLIGOCENE (RUPELIAN-CHATTIAN)</td>
<td>MANIYARA FORT</td>
<td>Foraminiferal limestone/shale with coral bioherm and lumpy claystone</td>
</tr>
<tr>
<td></td>
<td></td>
<td>—Unconformity—</td>
</tr>
<tr>
<td>MIDDLE EOCENE (LUTETIAN-BARTONIAN)</td>
<td>FULRA LIMESTONE</td>
<td>Dense foraminiferal limestone</td>
</tr>
<tr>
<td>EARLY MIDDLE EOCENE (LUTETIAN)</td>
<td>HARUDI</td>
<td>Claystone/limestone. coquina</td>
</tr>
<tr>
<td></td>
<td></td>
<td>—Unconformity—</td>
</tr>
<tr>
<td>LATE PALEOCENE to EARLY EOCENE (TH ANETIAN-YPRESIAN)</td>
<td>NAREDI</td>
<td>Ferruginous claystone. limestones, gypseous shale. (NO BRYOZOA)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>—Unconformity—</td>
</tr>
<tr>
<td>EARLY PALEOCENE (THANETIAN)</td>
<td>MATANOMADH</td>
<td>Volcanoclastics, sandstone, bentonite. (NO BRYOZOA)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>—Unconformity—</td>
</tr>
<tr>
<td>LATE CRETACEOUS - EARLY PALEOCENE (IMAASRICHTIAN-DANIAN)</td>
<td>DECCAN TRAP</td>
<td>Basalt</td>
</tr>
</tbody>
</table>

Table 2. Distribution of family/genus/species of Cyclostomata and Cheilostomata in different formations (F-family, G-genus and S-species with number of colonies within parenthesis). Mio = Miocene; O = Oligocene; Eo = Eocene.

<table>
<thead>
<tr>
<th>Cheilostomata</th>
<th>Cyclostomata Anasca</th>
<th>Ascophora</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>G</td>
</tr>
<tr>
<td>Chhasra</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(late Early Mio)</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Khari Nadi</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Early Mio)</td>
<td>12</td>
<td>17</td>
</tr>
<tr>
<td>Maniyara Fort</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(O)</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Fuira</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Middle Eo)</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Harudi 5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(early Mid. Eo)</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>MATANOMADH</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>6</td>
</tr>
</tbody>
</table>
The Kachchh area is unique among other marine Phanerozoic fossiliferous rock formations of the Peninsular India as bryozoans, with varying density and diversity, occur in successive horizons that are precisely dated by large benthic Foraminifera. The high diversity of Kachchh bryozoans, evident from the comparable number of taxa at different hierarchical levels, is a distinctive feature. Quite a few genera and species have shown some novel features in morphology, which have evolutionary and phylogenetic significance while some others have been proved important in paleobiogeographical reconstructions. These are discussed in following sections.

3.1 Evolutionary significance of species of Thalamoporella

The genus *Thalamoporella* Hincks, 1887 is an important constituent of the Kachchh Bryoza with fifteen new species occurring in the Harudi, Maniyara Fort, Khari Nadi and Chhasra Formations (Guha & Gopikrishna 2004a). The Harudi Formation (early Middle Eocene) has four species with 4% of *Thalamoporella* colonies, the Maniyara Fort Formation (Oligocene) has one, the Khari Nadi Formation (Early Miocene) has eight species with 92% colonies and the Chhasra Formation (late Early Miocene) has three species. The Kachchh species of *Thalamoporella* are distinctive in their occurrence, distribution and morphology when compared to species reported elsewhere. This assemblage has increased the number of its i) fossil taxa from 15 to 30, ii) Eocene species number (T. domifera, T. minuta, T. reniformis and T. dorothea (Guha & Gopikrishna, 2004)) from three to seven and iii) fossil species without avicularia (T. reniformis, T. dorothea, T. archiaci, T. tewarii and T. wynnei (Guha & Gopikrishna, 2004)) from one to six. Further, some novel features observed in this assemblage are a) the smallest mean ratio (1:0.24) between mean zooid length and mean avicularium length and or 8-shaped avicularium as in T. minuta, b) four-sided erect colonies as in T. dorothea, c) kidney-shaped opesiules as in T. reniformis, d) transverse avicularia as in T. transversa Guha & Gopikrishna, 2004 and e) the smallest avicularia (\(\bar{x} = 0.140\)) as in T. voigti Guha & Gopikrishna, 2004.

Cluster analysis of twenty-five qualitative characters grouped the fifteen species into three distinct assemblages (Guha & Gopikrishna 2004a), each assemblage representing a particular set of similar morphological characters, especially the features of avicularia (Table 4). The Assemblage I includes four species of *Thalamoporella* ranging in age from early Middle Eocene to late Early Miocene with avicularia of differing size and shape. Assemblage II has five species without avicularium that occur in successions that range in age from early Middle Eocene to Early Miocene. Assemblage III includes a complex group of six species with an agerange similar to that of the Assemblage I. The four Early Miocene species of Assemblage III have acute mandible of differing disposition i.e. torqued and transverse, indicating a possible link in the evolution of these avicularium features. Further the Assemblage III includes the species T. minuta, having the smallest avicularium.
Table 4. Results of cluster analysis of *Thalamoporella* species giving the assemblage-wise grouping, occurrence, age, mean ratio (between zooid length and mean avicularium length) and shape of mandible.

<table>
<thead>
<tr>
<th>Species of <em>Thalamoporella</em></th>
<th>Assemblage</th>
<th>Formation</th>
<th>Age</th>
<th>Mean ratio</th>
<th>Shape of mandible</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. vinijhanensis</em></td>
<td>I</td>
<td>CN</td>
<td>late E. Miocene</td>
<td>1:1.22</td>
<td>Acute</td>
</tr>
<tr>
<td><em>T. kharinadiensis</em></td>
<td>I</td>
<td>KN</td>
<td>Early Miocene</td>
<td>1:1.22</td>
<td>Round</td>
</tr>
<tr>
<td><em>T. kachchhensis</em></td>
<td>I</td>
<td>KN/CH</td>
<td>late E./E. Miocene</td>
<td>1:0.69</td>
<td>Gothic arch</td>
</tr>
<tr>
<td><em>T. domifera</em></td>
<td>I</td>
<td>HA</td>
<td>early Mid. Eocene</td>
<td>1:1.09</td>
<td>Round</td>
</tr>
<tr>
<td><em>T. wynnei</em></td>
<td>II</td>
<td>KN</td>
<td>Early Miocene</td>
<td>Avicularia absent</td>
<td></td>
</tr>
<tr>
<td><em>T. tewarii</em></td>
<td>II</td>
<td>KN</td>
<td>Early Miocene</td>
<td>Avicularia absent</td>
<td></td>
</tr>
<tr>
<td><em>T. archiaci</em></td>
<td>II</td>
<td>MF</td>
<td>Oligocene</td>
<td>Avicularia absent</td>
<td></td>
</tr>
<tr>
<td><em>T. reniformis</em></td>
<td>II</td>
<td>HA</td>
<td>early Mid. Eocene</td>
<td>Avicularia absent</td>
<td></td>
</tr>
<tr>
<td><em>T. dorothea</em></td>
<td>II</td>
<td>HA</td>
<td>early Mid. Eocene</td>
<td>Avicularia absent</td>
<td></td>
</tr>
<tr>
<td><em>T. setosa</em></td>
<td>III</td>
<td>CH</td>
<td>late Early Miocene</td>
<td>1:0.92</td>
<td>Bristle-like</td>
</tr>
<tr>
<td><em>T. voigti</em></td>
<td>III</td>
<td>KN</td>
<td>Early Miocene</td>
<td>1:0.28</td>
<td>Acute</td>
</tr>
<tr>
<td><em>T. arabiensis</em></td>
<td>III</td>
<td>KN</td>
<td>Early Miocene</td>
<td>1:0.76</td>
<td>Acute</td>
</tr>
<tr>
<td><em>T. rhombifera</em></td>
<td>III</td>
<td>KN</td>
<td>Early Miocene</td>
<td>1:0.98</td>
<td>Acute</td>
</tr>
<tr>
<td><em>T. traversa</em></td>
<td>III</td>
<td>KN</td>
<td>Early Miocene</td>
<td>1:0.52</td>
<td>Acute</td>
</tr>
<tr>
<td><em>T. minuta</em></td>
<td>III</td>
<td>HA</td>
<td>early Mid. Eocene</td>
<td>1:0.24</td>
<td>Round</td>
</tr>
</tbody>
</table>

[Abbreviations: HA, Harudi; MF, Maniyara Fort; KN, Khari Nadi; CH, Chhasra.]

Soule et al. (1992, 1999) held that larger avicularia with high mean ratio between mean zooid length and mean avicularium length, and rounded mandible are primitive features while reduction in size of avicularium and its absence were advanced features found in younger taxa. The features of the present assemblage of *Thalamoporella* species from Kachchh indicate that evolution of species without avicularia and a low mean ratio took place at an early date (early Middle Eocene). Alternately, the reduction in size or loss of avicularia might represent some ecological change or alteration in the predator/prey relationship and not a linear progression (Soule, pers. comm. 2003).

3.2 Astogeny of *Thalamoporella kachchhensis*

Boardman & Cheetham (1969) noted the importance of zooidal size as the most consistently applicable index of change. Even the range in zooidal size of a particular generation may be as great as the observed range of the parameter in the whole colony. In the zone of astogenetic change of a bryozoan colony, individuals in each generation in a distally directed series from the ancestrula express morphological characters unique to that generation (Boardman et al. 1969). There is a constant change in zooidal and apertural dimensions in zoecia belonging to different generations.

The Early Miocene species *Thalamoporella kachchhensis* Guha & Gopikrishna, 2004 occurring in the Khari Nadi and Chhasra Formations (Early Miocene) has large erect-rigid foliaceous bilaminar fronds and makes up about 9% of total bryozoan colonies from Kachchh and 26% of colonies in the Khari Nadi Formation. At the bifurcation of a series of zoecia in this species an adult zooid (mother zooid) gives rise to a pair of zoecia, one of which is decidedly shorter (S generation) in length than the other (L generation) or to one avicularium and one sibling zooid. These twin buds of unequal length grow independently by distal budding to form two linear series until they again give rise to mother zooids that are distally wider, generally shorter in length and have smaller apertural dimensions. Guha & Gopikrishna (2004a) studied (a) the stages of astogenetic repetition in zooidal series arising out of two dissimilar buds and (b) evolution of this species from the early to late phases of the Early Miocene.

Measures of the mean zooidal length of S and L generations and mother zooids in colonies of the Khari Nadi and Chhasra Formations indicate that maturity of zooids in colonies belonging to the older formation was attained by the 6th or 7th generation whereas the same was attained by the 2nd or 3rd generation in colonies of the Chhasra Formation. Similar indications are noted when other parameters like zooidal width and apertural dimensions are considered (Guha & Gopikrishna 2004a, fig. 40). The mean length of zoecia, avicularia and apertural height measured on twenty colonies each from the Khari Nadi and Chhasra Formations is decidedly smaller in colonies belonging to the younger formation. For zooidal width and dimensions of aperture and avicularium similar trends have been observed (Guha & Gopikrishna 2004a, fig. 41).

The zoarial growth form of *T. kachchhensis* being erect-rigid foliaceous eschariform, the chance of its influencing the time and stage of maturity of zooids in a colony and consequent increase in size is quite restricted. The environment of these formations may have a role to play. The Khari Nadi Formation, being
mainly arenaceous, might have helped zooecia to attain increased dimensions and maturity at 6th or 7th generation. In contrast, the Chhasra Formation, being chiefly argillaceous, might have motivated the zooids to attain early maturity with the appearance of mother zooecia in the 2nd or 3rd astogenetic stage where a bifurcating zooid may give rise to an avicularium, used as protective/cleaning apparatus. This might have been responsible for a luxuriant growth of *T. kachchhensis* to flourish more in the Khari Nadi Formation (549 colonies) than in the Chhasra Formation (40 colonies).

3.3 Evolutionary and biogeographical significance of Steginoporellids

In the present assemblage the family Steginoporellidae Hincks, 1884 is represented by three genera (*Labioporella* Harmer, 1926, *Steginoporella* Smitt, 1873 and *Reniporella* Guha & Gopikrishna, 2004) with four species, accounting for 6% of total number of colonies collected. The presence of three of the five Tertiary steginoporellid genera makes this area as one of the important centres for the evolution of the family Steginoporellidae during the Tertiary Period.

*Steginoporella bhujensis* Gopikrishna, 2003 is an important taxon of the Maniyara Fort, Khari Nadi and Chhasra Formations ranging in age from Oligocène to late Early Miocene. Based on the shape of main sclerite of B-opercula, this species can be placed under Group I-A of Harmer (1900, 1926: from Pouyet & David 1979b). Most of the species under this group evolved during the second stage of radiation of the genus *Steginoporella* (Pouyet & David 1979a, b) that took place in the European Tethyan Province during the Late Oligocène and Early Miocene when the Kachchh area probably became a part of the same province, a view confirmed by the above authors who suggested that the Indian Ocean and the western Pacific was the geographical source of this genus.

The geographical distribution of *Steginoporella* never extended beyond the 40° N or S and was within the regime of most important warm ocean currents (Pouyet & David 1979a, b). The presence of *Steginoporella* in the Kachchh Basin during the Oligocène to Early Miocene seems to indicate that warm tropical currents that were suitable for the optimum growth of bryozoans influenced it. *Reniporella gordoni*, Guha & Gopikrishna, 2004 from the Harudi Formation (early Middle Eocene), has revealed some interesting information on the evolution of the Tertiary steginoporellids. Though its polypidian tube was not visible, Pouyet & David (1979b, p.796) considered the Eocene genus *Gaudryanella* Canu, 1907 as more primitive than and nearest to *Steginoporella* Smitt, 1873 and put it at the rootstock in the phylogeny of the family Steginoporellidae Hincks, 1884. But the new Eocene genus *Reniporella* from Kachchh has a calcified polypidian tube and shows zooecial dimorphism (normal A-zooecia and avicularium B-zooecia) indicating a closer relationship with *Steginoporella* than any other belonging to the same family. It may be regarded as the most primitive taxon in the family (Figure 2). In the probable phylogenetic lineages of the genus *Steginoporella*, Pouyet & David (1979a, b) put the French Miocene species *S. rhodanica* Buge & David, 1967 at the base of the *S. rhodanica* group but left its antecedent uncertain. *S. rhodanica* is quite similar to *Reniporella gordoni* in zooecial and apertural aspects but lacks large kidney-shaped opesiules. Both the species have calcified polypidian tubes and the genera *Steginoporella* and *Reniporella* are considered more akin to each other in the family phylogeny (Guha & Gopikrishna, 2004b). If it is assumed that loss and/or reduction in the size of opesiules represent valid evolutionary changes with time, then species with large opesiules (*Reniporella gordoni*) may stand as the possible precursor to the French Miocene species *Steginoporella rhodanica* whose origin is so far unknown.

In the aspects of kidney-shaped opesiules, general colonial growth habit, beaded nature of lateral walls and smooth depressed frontal, *Reniporella gordoni* Guha & Gopikrishna, 2004 has an overall similarity with *Thalamoporella reniformis* Guha & Gopikrishna, 2004 occurring in the same horizon and locality. Based on these similarities and their coexistence in the Harudi Formation (early Middle Eocene) of Kachchh, one is inclined to infer that species with kidney-shaped
opesiules under *Reniporella* and *Thalamoporella* Hincks, 1887 might have evolved from a common ancestor or there might have been a parallel evolution of these two taxa with a possible link between their respective ancestors.

### 3.4 Evolutionary and biogeographical significance of *Therenia indica*

David & Pouyet (1978) described *Herentia* Gray 1848 (a genus unrecognised by Bassler 1953) under two subgenera *Herentia* and *Therenia* David & Pouyet, 1978, and put the Eocene species *H. (Therenia) americana* as the rootstock of *H. (T.) porosa* group, from where the French Miocene species *H. (T.) falunica* evolved as a side branch (David & Pouyet 1978, p. 184). Since the *Therenia indica* Gopikrishna, 2003 is from the Harudi Formation (early Middle Eocene) of Kachchh; it might share the same position with *H. (T.) americana* and probably can be directly linked to *H. (T.) falunica* that has similar zooecial features.

Figure 3 shows the probable position of *Therenia indica* in the phylogenetic chart of *Herentia* Gray, 1848 with its two subgenera *Herentia* and *Therenia* by David & Pouyet (1978, p. 184, fig. 5).

that the early evolution of *Therenia*, known to have occurred in the Atlantic and its Caribbean and Mediterranean parts (David & Pouyet 1978, p. 188), took place in the Indo-Pacific province also.

### 4 PALAEOECOLOGY OF TERTIARY SEQUENCES YIELDING BRYOZOANS

#### 4.1 Growth form classification

Bryozoans, a common group of benthic microfauna in the Tertiary sequences of western Kachchh, have a varied spatial and vertical distribution in the Harudi, Fuira, Maniyara Fort, Khari Nadi and Chhasra Formations. For classification of colonial growth types the procedure of Nelson et al. (1988) has been adopted. Eleven colony forms (stomatoporiform, unilaminar diastoporiform, idmidroniform, membraniporiform, celleporiform, eschariform, adeoniform, vinculariiform, reteporiform, cellariiform and lunulitiform) belonging to eight major growth forms, namely, ENul (encrusting unilaminar), ENml (encrusting multilaminar), ERde (erect-rigid delicate), ERfo (erect-rigid foliaceous), ERfe (erect-rigid fenestrate), ERro (erect-rigid robust), EF (erect flexible) and FL (free-living) have been recognised. The relationship of species number and density of colonies of these assemblages is often interesting. Since many colonies are fragmentary and of variable dimensions it is apparent that the estimates of density
Table 5. Formationwise distribution of species number (number of colonies within parenthesis) under different growth forms (for abbreviations see text) and ER/EN ratio of species under erect and encrusting growth form groups (same ratio of colonies within parenthesis).

<table>
<thead>
<tr>
<th>Formation (Age)</th>
<th>ENul</th>
<th>ENml</th>
<th>ERfo</th>
<th>ERde</th>
<th>ERro</th>
<th>ERfe</th>
<th>EF</th>
<th>FL</th>
<th>ER/EN</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chhasra (lateEarly Miocene)</td>
<td>04(107)</td>
<td>01(186)</td>
<td>06(247)</td>
<td>04(354)</td>
<td>01(55)</td>
<td>01(05)</td>
<td>04(68)</td>
<td>2.4(2.26)</td>
<td></td>
</tr>
<tr>
<td>Khari Nadi (Early Miocene)</td>
<td>31(903)</td>
<td>03(837)</td>
<td>04(580)</td>
<td>07(196)</td>
<td>01(12)</td>
<td>04(59)</td>
<td>02(235)</td>
<td>04(252)</td>
<td>0.53(0.62)</td>
</tr>
<tr>
<td>Maniyara Fort (Oligocene)</td>
<td>01(01)</td>
<td>01(80)</td>
<td>04(76)</td>
<td>03(136)</td>
<td>01(39)</td>
<td>01(54)</td>
<td>4.5(3.77)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fuira (Middle Eocene)</td>
<td>05(109)</td>
<td>01(03)</td>
<td>03(68)</td>
<td>01(68)</td>
<td>01(31)</td>
<td>01(54)</td>
<td>4.5(3.77)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Harudi (late Mid. Eocene)</td>
<td>20(1897)</td>
<td>06(85)</td>
<td>01(03)</td>
<td>03(68)</td>
<td>01(31)</td>
<td>01(54)</td>
<td>4.5(3.77)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

are only an approximation of relative abundance. In this analysis 6675 colonies were studied.

The distribution of number of species and colonies under each growth form along with the ER/EN (erect/encrusting) ratio for both species number and density in different formations is shown in Table 5. The ENul growth habit is the most taxonomically diverse (56 species) and dense, accounting for 45% of total colonies. The ENml growth form, though represented by only three species, has 16.5% of colonies. The ERfo growth form with 12 species is an important constituent of this assemblage represented by 13.6% of colonies. The ERde growth form accounts for 18 species and 12.6% of colonies. The FL and ERfe forms have 4 species each, and share 5% and 2.5% of total colonies respectively. The EF category with two species (3.6% of colonies) and ERro growth form with one taxon (1% of colonies) make up the rest.

4.2 Palaeoecology of bryozoans in the Kachchh Basin

In general the rocks of these formations yielding bryozoans are wackestones, packstones and mudstones with a fairly high content of terrigenous material. Five distinct taphonomic associations of bryozoan colonies with other organisms are identified. They are (a) with algae; (b) with saddle-shaped shells of Foraminifera; (c) with bivalve shells, chiefly oysters; (d) with high-spired gastropod shells; and (e) with fossil barnacles. The b-type is observed only in the Harudi Formation; a-, c- and d- types are common in the Khari Nadi Formation, while a- and e- types are common in the Chhasra Formation.

In the Harudi Formation fossiliferous bands within a chiefly argillaceous sequence contain a dense but less varied (with respect to number of growth forms) assemblage that accounts for 66 p. c. of total encrusting colonies in the present collection. Hard substrate provided by the large saddle-shaped and undulating tests of discocyclinid Foraminifera is the chief encrusting surface. The ER/EN ratio is 1:0.27, which indicates that the bryozoan horizon within the Harudi Formation developed in an inner shelf area (Schopf 1969).

Thick sequences of white to buff-coloured bedded foraminiferal limestones (often showing sorting of foraminiferal tests by size) belonging to the Fuira Formation have rare bryozoan colonies. Large mio- gysinids and discocyclinids (often over 2.5 cm in diameter) with broad equatorial faces buried in lime mud form the bulk of this sequence. The general ambience of the Basin during the deposition of the Fuira Formation was something peculiar that supported a restricted development of bryozoans with thickly calcified skeletons.

During the deposition of the Maniyara Fort Formation the taphonomic aspects remained somewhat similar to those of the preceding Fuira Formation but a gradual opening up of a variety of conditions resulted in appearance of more diverse growth habits. The advent of multilaminar celleporiform (species under Turbicellepora Ryland, 1963 encrusting algae) and erect-fenestrate (species under Reteporella Busk, 1884) colonies are notable additions. The absence of unilaminar encrusters (ENul) and high dominance of erect growth forms (ER/EN ratio for both species and colonies hovering around four) indicate a deepening of the basin and high turbulence.

The Early Miocene phase of the Kachchh Basin, when fossiliferous beds and lenses of impure wackestones and packstones of the Khari Nadi Formation were laid down, was the most productive stage for the optimum development of bryozoan colonies in a large number of taphonomic associations like those with algal colonies, on localised shell banks of bivalves and high-spired gastropods and free-living colonies as ‘sand fauna’. All the growth form groups have been encountered in this formation (Table 5). As evident from the presence of appreciable number of colonies having free-living (FL), erect-flexible (EF) and erect-rigid fenestrate (ERfe) growth aspects, the basin might have become somewhat shallower during the early part of Early Miocene. This is reflected in the ER/EN ratio for this formation, which veers around
5 CONCLUSIONS

Ninety-nine bryozoan taxa belonging to 62 genera in 38 families were collected from the Harudi, Fuira, Maniyara Fort, Khari Nadi and Chhasra Formations (early Middle Eocene to late Early Miocene) of western Kachchh, Gujarat. The present database of the Tertiary Bryozoa from Kachchh has provided much significant information on the diversity, evolution and palaeoecology.

The bryozoan radiation in the Kachchh basin peaked during the Khari Nadi times (Early Miocene) with 55 species grouped under 39 genera followed by the Harudi Formation (early Middle Eocene) with 25 species under 19 genera and the Chhasra Formation (late Early Miocene) with 21 species under 16 genera. The Fuira (Middle Eocene) and Maniyara Fort (Oligocene) Formations are less diverse with 10 and 11 species respectively. Besides preserving some hitherto unknown features like smallest mean ratio (between mean zooid length and mean avicularium length), transverse avicularium, smallest avicularium, the assemblage of Thalamoporella from Kachchh has increased the number of i) its fossil taxa from 15 to 30, ii) its Eocene species from three to seven and iii) its fossil species without avicularia from one to six. Furthermore, the number of Thalamoporella species with avicularia torqued toward sibling zooid is raised from one to three. The absence of avicularium and low mean ratio were proposed to be progressive features attained by younger taxa (Soule et al. 1992, 1999). However, in the present assemblage these features occur in taxa from the Harudi Formation (early Middle Eocene). Thus, the above scheme of evolution may need some revision as more number of older fossil taxa of this genus is described.

The zooids belonging to the Early Miocene (Khari Nadi Formation) colonies of T. kachchhensis mature at sixth or seventh astogenetic stage, while those belonging to late Early Miocene (Chhasra Formation) show significant shortening of zooolial, apertural and avicularial dimensions due possibly to their early maturity by the second or third stage only.

The presence of three out of five Tertiary steginoporellid genera makes the Kachchh area as one of the important centres for the evolution and radiation of this family. Steginoporella bhujensis in the present assemblage indicates that the Kachchh Basin might have experienced warm tropical oceanic currents suitable for optimum growth of bryozoans during the period from the Oligocene to Early Miocene.

The monospecific genus Reniporella, the fifth Tertiary steginoporellid genus, might share the same place with the Eocene genus Gaudryanella as root-stock of the family phylogeny and might be the precursor to the French Miocene species Steginothalamus rhodanica, whose origin is so far unknown. The similarity in opesial morphology and coexistence of Reniporella gordoni and Thalamoporella reniformis in the present assemblage indicate a common ancestor or parallel evolution with a link between their ancestors.

Therenia indica from Kachchh extends the biogeographical distribution of the genus to Indo-Pacific province also. Further this Middle Eocene species possibly share the same place with H. (T.) americana in the phylogeny of this genus.

The assessment of relative abundance of different zoarial growth forms, in terms of their diversity and density under each formation and correlation of colonial growth forms with their habitats, revealed two episodes of deepening (Oligocene and late Early Miocene) between periods of shallowing (early Middle Eocene and Early Miocene). Beginning from the early Middle Eocene when the bryozoans shared restricted niches the ambience gradually opened up with great variation and reached its peak during the Early Miocene (Khari Nadi Formation).

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REFERENCES


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Distribution of the Kachchh Bryozoa belonging to different Tertiary Formations of western Kachchh, Gujarat with their family affiliation and frequency of colonies within parenthesis. Abbreviations of Formations: FIA-Harudi (Early Mid. Eocene, FU-Fulra (Mid.Eocene); MF-Maniyara Fort (Oligocene), KN-Khari Nadi (Early Miocene) and CH-Chhasra (Late Early Miocene).

<table>
<thead>
<tr>
<th>Family</th>
<th>Genera &amp; species (No. of colonies)</th>
<th>HA</th>
<th>FU</th>
<th>MF</th>
<th>KN</th>
<th>CH</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Multisparsidae)</td>
<td>Idmidronea sp. (15)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(Incetae sedis)</td>
<td>Discosparsa lakhatensis (10)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(Oncousoeciidae)</td>
<td>Oncousoecia narediensis (129)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(Plagioeciidae)</td>
<td>Plagioecia taylori (12)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Tubigerina sp. (6)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
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<td>-</td>
<td>-</td>
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<td>-</td>
</tr>
<tr>
<td></td>
<td>Voigtopora reticulata (27)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>(Membraniporidae)</td>
<td>Biflustra mitiae (3)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4-</td>
</tr>
<tr>
<td>(Electriidae)</td>
<td>Conopeum gohelaensis (7)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4-</td>
</tr>
<tr>
<td></td>
<td>Herpetopora haimei (196)</td>
<td>+</td>
<td>-</td>
<td>-</td>
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<tr>
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<td>Aploisina sp. (24)</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Copidozoum feddei (4)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4-</td>
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<tr>
<td></td>
<td>Crassimarginatella blanfordi (37)</td>
<td>-</td>
<td>+</td>
<td>-</td>
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<tr>
<td></td>
<td>Crassimarginatella ukirensis (10)</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Marginaria senguptai (3)</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
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<td></td>
<td>Planicellaria kharaensis (8)</td>
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<td>+</td>
<td>-</td>
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<tr>
<td></td>
<td>Planicellaria naliyaensis (14)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>Reptoporina chhasraensis (79)</td>
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<td>-</td>
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<td>Akatopora aidaensis (21)</td>
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<td></td>
<td>Antropora gadhavii (14)</td>
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<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>(Quadricellaridae)</td>
<td>Nellia kutchensis (410)</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>4-</td>
</tr>
<tr>
<td></td>
<td>Nellia naryani (6)</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td></td>
<td>Nellia quadrangularis (260)</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>4-</td>
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<tr>
<td></td>
<td>Nellia walasaensis (4)</td>
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<td>-</td>
<td>-</td>
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</tr>
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<td>(Vinculariidae)</td>
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<td>-</td>
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<td>(Cupuladriidae)</td>
<td>Discoporella misrai (180)</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>4-</td>
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<td>(Chlidoniidae)</td>
<td>Crépis gurjarensis (226)</td>
<td>-</td>
<td>-</td>
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<td>Micropora vredenburgi (7)</td>
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<td>-</td>
<td>-</td>
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<td>Microporina biswasi (23)</td>
<td>4-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>(Onychocellidae)</td>
<td>Onychocella torquata (20)</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>4-</td>
</tr>
<tr>
<td></td>
<td>Floridina pentagonus (11)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4-</td>
</tr>
<tr>
<td>(Steginoporellidae)</td>
<td>Labioporella bassleri (5)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>4-</td>
</tr>
<tr>
<td></td>
<td>Labioporella hariparensis (329)</td>
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<td>-</td>
<td>-</td>
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<td>4-</td>
</tr>
<tr>
<td></td>
<td>Sleginoporella bhujensis (51)</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>4-</td>
</tr>
<tr>
<td></td>
<td>Reniporella gordonii (32)</td>
<td>+</td>
<td>&quot;</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
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ABSTRACT: The following revised definition of the phylum Bryozoa is given after a critical discussion of their main biological characters in the light of recent advances and controversies in our knowledge of this taxon. Colonial animals which are morphologically and anatomically unsegmented, triploblastic, with embryonic radomesderm and generally abortive endodermic macromeres (excepted some primitive and specialized Cheilostomes); endocelomates without archimery, in both larva and adult; two-layered - ectodermic and mesodermic tegument, each layer with peculiar morphological and ontogenetical capacities, in both the larva and the adult; according to the cases, chitinous or chitino-calcareous exoskeleton; embryologically with protostomian larva, but atypical deuterostomian ancestrula (and consequently it is also the case for the functional wtozoecia); neither hyponeurian nor epineurian in the adult stages; some epidermal cell lineages, true stem cells, retaining a permanent totipotence from the larval metamorphosis to the death of the zoarium, the latter proceeding by clonal development from a single larva; presenting, according to the different phylogenetic trends, various types of ontogenetic capacities of morphogenetical substitutions; capacities of epidermal cells art polarized; each neopolaripodial morphogenesis is an predetermined biological phenomenon, probably under hormonal influence; devoid of some physiological systems (respiration, circulation, excretion); adult constituted by a visceral component, the polypide, and a tegument, the eystid; with a row of peribuccal tentacles in the adult, and of ectodermal origin; cctoprocts; generally with an intermittent digestive system (= main part of the polypide), periodically degenerating and renewed from an epidermic proliferation to the inside (consequently: 1° the adult epidermis has kept some morphogenetic capacities of a gastrula; 2° the budding - by disappearing of an inhibition factor from an eotodermis, of an organ with a digestive vocation, contradicts the classical theory of embryological layers); digestive system U-shaped, without digestive gland; without coelom in the larva, the coelomic cavity appearing by schizocoelieonly during the metamorphosis. Some evolutionary trends genetically "programmed" and predetermined, characterized by embryological apoptosis and pre-differentiations, events obvious from the embryological stages. Elaborate coloniality (interzoidal pore and funicules-rosettes system); presenting capacities of both asexual and sexual reproduction and a very complicated metamorphosis. The species are mainly sedentary and benthic, exceptionally free-living; always aquatic, generally marine; filter-feedings with a predominantly vegetarian diet. They often display an interzooecial polymorphism corresponding to a functional specialization of individuals'.

Bryozoa are:

1 UNSEGMENTED TRIPLOBLASTIC ANIMALS WITH AN ENDOMESODERM

The Bryozoa are triploblastic animals, in which the mesoderm proceeds from an embryonic endomesoderm, topographically distinct in the young embryo from the ectoderm. Generally, the endodermal cells degenerate before the end of embryogenesis, but sometimes origin to a functional larval digestive tract in some specialized and presumed primitive Cheilostomes (Malacostegans sensu stricto) or an abortive structure with various destinies according the evolutionary lineages (d'Hondt 1976). Coelomogenensis in the Eurystomes (it is unknown in the Stenolaemates) occurs not during the embryogeny but only during metamorphosis (d'Hondt 1974, 1982), and later a part the ancestral coelom is transmitted at each budding to a new zoocelia by the ancestrula, and further from each mother-zooecia to her daughter-zoecia. A reinterpretation of the old observations on the
embryogenesis of the Phylactolaemates (d’Hondt, ms. in writing) reveals that the coelomogenesis and the embryological origin of the mesoderm may be constitute only and simply a variant of the same general process.

During embryogenesis of the Bryozoa, in lectiotrophic as in cyphonautes and pseudocyphonautes larvae (Barrois 1877, Prouho 1890, 1892, Calvet 1900, Pace 1906, Marcus 1938, Correa 1948, d’Hondt 1977c), the 4 initial macromeres of the vegetative pole of the blastula undergo a transversal division, to produce 4 outer (epidermic) and 4 inner daughter-macromeres, these last situated in the vegetative region of the blastocoele and evolving in a primary endoblast. Further, when the endodermic cells constitute a compact sphere, topographically completely individualized from the epidermis, a small lens of flat and monostratified cells (at this stage, 4-5 cells are obvious in a transverse section) is observable. This embryological rudiment of the mesoderm, where each cell exhibits a large nucleus and a voluminous nucleolus, is obvious closely covering the apical region of the endoblast; this lens is isolated from the epidermis and without contact with its cellular membrane (d’Hondt 1983). The first stage of the anatomical differentiation of this lens (probably by delamination of the upper part of the endoblast from some macromeres) has not been observed and so the complete morphogenetic process of the mesodermogenesis remains unknown; but the mesoderm of the Bryozoa is indubitably an endomesoderm. Later, this monostratified layer surrounds completely the endodermal primordium, before differentiating into mesenchymous tissue with various types of mesodermic cells (d’Hondt 1973b, 1983). At this moment, the endodermal cells differentiate according to various evolutionary trends, or disappear in some phylogenetic lineages of Bryozoa.

The embryological degeneration of the endoderm in most lectiotrophic larvae, or its regression in the pseudocyphonautes as in some peculiar lectiotrophic types (Bowerbankia imbricata (Adams, 1798); Alcyonidium Lamouroux, 1813 sensu stricto), is a preprogrammed phenomenon resulting from apoptoses. In the non-cyphonautes larvae, the mesenchyme remains a full and compact cell mass, without coelomic cavity. Coelomogenesis is unknown in the cyphonautes larvae, in which a functional digestive tract is differentiated. The coelom, according our observations (resulting from the study of histological sections of morphogenetic stages fixed each ten minutes during about ten hours after the beginning of metamorphosis) on various lectiotrophic and the pseudocyphonautes larvae, essentially Ctenostomes, appears only during the metamorphosis, at begin by the differentiation of a cavity inside a compact mass of mesodermic cells so proceeding from an initial embryonic entomesoderm, followed by the organization of these cells in a peripheric mesodermic layer (more and more thin), this morphogenesis constituting a schizocoely according Lütter’s definition (2000). The embryo and the larva of bryozoans are unsegmented during their whole life, without external or internal trimery, without differentiation of a prosome, a mesosome or a metasome and without protocoely, mesocoely and metacoely. The tentacular coelom will be constituted only by a part of the single coelomic cavity, confined during the tentacle retroflexion (d’Hondt 1973b, 1977a, b, 1986a). According Brusca and Brusca (1990), the schizocoely characterizes normally organisms with spiral cleavage and stereoblastula, the enterocoely the animals with radial cleavage and coeloblastula; but in the Bryozoa, the cleavage is radial and the blastula a stereoblastula.

During metamorphosis, the various mesenchymatous larval cell types evolved individually. Some, initially free and ameoboid, are arranged afterwards to constitute a flat cell layer lining the epidermis (d’Hondt 1974), constituting then the somatopleure, in continuity with the thin splanchnopleure lining the polypide, and delimiting between two layers (both monostratified) the single coelomic cavity; others become phagocytes, other muscular cells - their differentiation is easy to follow; the larval mesodermic yolk cells are directly transferred from the larva to the ancestrula. Our cytological observations disagree with the Zimmer’ hypothesis (1997) according to “some of the mesodermal primordia are reported to be of epidermal origin”; after our studies, the mesoderm of the Bryozoa is exclusively an endomesoderm. This difference of point of view arises, in our opinion, owing to the fact that the study of the development of the Ctenostomes and of the is objectively not to easy to interpret that in some other Ctenostome taxa, where many cell types present a very obvious natural cytological characters that are not ambiguous.

Therefore, the Bryozoa, in contrast to Brachiopods and the Phoronids, present any outpocketing from the often temporary digestive tract rudiment of the lectiotrophic and pseudocyphonautes larvae; the Bryozoa are not archimeric animals (d’Hondt 1986a, 1999). Coelomogenesis is not by enterocoely in the Bryozoa, because these animals are not characterized by a separation of an archenteral diverticule as in Brachiopods (Lütter, 2000) or a differentiation of a secondary body developed from an enterocoel; the embryology of the Bryozoa occurs without development of coelomic pouches from the archenteral cavity. The coelomic cavity does not proceeds from the archenteral lumen. The general coelom of the zoecium remains in communication with its diverticules, the epistomial (in the Phylactolaemates) and lophophoral coelomic cavities, proceeding ontogenetically from it; but these cavities do not constitute, in
contrary to Brien’s opinion (1960), other independent coeloms (protoeoele and mesoeoele). The larval mesoderm originates from the same cellular lineage from the embryo to the ancestrula, and then by budding to the other zoecia of the same zoarium. A colony of Bryozoa constitutes a clone, where the mesodermal cells as some of the epidermic cells of all the zoecia arises directly from cell lineages identified in the embryo. Only the larval digestive tract (functional in the cyphonautes, abortive in the pseudocyphonautes and in those of Alcyonium) is derived from embryonic development; the first and all the other digestive tracts of the ancestrula, and all the ones of the other autozoecia arise from an epidermic origin.

Remark: Some different larval (and morphogenetical) types are known in the Bryozoa, differing by the embryological evolution of various epidermal cell lineages, and by many of morphogenetic substitutions (d’Hondt 1976, 1977c), the apoptotic events corresponding to various ontogenetic trends revealed during embryogenesis: cyphonautes (bivalve planotrophic larva, with functional digestive tract); pseudocyphonautes (bivalve lectotrophic larva, with abortive digestive tract modified as site of accumulation of glycogen); various types of columnar lecithotrophic larvae, i.e.:

1° - Bowerbankia Farre, 1837 and the other Vescularines, where the ancestrual epidermis is derived almost totally from the pallial tissue, with the invaginated neck of the internal sac (incorrectly named “metasomal sac” by Woollacott & Zimmer 1978), and inner undifferentiated cells from infracoronal origin producing the first ancestrual polypide;

2° - Alcyoniumidium, where the internal sac and the pallial tissue contribute to formation of the ancestrual epidermis, with abortive digestive tract transformed in a hard concretion, transverse interpalial muscles and where the first polypide proceeds essentially from a ring of infracoronal undifferentiated cells (N.B.: according the photographs of d’Hondt 1973, larvae of Alcyoniumidium present striated muscles, as the cyphonautes);

3° - Bugula Oken, 1815, Microporella Hincks, 1877 and almost all the Cheilostomes, with too well differentiated infracoronal cells to act in the polypidial differentiation, the polypide developing only from suprapallial cells (“upper blastema”), and where the ancestrual epidermis arises for its main part from the internal sac. The cells of the pallial tissue are too highly differentiated to contribute to the formation of the ancestrual epiderm;

4° - and some other types are poorly known (bibliographical references in d’Hondt 1977c, 1982, 2001).

2 WITH INTEGUMENT CONSTITUTED BY TWO CELLULAR LAYERS, EACH HAVING PECULIAR MORPHOGENETICAL CAPACITIES

The fundamental functional unity of the Bryozoa consists in a tegument constituted by two superposed cellular monostratified layers, the epidermis (external) and the mesoderm (internal), constantly associated from the young embryo to the functional zoecium, and each having its own morphogenetical capacities. At each stage of the life of an individual of Bryozoans (embryo, free-living larva, metamorphosis, post-larval morphogenetic stages, ancestrula, functional autozoecium, autozoecium in polypidial regeneration, coeno- and heterozoecium), we can observe the permanent association of both layers. The mesoderm is absent only during the differentiation of the embryo, but then it is precociously present as a compact mass between the epidermis and the (transitory or not) endoderm (d’Hondt 1974). In the larva, the mesoderm (somatopleure) constitutes a continuous inner lining flattened along the whole epidermis, including the autozoecial walls, the internal sac, the pallial tissue, in continuity with the peripolypidial splanchnopleure. When a new polypide is budded to the inside from the proliferation of the cells of the epidermic layer of the tegument, it pushes away the somatopleure to the inner. Further, in each polypide cycle, after each degeneration of the polypide, the phenomenon is identical and the epidermal proliferation pushes back the mesodermal layer, which ends by completely surrounding it. Thus a part of the somatopleure progressively becomes the splanchnopleure, with extension of the epidermal bud, which becomes the zooecial digestive tract, a structure in other bilateria derived from endodermic origin. Probably many hormonal inductions must act during this period. At each polypidal degeneration, the previous splanchnopleure disappears through cell death, and will be replaced by a newly formed splanchnopleure which was formerly a localized area of the somatopleure (Prouho 1890, Calvet 1900, d’Hondt 1982).

Then, the epidermic layer of the integument secretes a cuticle, originally proceeding from some types of ectodermal larval cells that certain peculiar cytoplasmic inclusions (d’Hondt 1974, 1977a, b). In all the Bryozoa, an external chitinous layer is produced first; according the species, it can be thin or thick. The cuticle remains exclusively chitinous in the Ctenostomes and the Phylactolaemates. A second layer, calcareous, is secondarily secreted underneath the chitinous bed by the epidermis in the Cyclostomes (according to Nielsen 1970 and d’Hondt 1977d, the chitinous layer is yet differentiated in the invaginated pallial groove of the larva of Crisia Lamouroux,
3 TYPICALLY NEITHER PROTOSTOMIANS NOR DEUTEROSTOMIANS

With reference to Lender & al. (1994), a protostome animal is an “animal triploblastique chez lequel la bouche dérive de la région antérieure du blastopore” and a deuterostome is an ‘animal triploblastique chez lequel la bouche est une formation secondaire, le blastopore de la gastrula est à l'origine de l'anus’. These referring definitions not precise if “animal” designate the adult or the larva, and it means implicitly that it could be applied to both cases.

In the cyphonautes, planctotrophic organisms (Strieker, Reed & Zimmer 1988a), according to its topographical situation, the larval mouth could be derived apparently from the blastopore (Kupelwieser 1906, Marcus 1938, Strieker 1988, Strieker, Reed & Zimmer 1988b); therefore, this larval type may be fundamentally protostomian. But, in fact (Zimmer 1997), this interpretation is probably wrong: “The blastopore closes at the vegetal pole”, probably in the cyphonautes and the non-cyphonautes larvae both, and gut “are completed by stomodeal (oral) and procotodea (anal) invaginations”. In the lecithotrophic and pseudocyphonautes larvae, devoid of functional digestive tract, the blastopore disappears during the embryogenesis and its topographical situation cannot be localized by external observation (but only in histological sections in AlcyonitUum and Flustrellidra Bassler 1953). During the metamorphosis of the non-cyphonautes larvae an inversion of polarity, firstly described by Calvct (1900) occurs; the autozoocical aperture appears at the aboral pole of the ancestrula, diametrically opposed to the situation of the blastopore, under the influence of badly known factors (hormonal secretions, induction effects, external parameters, gravity?). If (after Zimmer 1997) the larval mouth of the cyphonaute is a neoformation, and considering that the oralifice of the ancestrula appears on the aboral pole, the Bryozoa are doubling deuterostomes - but however different of some other deuterostomian taxa by two characters: the mesoderm formation (non archenteral) and the coelogenesis (non enterocoelous).


1° - the protostomes are triploblastic and schizocoelic animals where the mouth arises from the anterior part of the blastopore; it is the case for the cyphonautes and the non-cyphonautes larvae of Bryozoa. Ecto-mesodermic muscles; determinant cleavage. Contrarily to the Bryozoa, the cleavage is spiral.

2°- the deuterostomians are triploblastic and enterocoelic animals in which the mouth is a secondary or a neo-formation (it is the case, for the adult individuals of Bryozoa, the ancestrula and all the autozooids), the blastopore of the gastrula being at the origin of the anus (it is not the case to the case of the Bryozoa); the cleavage is indeterminate and radial; mesodermal muscles.

The cyphonautes present the same type of inversion of polarity that the other bryozoan larvae. Su the blastopore close during metamorphosis, and the mouth and the anus of the adult autozooid forms new structures that appear secondarily in the aboral region; a peculiarity of the Bryozoa is the confluence of the buccal and anal regions in the same original and inner anatomical common structure, from epidermal origin, the tentacle sheath. The Bryozoa are not particularly either protostomians nor deuterostomians according to the traditional definitions of these terms (d'Hondt 1986a). It was also Brien's (1970) point of view; in this fundamental paper, He wrote: “Le cystide est l'élément primordial et fondamental, c’est lui qui dérive de la larve après sa métamorphose ou du bourgeois (...); dès qu’il est formé, il édifie par prolifération d’une région de sa paroi frontale, le ‘bourgeon polyptidien’ qui en se développant constitue les organes indispensables à la zoécie fonctionnelle: l'axe digestif et le système nerveux. Le polypide de la zoécie est une évolution du cystide”.

According to Nielsen (1987, 1994, 1995), the Bryozoa present more protostomian than deuterostomian characters, but art not typical Protostomes. An argument in favour of their greater affinities with the protostomians are the presences firstly of ciliary bands with compound cilia inserted on multiciliate cells, secondly of a central nervous system with an apical ciliated and senssoiy cap. But, contrary to other Protostomes, they are devoid of ventral nervous cord. According to d’Hondt (1997a), the Bryozoa exhibit a third developmental pathway, different both from protostomy and deuterostomy.

Remark: Many marine zoological groups present free living and planktonic larvae, sometimes called “trophophore-like”, exhibiting normally some ciliary bands. These bands, adaptive and functional features, are considered as main systematic and phylogenetic characters and, according to the cases, as homologies or analogies. The corona, locomotory structure of the bryozoan larvae, is not homologous ontologically of the entoprocts one (d'Hondt 1986a). Nielsen's works (1985,1987) show that homologies and analogies can be put in evidence between troches of larvae of different systematic groups, according to the fact that they are constituted respectively by monociliate (case of the Gastroneuralia) or multiciliate (character of Notoneuralia) cells the cilia sometimes compound,
according to different types corresponding respectively to various evolutive trends. The interpretation is difficult in the case of the Bryozoa, because if the larval corona is constituted by a ring of cells bearing a single cilium, multiciliated cells exists near the mouth of the cyphonautes.

4 NEITHER HYPONEURIAN NOR EPINEURIAN IN THE ADULT (ZOOID)

In the Bryozoan larva, the central nervous system is axial, obliquely oriented forwards, arising from a sub-apical ganglion (surmounted by neurosensory cells), situated in the anterior and inner part of the apical disc, and finishing at the pyriform organ, neurosensory and glandular complex localized in the anterior part of the larva. One equatorial nervous ring curves round the whole circumference of the animal, in subie. Akyunidium or medio-fie. Bowerbankia coronal situation, arising at each side of the pyriform organ from a subepidermal nervous plexus, and presenting connections with sensorial cells intercalated between coronal cells (Reed & Cloney 1982). So, the central nervous system in the larva of the Bryozoa is epineural and anterior; the main ganglion is aboral, as in the trochophore-like larvae of many marine animal species in various phyla.

The nervous system in the adult is neither hyponeurian nor epineurian? The nervous center is ring-shaped and situated at the base of the lophophore; it comprise several ganglions (Bronstein 1937, Lutaud 1973, 1977b, Gordon 1977). Two pairs of main nerves proceeding from the cerebral ganglion, and emits some nerves arising along the tentacle sheath, in the mesoderm (peculiarly funiculus, muscles, interzoooidal connections via the "rosettes" and basat plates) (Lutaud 1979), along the walls, degenerating and reconstituted at least in great part at each new polypidal regeneration. The ganglion is renewed at each polypidal regeneration. Then, it is necessary that new neural connections must be re-established by proliferation and lengthening of the axonal fibres, some closely to the parietal muscles and opercular muscles (Lutaud 1977), which do not degenerate. The adult nervous system is neither a dorsal nor ventral, but lateral in the Bryozoa. From a peribuccal nervous ring arise symmetrically bilateral main nerves, further ramified in the various directions in the space to unnerv the whole autozooid (Lutaud 1976, 1982) and, via the "rosettes", the hetero and the coenozooeo-cia (Lutaud 1969, 1974, 1977b, 1979).

In the Bryozoa, the disposition of the central nervous system is very peculiar. It must, perhaps, derive secondarily from an epineury, but it corresponds during evolution to an infraction of the theory of the differential growth of the nervous axis proposed by Lacalli (1995, 1996, 1997) and adopted by Nielsen (1985). Could this fact be explained by a possible and complex intervention of hox-genes?

5 IN WHICH SOME EPIDERMIC CELL LINEAGES KEEP, FROM THE EMBRYO TO THE ZOOID, A CERTAIN TOTIPOTENCE AND PRESENT CAPACITIES OF MORPHOGENETIC SUBSTITUTIONS ACCORDING PHYLOGENETICALTRENDS

During embryogenesis, the larval epidermis differentiates some cellular categories, many of them distributed according to successive oral-aboral rings, each having their own cytological and sometimes biochemical characters and a specialized function. Some of them have only a transitory existence, and disappear during metamorphosis (d'Hondt 1976); it is for example the case for: 1° the secretory cells of the pyriform organ and for the neck of the internal sac, tissues assuming respectively the primary and the secondary adhesions of the larva to the substratum at the beginning of metamorphosis; 2° the multiciliated cells of the pyriform organ, locomotion and probably also sensorial organ; 3° the larval nervous system, the locomotory cells of the corona; 4° the muscles, all degenerating. The differentiated infracornoral cells of the lecithotrophic cheilostome larvae disappear also during metamorphosis. Some cellular epidermic types are transmitted from the larva to the ancestrula:

- the pallial tissue and the internal sac from which originates (from one of them or from both according the taxa) the ancestrular epidermis, which is then transmitted by budding to the epidermic layer of the daughter-zooids, and finally the first budded of all the zooids of the zoarium;
- the undifferentiated epidermal cells of the apical disc ("Upper blastema" of Woollacott & Zimmer 1971);
- the infracornoral cells of the Bowerbankia and Akyunidium larvae, from which arises the polypide primordium according the phylogenetic lineages.

Normally, two types of larval epidermic cell lineages, the pallial tissue and the internal sac generate (in different proportion according the larval type) the ancestrular epidermis; likewise, two other types of undifferentiated cells, infracornal and suprapallial, contribute (each more or less, according to the phylogenetic lineage) in the elaboration of the rudiment of the first ancestrular polypide. In some lineages of Bryozoa, the cells of one of the members of each of theses two "couples" may be programmed to follow a divergent developmental path, and are characters of
stem cells of Bryozoa must constitute a new field of research open to bryozoologists (Jacob 2002). When the ancestrula buds a daughter-zooecium, it produces a swelling, later isolated by a peripheral septum, future interzooecial wall, increasing in distal direction, and covered by a diermic integument (ectoderm and mesoderm), the “rosette” remaining as unique communication between both (Bobin 1958, 1964, 1965, 1971). The ectoderm and the mesoderm of the daughter-zooecia constitute a part of the double-walled integument between the two eystids, even after closing by the interzooecial wall, but always in direct continuity by the means of communication. When a daughter-zooecia buds a polypide, or when the ancestrula reconstitute a new polypide after necrosis of the previous polypide, elaborating a hernia of undifferentiated ectodermic cells first, they derive always from the same lineage of the larval epidermic stem cell: later it differentiates numerous cytological cells, constituting the various regions of the digestive tract, and nervous cells. These phenomena can logically be under the control of inductions or of hormonal secretions.

6 OF WHICH THE ADULT INDIVIDUAL HAS PRESERVED SOME MORPHOGENETIC CAPACITIES OF A GASTRULA

After the degeneration of a previous polypide inside an autozooecium, the ectodermic layer of the cystid, constituted by true stem cells, buds a replacement new polypide, which will have as temporary a life as its predecessor (except in Phylactolaemates where the polypide does not degenerate), and which elongates in stretching the mesodermic lining; this growth requires, for its nutrition, the metabolization of the glucidic and lipidic vacuoles present in the zoocellular cells and arising peculiarly from the degeneration of the preexisting polypide. The new polypide differentiates the different segments of its digestive tract and the adult nervous center, all proceeding from the same larval epidermic cell lineage. This epidermic proliferation to the inside is realized to the basal membrane on the inside (but later the bud will become isolated from the epidermis) and will evolve further to become a polypide, in a word essentially a digestive tract. This morphogenetic capacity is comparable with the typical one of a gastrula, where the division of some undifferentiated cells (some macromeres) to the inner produces an endodermic tissue. Some epidermic cells of the larva, then of the zoocellular cystid, have retained the morphogenetical capacity to produce organs with digestive vocation, and transmitted this capacity to its daughter-zooecia, which constitutes an infraction of the classical theory of the predetermination of the embryonic layers (d’Hondt 1986a, 1999).

7 WHERE THE CAPACITIES OF THE EPIDERMAL CELLS ARE POLARIZED

The epidermal cells of the Bryozoa, as all epithelia, are polarized; the capacities of it proximal and it distal parts of the cells being different. Distally, the epidermal cells secrete the cuticle; according the groups of Bryozoa, the cuticle is completely chitinous, or externally chitinous and inwardly calcified. Primarily, the epidermal cytoplasm is uniform, unspecialized and its cells are totipotent, keeping characters of undifferentiation. Proximally (only), the epidermal cells are able to multiply by division, at least at some topographic places on the cystidial wall, for differentiate a polypide, probably by an external induction from the upper part of the cells that probably differentiates the autozooecial aperture.

8 WHERE THE NEOPOLYPIDIAL MORPHOGENESIS IS AN AUTOMATIC PHENOMENON UNDER HORMONAL INFLUENCE (LIFTING OF AN INHIBITION?)

An autozooecium can be devoid of polypide, independently of its size, its age or its place in the biological cycle. This occurs in various circumstances, naturally after a polypidial degeneration, or experimentally after a surgical ablation of the polypide (d’Hondt 1976b). Then, it acquires immediately the capacity of budding a new diermic polypidial rudiment beginning by inner proliferation of the cystidial epidermic cells, apparently localized (see above). It is very probable that in the non-Phylactolaemates Bryozoa (the Phylactolaemata keeping always the same polypide) a hormonal factor induces without delay the elaboration of a new polypide when the previous one ceases to be functional or disappears. Probably the disappearance (sensu lato) of the polypide or polypidial degeneration lift and inhibition...
and suppress some influence linked to the presence of an active polypide. The influence must be a neurosecretion, the degeneration of the polypide including necrosis of the central nervous system (the nervous lophophoral ganglion of a bryozoan being quickly differentiated during the polypidial organogenesis). This fact could explain why the inhibition reappears early during polypidial regeneration (except perhaps in Alcyonium duplex Prouho, 1892). were the effect must be more slowing or altering, because several (not numerous) autozooecia can sometimes contain two polypides.

When a polypide begins its differentiation into an autozooecium, it generally inhibits the genesis of a second polypide in the same zooecium. Also, immediately after cisternisation of an ancestrula from which the polypide have been surgically removed, the integument differentiates the rudiment of the new polypide because anyone inhibition is then exerted: but if the zooecium is too small, the young polypide may be incapable of normal development, because of lack of nutriments (d'Hondt 1982). In the Phylactolaemata, the constant presence of the same initial polypide in a same zooecium constitutes a permanent inhibition to the regeneration of a neopolypide; this absence of polypidial regeneration in the Phylactolaemates proceeds perhaps also from the frequent incomplete interzooecial partition and from a more important interzooecial hormonal diffusion. Perhaps the unusual longevity of the Phylactolaemate polypide must be linked to the greater dimensions of the individual and consequently to a better facility to eliminate the metabolic wastes. Osmoregulation in the Phylactolaemates is not such a fundamental function as in the marine Bryozoa, and consequently the polypide is perhaps not so much physiologically stressed and ‘tired’ as in marine species.

9 DEVOID OF SOME PHYSIOLOGICAL APPARATUS (RESPIRATION, CIRCULATION. EXCRETION)

The Bryozoa are devoid of respiratory, excretory and circulatory apparatus. They do not possess any nephridies. The metabolites circulate in the colony from mother-zooecia to daughter-zooecia through the irregular lacunae between the mesodermic cells of the funiculus (Lutaud 1982b, Carle & Ruppert 1983) and via the specialized cells, the ‘rosettes’, according to a given polarity (Bobin 1965, 1971).

Excretion is assured in large part by various mechanisms: accumulation of wastes in the (originated from epiderm) cells of various segments of the digestive tract (Gordon 1977), particularly in stomach, caecum and intestine, pylorus and rectum; this storage results in deforming and to making the various segments of the digestive apparatus mechanically and physiologically unfunctional, and finally poisoning the polypide. This “paralysis” of digestive function induces both the death of the polypide and of the nervous lophophoral center (suppressing the inhibition to the bud of a new polypidial rudiment), but not of the epidermis and of mesoderm-lining of the cystid, which remains unaltered. The constraint linked to this periodical phenomenon, the constant cycle of polypidial regeneration-degeneration, resulting from the lack of excretory system, is the main characteristic feature of the Bryozoa.

The mechanism of invagination and devagination of the polypide proceeds from a hydrostatic process affecting the intrazooecial fluids; for this reason, the retracted polypide inhabits only a small part of the cystidial cavity, the main part of the volume of the zooecium being occupied by an intrazooecial liquid containing free mesodermic cells and gametes. The size of the mouth implicates the absorption only of small particles (microphagic diet by ‘filtration’), and the enzymatic equipment is adapted to the digestion of nutriments from vegetable origin (d'Hondt 1986b). The bacterial pockets present in the vestibular glands of some cheilostomes (Lutaud 1965) apparently do not have a metabolic function.

10 WITH TENTACLES FROM EPIDERMIC ORIGIN

The embryological origin of the tentacular epithelium is ectodermal, because the tentacles are the first morphological structure differentiated, very precociously, from the upper part of the ectodermal layer of the polypidea, immediately after individualisation. This primordium constitutes initially a closed spherule, becoming cup-shaped (“coupe prétentaculaire”, according d'Hondt 1982), open at the lop, the edges of this cup turning up to become a bistrati fied ectodermal neck imprisoning the mesodermic cells, lining it, between its two layers. The tentacles are differentiated later: by longitudinal partition and rearrangement of the cells of this neck in a given number of lots, each lot corresponding to a presumptive tentacle; later, each of these lots of cells becomes a tentacle by gradual deepening of the radiating incisions, then fissures, which will it demarcate. The tentacular and lophophoral coelomic cavity arises from some diverticulae of the general single coelomic cavity, in continuity with it, and the intratentacular lingingmesoderm is in complete continuity with the splanchnopleure (the splanchnopleure being, according the Lender. Delavault & Le Moigne's definition (1994) applicable in the case of the Bryozoa: “chez les coelomates l’un des deux feuillets mésoédermiques résultant du creusement des lames latérales en une
11 ECTOPROCTS

One of the main particularities of the Bryozoa, without equivalent in the other animal phyla, consists of the anatomy of the temporary digestive tract, constantly renewed during the whole life of the autozooid. The two extremities of this tract, the mouth and the anus, are confluent side by side in a peculiar and common ectodermal protractile formation, playing a function of relation between the external environment and the two digestive openings, necessity of which not seeming evident, the tentacular sheath. This sheath is, like the polypide, renewed at each genesis of a new polypidal rudiment, and before the complete differentiation of this later (the formation of the intestine, pylorus and rectum occurs after the tentacular sheath differentiation and are the last segments of the digestive tract to differentiate). The tentacles are obvious at the time when the tentacular sheath is differentiated from epidermis; the sheath grows out during the migration of the polypidial primordium from the epidermal region to the center of the zooecium, and at the same time the mesodermal lining organizes itself in splanchnopleure. When the polypide will differentiate its different segments, the splanchnopleure becomes finally directly in continuity with the mesodermal cells lining the tentacular sheath and the inner side of the tentacle cavities. It is only belatedly that the anus perforates the tentacular sheath and emerge in it, this phenomenon occurring at the end of the polypidial differentiation (Calvet 1900).

12 WITH CURVED DIGESTIVE SYSTEM, U-SHAPED, WITHOUT DIFFERENTIATED DIGESTIVE GLAND

The digestive tract of the Bryozoa is U-shaped, with the following differences according to the species; more or Jess long pylorus, shape and level of insertion of the digestive caecum (morphology of which being a little variable with age), respective length of the segments, presence or absence of a gizzard (primitive or elaborated), obvious delimitation between stomach, intestine, pylorus and rectum; the intestine and the oesophagus are more or less elongated and folded during the polypidial invagination. Only some segments of the tract have ciliated cells: pharynx, pylorus; the gizzard presents different arrangements of chitinous teeth; the pharynx have a more or less columnar epithelium. Digestion is restricted to the last segments of the tract (caecum, stomach, intestine, pylorus) (d’Hondt 1986).

Only the cyphonautes, specific larval type of the malacoslegous Bryozoa, present a functional digestive tract, U-shaped but without caecum, like larvae of other groups of deuterostomic organisms (ie. Phoronida, some Brachiopods). But phoronids and many brachiopods larvae have a direct development, contrary to the case of the Bryozoa where sexual development is indirect and via a complicated metamorphosis. Different digestive segments are individualized in the cyphonautes larvae as in the other taxa mentioned. But in Brachiopoda and the Phoronida, the digestive tract, appearing during embryogenesis, is transmitted directly from the larva to the adult; it is not the same in the non-cyphonautes Bryozoa: before the end of embryogenesis, either this tract degenerates (general case); it is vestigial in few genera, only, evolving ro a pocket rich in glycogen (pseudocyphonautes), or is transformed in a concretion (Alcyonium). In the cyphonautes, the transitory functional larval gut degenerates quickly and completely during the first stages of the metamorphosis.

Note: in some Ctenostome families, the larvae - imperfectly known - present the general morphology of cyphonautes, but apparently not the whole organisation.

13 WITH ELABORATED COLONIALITY

Colonial ity in the Bryozoa reaches a high degree of specialisation. Some individuals are specialized for incubation of embryos (ovicells), settlement and attachment (some types of coenozoecia, stolons, rhizo­oids), chemoreception and the defence (avicularia; vibracuiaria), the functions of relation and the transferring of metabolites (some stolonial coenozoecia), asexual reproduction (hibernacula, statoblasts); in the case in functional autozooecia: for nutrition, gamogenesis and sexual reproduction, and the elimination of the metabolic wastes. The system of transfer of biochemical information and of metabolites via the complex funiculus-rosettes at the level of the interzooecial pores is polarized, the molecules moving from the mother-zooecia to daughter zooecia (Bobin 1965, 1971), in the direction of the colony growth. In reciprocity, exchanges of sensory information take place in the opposite direction, from daughter-zooecia to mother-zooecia via the nervous filaments traversing the interzooecial pores, and then moving through the whole colony along the funicular system.

The zooecia are more or less closely connected one with another according to the species. The zoarium of the Arachnidiidae, the Nollellidae or the Chaperiidac is often disjoined. The specialization of zooecial types varies according to the taxa, to the most extreme situation of the Batopondae and the Clavopondae where the functional autozooecia are reunited in a quasi-spherical capitulum situated at the top of a excessively long and
thin peduncle. Two other very different cases of evolution in the Bryozoa are presented by the lunuliform Bryozoa, characterized by their conical zoarial shape and their very peculiar capacities of locomotion (Cook and Chimonides 1978), and by the motile and mesop-sammic Monobryozooidae, reduced to two zoecia, one single functional autozooecium and a bud.

14 PRESENTING BOTH CAPACITIES OF SEXUAL AND ASEXUAL REPRODUCTION

Independently of the clonal asexual reproduction of the Bryozoa by budding of daughter-zoecia, contributing to the increase of the colony, these animal present two types of reproduction via the differentiation of a free-living founder-individual: the first is asexual, the other sexual. This later corresponds to indirect development (with the exception of the Phylactolaemate larvae, in which the development is direct, the “larva” being constituted, in fact by one (or two) miniature adult zoecia).

Some genetically programmed events occurring during embryogenesis condition the expression of corresponding characters in the larvae according to the phylogenetic lineage. 1° - larval morphology and anatomy conditioning the processes of metamorphosis and of post-larval organogenesis; 2° anatomical interspecific differences. Those two suites of characters allow definition of the main evolutionary trends in the Bryozoa.

According these main lineages, one or other cell type can, during embryogenesis, either be abortive, or remain undifferentiated, or may acquire cytological and functional differentiations, or evolve following various specialisation following a given ontogenetical program to obtain some specialisation different according these trends, or follow an allometric development. When the larva is emitted at an undifferentiated morphological stage, it is also physiological immature; thus a long delay, both of growth and maturation, is necessary (d'Hondt 1981): but when the larva is morphologically mature before its liberation, only a short physiological maturation may be necessary later.

One of the most obvious programmed morphological events concerns the bi laterality of the embryo, which can be: a - more or less cylindriform, with an anterior pari materialized by the pyriform organ, with a palliai tissue remaining invaginated and stretching out only at metamorphosis, and with an equatorial corona (general case); b elongated and laterally compressed, with always an anterior pyriform organ, but characterized by a precocious devagination of the palliai tissue (secreting a pair of symmetrical valves before the spawning) and with a corona rejected to the ventral side (cyphonautes and pseudocyphonautes). In the case of the cylindrical larvae, the ancestrular cuticle is secreted after spawning, only during metamorphosis. The claimed “non-coronate larvae” of some authors are incorrectly named, being in fact true “coronate larvae” in which the corona is secondarily displaced and situated in ventral position, following the development of the valves. The definitive larval morphology proceeds from a lot of apoptoses phenomena.

In the Phylactolaemates, the ontogenetically preprogrammed larval particularities consist in the telescoping of various morphogenetical events which occur, in the other Bryozoa, after spawning. The claimed “larva” of the Phylactolaemates is in fact a young free-living colony, generally with two functional autozooecia, able to adhere to a substratum and to grow. The larval development is realized in the mother-autozooecium, before the spawning, and the organism emitted is no longer true larva. The sexual reproduction of the Phylactolaemates constitutes an exception among the Bryozoa, a case of direct development (Brien 1953).

Generally, a single embryo produces a single larva. However, the phylogenetic lineage of the Cyclostomes, whose reproduction remains rather badly known, presents an other original mode of asexual reproduction, interpreted as primitive: the phenomenon of polyembryony (Harmer 1893); an exception resulting perhaps from the lack of the hormonal regulation acting in other Bryozoa and expressed by the capacity of scission of the embryos during development. This phenomenon can be compared with the duplication of the polypidial primordial in Akyonidium duplex, resulting probably also from a deficiency of the normally regulation controlling the maintenance of a single and indivisible rudiment. The mechanism of the polyembryony is the following: the initial embryo, spherical and hollow, like a coeloblastula, differentiates a sort of protuberance, later detached to become a secondary embryo, and budding itself likewise tertiary embryos.

The most classical phenomenon of asexual reproduction in the Bryozoa concerns only certain (and few) genera (Ctenostomes, Phylactolaemates): it is the elaboration of "sleeping buds" and of “resistance structures” (hibernacula, statoblasts). Both arc answers to the effect of constraining factors, fluctuating during the year, in fresh- and brackish-water (where the eco-physiological conditions are less homogeneous than in marine environments).

15 WITH A COMPLEX METAMORPHOSIS, PREDETERMINED DURING THE EMBRYOGENY, AND PRODUCING VARIOUS LARVAL TYPES, RESULTING RESPECTIVELY FROM DIFFERENT APOPTOSIS PHENOMENA

Embryonic development varies according to the phylogénie lineages of Bryozoa and leads to the
individualization of various larval types, each corresponding to a given taxon. The differences between larval types may correspond to various systematic levels, some characteristics being diagnostic either for species (Barrois 1877, Calvet 1900. Humphries 1975, Reed & Clooney 1982), genera (d'Hondt 2001b), families and superfamilies (d'Hondt 1977c) or higher systematic levels (d'Hondt 1977c, 1997b). The respective importance and significance of one or another morphological, anatomical or cytological larval characteristic varies independently, and only experiments would allow us to understand the true phylogenetical value of each morphological or ultrastructural particularity. Each larval type constitute a phylogenetic and systematic character.

Larval morphology and anatomy condition the type of metamorphosis, and results from the complex of its own preprogrammed apoptosis phenomena occurring during the embryogenesis, characteristic of each phylogenetic lineage. According to the respective capacities of differentiation of each of the larval tissues participant in morphogenesis in each given larval type, the ancestrula is structured according to various modalities; but when the ancestrula is completely formed, it will act the same function independently of the phylogenetic lineage to which belongs the species. Later, all ancestrulae will play the same function independently of their previous organogenesis and of the larval type from which they proceed.

The programmed atrophy, necrosis, apoptosis, conservation of totipotent characters and allometric growths of some organs, which characterize the embryological and larval development of the various phyletic lineages of Bryozoa, make these organisms constitute certainly a favoured experimental biological material.

According the number of the cytophysiological potential capacities presented by some of the cell lineages participating in the metamorphosis and their expressions, larval characters are diagnostic of each given taxon. It is the case, for example, of the hyperdevelopment of the corona and of the anatomy of the internal sac in the Vesicularines, of the predifferentiation of the infracorona! cells in the non-cyphonautes chislostomes, or of the precocious devagination and secretion of the palliai cuticle in the pseudocyphonautes and the cyphonautes. These events occurring during metamorphosis will determine the morphology of the ancestrula, and consequently (d'Hondt 1977c) induce the shape of the zoarium will be function of the larval morphology and anatomy.

16 NORMALLY SEDENTARY

The Bryozoa are almost always sedentary and sessile animals, erect or encrusting species, normally adhesive to a substratum. The adhesion is assumed according to many different modalities; fixation on the whole zoarial surface, by an encrusting disc or plate constituted by a small number of basal zooecia, by rhizoids issued from proximal or lateral autozoecia or coeno­zoecia. by a column or a peduncle of erect elongated zooecia. A lot of species live on a soft bottom in which the basal portion of the zoarium or rhizoids are inserted (i.e. Pseudalcyonidium d'Hondt, 1975, Metalcyonidium d'Hondt, 1975, Batoporidae): exceptionally, the zoarium is almost completely immersed in the sediment (Pachyzoon d'Hondt, 1983).

Amongst the boring bryozoans (Terebriporidae, Spathiporidae, Penetrantidae), the colonial morphology is tributary to the relief of the shells. Some genera are inquiline in other organisms (Harvieriella Borg, 1940, Hypophorella Ehlers, 1876) and fixed by adaptive cuticular processes (abortive zooecia, spurs); they are presumed mobile but we do not know if they are able to move from an individual-host to an other.

Various Bryozoa are free-living. For example, the interstitial ctenostomes belonging to the genera Achihozoon Hayward. 1978, Pachyzoon or Prazcnetula d'Hondt, 1983, living between the sand grains; these species are very probably mobile, but probably slowly, inside the substratum More peculiar is the case of the Monohryozoon Remane, 1936, constituted only by a functional autozoecia and its replacement bud; this genus has been described as motile in the sediment, thanks the mobility of it adhesive basal tubes which allows a temporary adherance to the sand grains; but probably also the movements are very slow in the Monohryozoon, and the animals cannot do spacious displacements.

The lunulitiform Bryozoa have been described (Cook and Chimomdes 1978) as able to moving slowly on the substratum, and to turn over if they are reversed, thanks the marginal specialized vibraculana of the (conical) zoarium. These organisms demonstrate the most elaborated and advanced case of coordination and integration, involving a whole zoarial response, among the Bryozoa.

17 ONLY AQUATIC

The Bryozoa are strictly aquatic organisms, mainly marine, with a small number of fresh- (about 100, essentially Phylactolaemates and Hislopidae) and brackish-water (about 200) species, on a total (now) approximately of 5700 recent species. The brackish-water species may be classified according to their gradient of tolerance (Winston 1977b, Occhipinti Ambrogi 1982, 1985, d'Hondt 2002); this classification of the brackish-water Bryozoa may not be superimposed on the systematics of the phylum, because some families comprise both typically marine
and widely distributed freshwater species (i.e. Victorellidae, Paludicellidae. Membraniporidae).

18 FILTER-FEEDERS WITH PREVALENT VEGETARIAN FILTER FEEDER DIET

The Bryozoa possess a short extensible mouth. Consequently, the diameter of the ingested particles, driven to the buccal aperture by the beating of the tentacular cilia, may be smaller or equivalent to the width of the buccal aperture. Enzymologique studies (d'Hondt 1986b) demonstrated that the digestive enzymes present in the bryozoan digestive tract are essentially adapted for the digestion of vegetable nutrients, very few for food of animal origin. Direct observations demonstrate essentially the absorption of small algae (Bullivant 1968, Winston 1977a).

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A review of non-commensal loxosomatids: collection, culture, and taxonomy, with new implications to the benefit of commensalism (Entoprocta: Loxosomatidae)

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ABSTRACT: Solitary entoprocts (=loxosomatids) have been recognized as a commensal animal, and a non-commensal mode of life is thought to be exceptional in this group. However, recent reports from the Okinawa Islands, Japan, together with the literature surveys of their habitats, indicate that non-commensal life is rather common in this group. In this report, the collection and culture methods as well as the taxonomy of non-commensal loxosomatids are reviewed. Some new observations on the non-commensal species in the Okinawa Islands indicated that they select their habitat to avoid overgrowth by neighbouring organisms. In commensal species, the host animals may protect loxosomatids from the overgrowth, and this may be a benefit of commensal life. Together with the previously postulated advantages (cf. avoiding predators and sedimentation), a major benefit of commensal mode of life seems to be that they can enjoy safe habitats.

1 INTRODUCTION

Entoprocts are suspension feeders that create water currents using ciliary tentacles and catch food particles in the currents. To date, a total of about 180 species have been recognized in this phylum, among which about 140 are solitary and others are colonial. Unlike the colonial species that mostly attach on non-living substrates, most of the solitary entoprocts (=loxosomatids) have been found in association with other animals (Nielsen 1964, Soule & Soule 1965), and thus, this animal group has been recognized as a commensal one (Hyman 1951, Brusca & Brusca 1990, Ruppert & Barnes 1994, Nielsen 2001).

Before Iseto (2001), only a few species had been recognized as non-commensal species (Table 1). *Loxomitra kefersteinii* (Claparède, 1867) was first described based on specimens found on bryozoans and hydroids at Naples. Later studies reported the same species living on plastic panels (Ryland & Austin 1960) and glass plates in an aquarium (Nielsen 1966b). Nielsen (1966b, 1989) concluded that this species is not associated with a host animal. *Loxosomella shizugawaensis* (Toriumi, 1949) was described from northern Japan based on the specimens found on algae. Konno (1971) reported the same species on sponges, gastropods, bivalves, solitary ascidians, and rocks, as well as on algae and recognized this as a non-commensal species (Konno 1978). *Loxosoma isolate* Salvini-Plawen, 1968 was described from the northern Adriatic Sea. This species was found in coarse sands and is the only representative to live interstitially (Salvini-Plawen 1968, 1986). *Loxosomella constricta* (O’ Donoghue, 1924) and *L. olei* Marcus, 1957 were reported from South Africa and the Brazilian coast, respectively. The two species have been found only on non-living substrates. So far only the above species have been recognized as non-commensals among loxosomatids.

However, Iseto (2001, 2002, 2003) reported ten non-commensal loxosomatids (Table 1) from Okinawa Island, the Ryukyu Archipelago, Japan and its adjacent islets. The ten species were found on non-living objects such as coral rubble and shell remains collected from shallow reef flats as well as on glass slides that had been placed on the reef flats and in a fishery port. The reports from the Okinawa Islands suggested that non-commensal species are common among loxosomatids.

Loxosomatids have been found associated with a variety of taxa such as polychaetes, bryozoans, sponges, sipunculans, ascidians, echinoderms, cnidarians, crustaceans, echiurans, molluscs, and pterobranchs (summarized in Nielsen 1964, Soule & Soule 1965). However, it seems unreasonable to always regard those animals as the host of loxosomatids. As Emschermann (1971) postulated, the host specificity is very low in several species, and some of them have
Table 1. List of non-commensal loxosomatids.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reference</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Loxosoma isolata</em></td>
<td>Salvini-Plawen, 1968</td>
<td>Sand (interstitial)</td>
</tr>
<tr>
<td><em>Loxocorone allax</em></td>
<td>Iseto, 2002</td>
<td>Stones, Glass slides</td>
</tr>
<tr>
<td><em>Loxocorone dicoxyledonis</em></td>
<td>Iseto, 2003</td>
<td>Stones, Glass slides</td>
</tr>
<tr>
<td><em>Loxomitra kefersteinii</em></td>
<td>Claparede, 1867</td>
<td>Bryozoans, Hydroid</td>
</tr>
<tr>
<td></td>
<td>Ryland &amp; Austin, 1960</td>
<td>Plastic pannels</td>
</tr>
<tr>
<td></td>
<td>Nielsen, 1966b</td>
<td>Aquarium, Solitary ascidian</td>
</tr>
<tr>
<td><em>Loxomitra mizugamaensis</em></td>
<td>Iseto, 2002</td>
<td>Stones, Glass slides</td>
</tr>
<tr>
<td><em>Loxomitra tetraorganon</em></td>
<td>Iseto, 2002</td>
<td>Stones, Glass slides</td>
</tr>
<tr>
<td><em>Loxosomella aloxiata</em></td>
<td>Iseto, 2001</td>
<td>Stones, Glass slides</td>
</tr>
<tr>
<td><em>Loxosomella constricta</em></td>
<td>O’Donoghue, 1924</td>
<td>Dead branch of a gorgonaccan</td>
</tr>
<tr>
<td><em>Loxosomella intragemmata</em></td>
<td>Iseto, 2003</td>
<td>Glass slides</td>
</tr>
<tr>
<td><em>Loxosomella lappà</em></td>
<td>Iseto, 2001</td>
<td>Stones</td>
</tr>
<tr>
<td><em>Loxosomella lecithifera</em></td>
<td>Iseto, 2003</td>
<td>Glass slides</td>
</tr>
<tr>
<td><em>Loxosomella monocera</em></td>
<td>Iseto, 2001</td>
<td>Stones, Glass slides</td>
</tr>
<tr>
<td><em>Loxosomella olei</em></td>
<td>Marcus, 1957</td>
<td>Stones</td>
</tr>
<tr>
<td><em>Loxosomella shizugawaensis</em></td>
<td>Toriumi, 1949</td>
<td>Algae</td>
</tr>
<tr>
<td></td>
<td>Konno, 1971</td>
<td>Algae, Sponges, Molluscs, Solitary ascidians, Rocks</td>
</tr>
<tr>
<td></td>
<td>Konno, 1978</td>
<td>NO DATA*</td>
</tr>
<tr>
<td></td>
<td>Konno, 1985</td>
<td>NO DATA*</td>
</tr>
<tr>
<td><em>Loxosomella stomatophora</em></td>
<td>Iseto, 2003</td>
<td>Glass slides</td>
</tr>
</tbody>
</table>

* Konno (1978, 1985) did not mention the substrate of the specimens collected in Sado and Shirahama, Japan. However, he noted in the former paper that this species has no host animal.

Table 2. List of loxosomatids that show low host specificity and/or low host dependency.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reference</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Loxosoma loricatum</em></td>
<td>Harmer, 1915</td>
<td>Bryozoans</td>
</tr>
<tr>
<td></td>
<td>Bobin &amp; Prenant, 1953b</td>
<td>Polychaetes</td>
</tr>
<tr>
<td><em>Loxosomella antarctica</em></td>
<td>Franzén, 1973</td>
<td>Ophiuroids</td>
</tr>
<tr>
<td></td>
<td>Emschermann, 1993</td>
<td>Ophiuroids. Polychaetes</td>
</tr>
<tr>
<td><em>Loxosomella antedonis</em></td>
<td>Mortensen, 1911</td>
<td>Crinoids</td>
</tr>
<tr>
<td></td>
<td>Ryland &amp; Austin, 1960</td>
<td>Settlement panels</td>
</tr>
<tr>
<td></td>
<td>Emschermann, 1993</td>
<td>Polychaetes, rocks, and other solid substrates</td>
</tr>
<tr>
<td><em>Loxosomella crassicauda</em></td>
<td>Salensky, 1877</td>
<td>Tubes of polychaetes</td>
</tr>
<tr>
<td></td>
<td>Harmer, 1885</td>
<td>Floor of a tank in laboratory.</td>
</tr>
<tr>
<td></td>
<td>Atkins, 1932</td>
<td>Tubes of polychaetes. Wall of a tank laboratory.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A solitary ascidian and bryozoans growing on the ascidian</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Stones</td>
</tr>
<tr>
<td><em>Loxosomella hispida</em></td>
<td>Marcus &amp; Marcus, 1968</td>
<td>Algae. Bivalves</td>
</tr>
<tr>
<td><em>Loxosomella leptoclini</em></td>
<td>Harmer, 1885</td>
<td>Colonial ascidians</td>
</tr>
<tr>
<td></td>
<td>Harmer, 1915</td>
<td>Pterobranchs</td>
</tr>
<tr>
<td></td>
<td>Prenant &amp; Bobin, 1956</td>
<td>Colonial ascidians</td>
</tr>
<tr>
<td><em>Loxosomella murmanica</em></td>
<td>Nius, 1909</td>
<td>Sipunculans</td>
</tr>
<tr>
<td></td>
<td>Nielsen, 1989</td>
<td>Body of sipunculans and inner side of its shelters.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tube of polychaetes</td>
</tr>
<tr>
<td><em>Loxosomella nitchei</em></td>
<td>Nielsen, 1989</td>
<td>On bryozoans, hydroids, algae, and stones</td>
</tr>
<tr>
<td><em>Loxosomella phascolosomata</em></td>
<td>Vogt, 1876</td>
<td>Sipunculans</td>
</tr>
<tr>
<td></td>
<td>Atkins, 1927</td>
<td>Bivalves*</td>
</tr>
</tbody>
</table>

*The bivalves, *Potidoma clarkiae* and *Mysella hindenteaia*, lived with sipunculans. Therefore, *L. phascolosomata* may have special affinity to sipunculans.
also been found on non-living substrates (Table 2). Such ambiguous commensal relationships indicate that those species have a high tolerance of the substrate, and that they are possibly not commensal species. The fact that most loxosomatids have been found on other animal groups is probably the result of a more intense search on such substrates. It seems likely that a noncommensal lifestyle is rather common in this animal group. To outline diverse lives of Loxosomatidae, not only the commensal species, but also non-commensal species should be surveyed in worldwide waters including the localities from which only commensal species have been reported so far. This paper reviews the current knowledge about non-commensal loxosomatids and also discusses the benefit of commensalism in this animal group based on some new observations on non-commensal species that cannot enjoy those benefits.

2 COLLECTION OF NON-COMMENSAL LOXOSOMATIDS

Iseto (2001, 2002, 2003) collected calcareous stones or dead coral rubbles from shallow reef flats (Fig. 1 A) and found several non-commensal loxosomatids on them using a binocular microscope. However, the surfaces of the substrates were usually rather complex and tiny loxosomatids on them were difficult to detect. He placed glass slides (26 mm X 76 mm) in slide boxes (Fig. 2A) and put them in reef flats or a fishery port (Fig. 1B) and found several loxosomatid species attached to the slides after a few months (Fig. 2B). This method drastically improved the efficiency of the collection process. In one case, more than 1,800 individuals of five species were attached to a single slide that had been immersed at a reef flat for two months; the density reached about 46
individuals/cm². In most cases the slides were kept in the field for about two months and this period seemed to be the best for collecting non-commensal species in the Okinawa Islands. Longer (e.g. four months) settlement was sometimes successful but the number of loxosomatids was usually low due to settlement of larger animals such as ascidians, bryozoans, sponges, and tube-building polychaetes. Ryland & Austin (1960) immersed plastic panels at a dock in Swansea, and found two loxosomatid species, *Loxosomella antedonis* Mortensen, 1911 and *Loxomitra kefersteinii*, attached to them. In this case the density of the loxosomatids reached approximately 5 individuals/cm². It seems that using settlement panels is the best way to collect non-commensal species.

Another unique collection method was introduced by Iseto (2001, 2003). He collected some objects from the sea and put them, together with glass plates, into a bucket filled with seawater and maintained it with an air supply. About one month later he found dozens of individual *Loxosomella lappa* Iseto, 2001 on the plates, which most likely proliferated by budding from original individuals attached to the objects. In this case, no food was added, and thus detritus that contaminated the original objects was sufficient for their asexual proliferation. This is another collection method effective for finding small individuals that otherwise would be overlooked by direct observation of the substrate surface.

### 3 CULTURE OF NON-COMMENSAL LOXOSOMATIDS

Culturing has great advantages in the studies of loxosomatids. It supports careful observations of morphological, behavioural, and reproductive characteristics including those that vary depending on the growth stage. There are, however, very few reports on the long-term culturing of loxosomatids. This may be because the majority of species studied so far are commensal species. The commensal species usually choose specific attachment sites, and seem to have special preference for particular substrates, and thus it is plausible that they have some difficulty living on culture dishes or other artificial objects.

On the other hand, the non-commensal species have been found on various substrates such as stones, plastic panels, glass slides, and animal bodies, and show high tolerance to substrate. Nielsen (1966b) suspended slides in an aquarium at Miami and obtained individuals of *Loxomitra kefersteinii* attached to the slides some days later. He kept those individuals in the aquarium for about 10 days so he could observe its budding process. Iseto (2001, 2002, 2003) cultured some non-commensal loxosomatid species found in the Okinawa Islands in the laboratory. The collected animals were grown in small (ca. 50 ml) glass dishes (Fig. 3). He supplied surplus amounts of microalgae *Nannochloropsis* (Marine Chlorella 100, Marine-Bio Co., Japan) as food once a day, and exchanged the seawater after about 30 minutes (Iseto, 2001). The excess food and excretions deposited on the bottom of the culture dishes were removed several times a week using thin wooden sticks (Iseto, 2003). By this method, *Loxocrone dicotyledonis* Iseto, 2003 was grown for about ten months. The original three individuals showed vigorous budding and the number of individuals reached 138 within the first 40 days (Iseto 2003). *Loxocorone allax* Iseto, 2002, *Loxomitra mizugamaensis* Iseto, 2002, and *L. tetraorganon* Iseto, 2002 were grown for two to three months, but it may be possible to culture them for longer time as they budded vigorously throughout the culture period. In the case of *L. allax*, for example, a bud was released from the parent approximately every three days. The liberated buds, some of which had already began to produce their own small buds, attached to the culture dish within one or two days and, after about one week, released their fully grown first buds. Culturing with a commercially available diet for invertebrates (Invertemin, Tetra, Germany) was also successful at least for short-term (about one month) culturing of several species. Therefore, food preference seems not to be strict, at least in the non-commensal species in the Okinawa Islands. It is worth noting that it proved impossible to grow one species, *Loxosomella aloxiata* Iseto, 2001, in the laboratory (Iseto 2003). The newly liberated buds of this species are known to have a slug-like foot at base of the stalk that enable the animal to glide over the substrate, but the foot is degenerated when the animal fixes on the substrate to become an adult form (Iseto 2001). I observed dozens of liberated buds of this species but they never fixed on the substrate. After several
days, their feet became half degenerated and the liberated buds failed to reach the normal adult form. This is somewhat curious because adults of this species were found in the field attached to glass slides that were a similar substrate to the glass dishes used in the laboratory. At present, the factors that obstruct the normal attachment and metamorphism in this species are completely unknown.

4 TAXONOMY OF NON-COMMENSAL LOXOSOMATIDS

Among about 140 species so far described in the family Loxosomatidae, 26 species (Nielsen 1996, Prpic 2001) are classified in the genus Loxosoma Keferstein, 1862, excluding the species those generic allocation is in question (see below). Among them, only L. isolata, which lives interstitially, is non-commensal (Salvini-Plawen 1968, 1986). All the other species of this genus have been known to associate with polychaetes of several families (Nielsen 1996), except Loxosoma jaegersteni Nielsen, 1966a, whose habitat is not known. This suggests a special affinity of the group to the Polychaeta. Salvini-Plawen (1986) noted that other two interstitial species were found in Florida but remain undescribed, and thus, Loxosoma may be a genus adapted also to interstitial habitats.

In the genera Loxomitra Nielsen, 1964 and Loxocorone Isotto, 2002, three of five and two of four species are non-commensals respectively. This indicates that the two genera have some affinities to non-commensal life style. In both genera, however, only a few component species have been described so far. Extensive studies are required to determine the generic properties of their commensalism.

Loxosomella Mortensen, 1911 is the most species genus in Loxosomatidae, consisting of about 90 species. Species have been found mainly on polychaetes, sponges, bryozoans, and sipunculans (Nielsen 1964, Soule & Soule 1965), and several species were found on ascidians (Harmer 1885, Atkins 1932), bivalves (Atkins 1927, Marcus & Marcus 1968), crinoids (Mortensen 1911), crustaceans (Soule & Soule 1965), echiurans (Marcus & Marcus 1968), hydroids (Claparède 1867), ophiuroids (Franzén 1973, Emschermann 1993), and pterobranchs (Harmer 1915). Such high diversity with regard to the host animal groups is a characteristic feature of this genus. It is intriguing that all loxosomatid species that have been reported from more than one host animal group belong to this genus (Table 2), except Loxosoma loricatum Harmer, 1915, of which the generic allocation is in question (see below). Such low host specificity is another characteristic feature of this genus. Moreover, some Loxosomella species have been found from both living and non-living substrates (Table 2), indicating that they have low host dependency as well as the low host specificity. This implies that they are basically non-commensal species. Such flexibility in habitat selection is a significant aspect of this genus.

The genus Loxomespilon Bobin & Prenant, 1953a is a monotypic taxon in which only L. prezi Bobin & Prenant, 1953a has been described. This species has been found exclusively on polychaetes. As such, the non-commensal species are known in four genera.

Nielsen (1996) postulated that for the eleven species originally described in the genus Loxosoma (L. breve Harmer, 1915; L. cingulatum Kluge, 1946; L. cocciforme Harmer, 1915; L. infundibuliforme Kluge, 1946; L. lanchesteri; L. loricatum; L. minutum Osbum, 1912; L. rotundum Kluge, 1946; L. sluiteri Harmer, 1915; L. subsessile Harmer, 1915; L. troglodytes Harmer, 1915), the generic affinities could not be ascertained because the original descriptions did not sufficiently define their generic characters. All of them are commensal species that have been found in association with host animals. Nielsen (1996) suggested that those species may in fact have belonged to the genus Loxosomella, because most of them were found on bryozoans or sipunculans, the common host animals of Loxosomella. One of them, Loxosoma loricatum, was found on polychaetes (Harmer 1915) and bryozoans (Bobin & Prenant 1953b). The low host specificity also suggests that this species is not a member of Loxosoma.

5 SOME IMPLICATIONS OF THE BENEFITS OF COMMENSAL LIFE

Nielsen (1964) summarized the loxosomatid-host animal relationships and postulated that most loxosomatids associate with animals that create water currents and attach to the positions where they can easily receive the currents. This indicates that their habitat selection is closely related to the host-generated water currents. Nielsen (1964) also postulated that several species have tentacles that seem too short to create sufficient water currents by themselves (cf. Loxosoma sam Nielsen, 1996, L. axisadvorsum Konno, 1972, and Loxomespilon perei, Loxosomella dispocoda Nielsen, 1964, Loxosomella varions Nielsen, 1964). Based on these observations Nielsen (1964) concluded that Loxosomatids are energy commensals that exploit host-generated water currents to get suspended food particles more efficiently than through self-generated currents only.

However, Nielsen (1964) noted that this concept was not applicable for all cases as some loxosomatids attached on to the bodies of animals where no host-generated current is supplied (e.g. on the pinnules of crinoids, on the outer surface of solitary ascidians, and on the bodies of hydroids). The ten non-commensal
species found in the Okinawa Islands live without host animals and they obtain enough food through self-generated water currents (Iseto 2001, 2002, 2003). Nevertheless, the ten species do not seem to have features that enable them to make stronger water currents than those generated by commensal species. This suggests that not only the non-commensal species but also the commensal species, except several short-tentacled species (mentioned above), can produce sufficient water current by themselves, and that the commensal species do not largely depend on the host-generated current (Iseto 2003). Exploiting the host-generated currents may not always be a major benefit.

Emschermann (1971) noted that the essential difficulty in culturing loxosomatids was to protect them from sedimentation. He concluded that the general reason why they live on animals is to avoid sedimentation and that the host-generated water current is not the decisive factor for their substrate selection.

Iseto (2003) postulated that non-commensal species were often found at narrow crevices on substrates. This may indicate that substrate preference in those species depend on whether the attaching point is preferable for the avoidance of predators. Although there are no reports on the predators of loxosomatids, flat worms and nudibranchs are known to eat colonial entoprocts (Canning & Carlton 2000). It is reasonable to assume that the same animals also eat loxosomatids. Based on these arguments Iseto (2003) suggested that the commensal lifestyle has the advantage for loxosomatids of avoidance of predators at least in cases where the loxosomatids associate with animals living in tubes such as polychaetes and sipunculans; In these cases the predators may hardly come into the host tubes. However, during my extensive surveys on non-living substrata in the Okinawa Islands, I found non-commensal species several times at sites where they seemed to be exposed to predators. Although avoiding predators is no doubt a benefit of commensal life, it seems to be not always a major factor of their habitat selection.

I observed several times that loxosomatids found on the glass slides were covered by growing bryozoans (Fig. 4). This is obviously lethal for loxosomatids, and thus, non-commensal loxosomatids are threatened with overgrowth by neighboring organisms. An intriguing property of non-commensal loxosomatids in the Okinawa Islands is that they are never found on substrates densely covered by larger animals but found on substrates almost free from those animals. These new observations imply that one factor in the habitat selection is whether they can avoid overgrowth by neighboring organisms. The commensal species may have the benefit of avoiding overgrowth by other animals by living on the host animals. These observations are consistent with the fact that many non-commensal loxosomatids appeared on glass slides

Figure 4. Loxomitra sp. found on a glass slide that was placed at the Ginowan Fishery Port for two months. The loxosomatid was half covered by Bryozoa. Scale bar = 1 mm.

I wish to express my gratitude to Professor Shunsuke F. Mawatari (Hokkaido University), Professor Terufumi

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Gigantism in Permian trepostomes from Greenland: testing the algal symbiosis hypothesis using $\delta^{13}C$ and $\delta^{18}O$ values

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ABSTRACT: Photosynthesizing endosymbiotic algae can result in gigantism in their hosts, but this has never been unequivocally documented in extant bryozoans. Unusually large colonies (up to 7 cm branch diameters) of the trepostome bryozoan *Tabulipora* sp. have been recovered from the Kungurian (Early Permian) Kim Fjelde Formation in eastern North Greenland. Håkansson & Madsen (1991) used carbon and oxygen isotope values from skeletal carbonate to test the hypothesis that the gigantism was caused by algal symbiosis. In this study, a more precise test of their hypothesis was conducted using a finer sampling protocol on a colony from the same formation and location. Skeletal carbonate reveals mean $\delta^{13}C$ and $\delta^{18}O$ values of 3.9‰ VPDB and —6.5‰ VPDB, respectively. Diagenetic effects were evaluated by discretely recovering cements contained within zooidal chambers; skeletal values are significantly higher than the surrounding cements. In consideration of the isotope value of the Permian ocean, it is concluded that this isotopic evidence is largely negative. We reject the algal symbiosis hypothesis based on the combined isotopic, morphologic, and paleoenvironmental evidence.

1 INTRODUCTION

Gigantism refers to a condition in organisms with a larger body size than in phylogenetically related organisms. It can be caused by disease (e.g. pathologic gigantism) or special growth conditions that result in rapid growth and/or longevity (e.g. island gigantism, polar gigantism, abyssal gigantism, or symbiotic gigantism). In particular, elevated dissolved oxygen levels are most commonly cited as the source of gigantism due to special growth conditions (Chapelle & Peck 1999). Symbiotic gigantism results from the presence of a wide range of photosynthesizing endosymbiotic organisms, but most common are the "zooxanthellae" algae which are single-celled autotrophic plants (dinoflagellates) that live symbiotically in the tissues of their heterotrophic animal hosts (Trench 1993). Symbiotic algae photosynthesize and release photosynthetic products (sugars and $O_2$), into the tissues of their host. The host metabolizes the photosynthetic products and releases $CO_2$ and waste. The symbiotic algae absorb the $CO_2$ and extract the nutrients from the waste (phosphate and nitrate) during photosynthesis. This allows organisms to live in nutrient poor environments (Stanley 2003). Additionally, the symbiotic algae receive protection from predators by living in their host’s tissues. This symbiosis with its efficient recycling of nutrients promotes calcification (Pearse and Muscatine 1971) sometimes at ‘staggering’ rates which may lead to skeletal giantism (Hallock 1981, 1996, Cowen 1983). This is primarily achieved in two ways: removal of $CO_2$ from the host’s tissues helps convert bicarbonate to carbonate and the addition of energy allows for caloricly expensive calcification. Algae-bearing hosts are generally an order of magnitude larger than their non-symbiont-bearing relatives (Cowen 1983). Algal symbiosis has resulted in gigantism in a wide variety of
clades, most notably foraminiferans (Lee & Anderson 1991), corals (Coates & Jackson 1987), and bivalves (Morton 2000). These extant clades also have extinct ancestors in the fossil record whose gigantism has also been attributed to algal symbiosis (e.g. foraminiferans (Lee et al. 1979), corals (Cowen 1988), and bivalves (Vogel 1975)).

1.1 Gigantism in bryozoans

Gigantism has been recognized in various bryozoans, including several Ordovician trepostomes (Raizen et al. 1999), the Mississippian trepostome *Stenophragmidium* sp. with >35 mm diameter branches (Wyse Jackson & Kora, unpublished data), the Cretaceous cyclostome *Pennipora anomalopora* with 22 mm diameter branches (Taylor & Voigt 1999), the Pleistocene cheilostome *Schizoporella* sp. (Cuffey & Fonda 1976), and the Recent cheilostome *Cellepora coronopus* with 20 mm diameter branches (Chapman 1933). Larger than all these is the Permian trepostome *Tabulipora* sp. from the Kim Fjelde Formation in Greenland (Fig. 1) in which branches reached up to 70 mm in diameter and 200 mm in length (Ross & Ross 1962, Håkansson 1979, 1987, 1994, Madsen & Håkansson 1989, Håkansson & Madsen 1991, Stemmerik 1997). These Greenland colonies are at least an order of magnitude larger than other stenolaemates specifically and bryozoans in general (Madsen 1991). In addition, Håkansson & Madsen (1991) argued that this example of gigantism was the result of endosymbiotic algae.

1.2 History of research on endosymbionts in bryozoans

Previously in earlier bryozoan research, plant cells were reported in brown bodies or in the gut wall of bryozoans (MacMunn 1887, Oltmans 1923, Zirpolo 1923). The cells in brown bodies most likely represent undigested food (Schopf 1977). Reports of cells in the gut wall are of more interest to this study. Of these previous studies, Zirpolo’s (1923) is most unequivocal in attributing the cells to symbiotic algae in the gut wall, but Buchner (1930) was unable to
substantiate Zirpolo's claim. Bryozoan-algal relationships were again invoked to explain zoarial habits of some Paleozoic fossil species including Archimedes sp. (Condra & Elias 1944, 1945). This bryozoan-algal relationship was quickly disproved (Easton 1944, Haas 1945, Shulga-Nesterenko 1949), but even if these relationships were genuine, they involved exosymbiotic, multicellular algae, not the endosymbiotic, unicellular algae that are the focus of this paper. Lutaud (1965) showed that bacterial cysts live within bryozoans, but once again they were non-symbiotic. This was the state of bryozoan-algae symbiosis until Cuffey (1970, p. 44) wrote, 'Single-celled algae (zooxanthellae) live commensally in the soft tissues of a few modern marine bryozoans.' But this statement was unsupported and was thus rejected by Schopf (1977, p. 181) who found no evidence that any modern bryozoan has a symbiotic relationship with single-celled algae. Taylor (1999) reviewed the literature and concluded that there are no known examples of modern bryozoans with skeletons which are modified by the presence of photosynthetic or chemosynthetic endosymbionts. Since then, Crowley & Taylor (2000) reported on hydroids living symbiotically with some ascophoran cheilostomes, and Kaselowsky et al. (2002) documented the presence of fungi growing in the metacoelom of bryozoans causing the formation of 'giant buds'. These are not the photosynthesizing endosymbiotic algae common in reef forming corals.

The most rigorous test to date for symbiotic algae in bryozoans came from a study by Hâkansson & Madsen (1991) who argued that for some Permian bryozoans gigantism was the result of endosymbiosis. The effectiveness of Hâkansson & Madsen’s original isotopic test of the algal symbiosis hypothesis for gigantism in bryozoans was limited by the sampling resolution of the technology available at the time. New micromilling technology with 1 m spatial sampling resolution and new mass spectrometers that require —20 p.g samples (sensu Wurster et al. 1999) allow better independent sampling of bryozoan skeletal walls and secondary cements. This is in contrast to Hâkansson & Madsen’s (1991)*1.5 mg samples. They recognized this on p. 154: ‘due to the comparatively high amount of carbonate material required by the available analytical facilities, all bryozoan samples analyzed contain a varying proportion of the diagenetic cement spar now occupying all zooidal cavities.’ It is the goal of this study to test the algal symbiosis hypothesis for gigantism in the Permian trepostome Tabulipora sp. using state-of-the-art stable isotope analytical technology.

2 MATERIALS

This study was based on a single Geological Institute of Copenhagen specimen (GI 90635-1) of the stenoporid trepostome bryozoan Tabulipora sp. The colony branch has a length of 63.0 mm and a diameter of 38.9 mm (endozone diameter = 20.7 mm, exozone width = 9.1mm). The sample was collected 10 km northeast of Kap Jungersen in southern Amdrup Land in eastern North Greenland (Hâkansson et al. 1981, Fig. 17, un-numbered dot NE of locality 16; 80°35’N. 15°59’W). It came from the top of the Kim Fjelde Formation of the Mallemuk Mountain Group (Hâkansson 1979, Stemmerik & Hâkansson 1989) and has an age of Early Permian (Kungurian stage) (Stemmerik et al. 1998). The Kim Fjelde Formation was deposited in the Wandel Sea Basin which developed in response to extension and rifting between Greenland, Norway and Spitsbergen (Hâkansson & Stemmerik 1989, Stemmerik et al. 1998). Deposition in the basin was controlled by a series of syndepositional extensional faults and grabens that developed parallel to the stable Greenland craton (Stemmerik et al. 1996). Sedimentation in Amdrup Land was restricted to a subsiding platform bounded to the west by the East Greenland fault zone and to the northeast by the Sommertonasserne fault (Hâkansson & Stemmerik 1995).

This formation consists of cliff-forming, normal marine, shallow to deeper shelf, finely bedded, cherty, fossiliferous limestones (Hâkansson 1979, Hâkansson et al. 1981, Stemmerik & Hâkansson 1989, Stemmerik et al. 1996). The giant bryozoans are preserved in a bryozoan rudstone facies which was deposited on the outer shelf below storm wave base (facies F4 of Stemmerik 1997). Stemmerik (1997) correlated this facies with modern, shelf edge, cool-water carbonates deposited in 140-250 m depth (James et al. 1992). This interpretation is supported by the presence of contemporaneous formations at slightly lower paleolatitude in the Norwegian-Greenland Sea Basin of East Greenland which reflect warmer water conditions (Stemmerik 1995) and at slightly higher paleolatitude in the Sverdrup Basin of Canada which reflect even cooler water conditions (Beauchamp & Desrochers 1997). The cold temperate conditions are also reflected in the diagenetic products in the Kim Fjelde Formation where LMC cements dominate (Hâkansson & Stemmerik 1995).

The general Late Paleozoic northward movement of Pangea and the cessation of warm water currents in response to mid-Permian, Proto-Atlantic rifting led to a shift to temperate cool-water carbonates in eastern North Greenland during the Kungurian (Beauchamp 1994, Stemmerik & Worsley 1995). This cooling has been linked to changes in the composition of the Permian bryozoan faunas of the higher latitudes in the northern hemisphere (Ross 1995). In eastern North Greenland, sedimentation occurred in cold temperate water (Stemmerik et al. 1996). The Kim Fjelde Formation was deposited in the Early Permian

3 METHODS

The bryozoan colony was mounted on a glass slide and thick sectioned (100 pm thick), and its exposed upper surface was polished. Micromilling was performed (sensu Wurster et al. 1999) on a robotic computer controlled three-dimensional positioning stage set under a fixed high-precision dental drill that results in 1 pm spatial sampling resolution. Enough carbonate was milled to generate samples of approximately 20 pg of powder for each carbon and oxygen isotope analysis. The carbonate samples were roasted in vacuo at 200°C to remove water and volatile organic contaminants that could interfere with carbonate analyses. Stable isotope values were obtained using a Finnigan Kiel-Ill automated carbonate preparation system directly coupled to the inlet of a Finnigan MAT 252 gas ratio mass spectrometer. Carbonate was reacted at 70°C with two drops of anhydrous phosphoric acid for 90 seconds. Isotope ratios were corrected for acid fractionation and 17O contribution and reported in per mil notation relative to the VPDB standard. Precision and calibration of data were monitored through daily analysis of NBS-18 and NBS-19 carbonate standards. 8\(^{18}\)O values of the samples are bracketed by those of the standards. Precision is better than ±0.1 for both carbon and oxygen isotope values. All isotope values in this paper are presented as 8\(^{18}\)O\(_{\text{calcite}}\), and 8\(^{13}\)C\(_{\text{calcite}}\) relative to PDB.

4 ISOTOPIC EFFECTS OF PHOTOSYNTHESIZING ENDOSYMBIONTS

Animals that do not secrete shell material in isotopic equilibrium with the surrounding water possess a vital effect (Lowenstam & Epstein 1954). The effect of photosynthesizing endosymbionts on stable isotope values of host organisms’ skeletons is complex and equivocal (Houston et al. 1999). Carbon isotope fractionation is complex as it is affected by a variety of factors (i.e. vital effects) including kinetic effects, that are controlled by growth and calcification rates, as well as metabolic effects, that are controlled by respiration and photosynthetic rates (Norris 1998). In contrast, 8\(^{18}\)O fractionation is relatively simple as it is predominantly correlated with water temperature and salinity (Norris 1998).
Conventional wisdom now is that the vital effect of symbionts is expressed as higher skeletal $^{13}$C values (e.g. Barrera et al. 1990, Stanley & Swart 1995, Norris 1996, 1998). This is in contrast to earlier studies that found the opposite (e.g. Weber & Woodhead 1970, Erez 1978, McConnaughey 1989). Conventional wisdom now also holds that the vital effect of symbionts is expressed as lower $^{18}$O values (e.g. Weber & Woodhead 1970, 1972, Buchardt & Hansen 1977, Erez 1978, McConnaughey 1989, Norris 1996, Houston et al. 1999), while other studies have found that symbionts have no effect (e.g. Barrera et al. 1990, Crowley & Taylor 2000). Similarly, the conventional wisdom is that $^{13}$C and $^{18}$O are positively correlated only in organisms lacking photosynthesizing endosymbionts (e.g. McConnaughey 1989, Stanley & Swart 1995, Spero et al. 1997), although others have suggested that symbiotic organisms can exhibit a similar relationship (e.g. McConnaughey 1989, Norris 1998, Crowley & Taylor 2000). Thus, using stable isotope values to differentiate between symbiotic and asymbiotic taxa in the fossil record is not at all straightforward. For the purposes of this study, it is assumed that the presence of photosynthesizing endosymbionts will be expressed as higher $^{13}$C and lower $^{18}$O values, with no positive correlation between the two.

5 RESULTS

Twenty carbonate samples were collected for stable isotope analysis (Table 1, Fig. 4). For the colony as a whole, the mean $^{13}$C is 3.7% (range 3.4 to 4.1%), and the mean $^{18}$O is -7.3% (range -8.2 to -5.5%). The $^{13}$C and $^{18}$O values are positively correlated (R$^2 = 0.89$, P < 0.01).

Table 1. Summary of stable isotopic values from the Permian bryozoan *Tabulipora* sp. (GI 90635-1).

<table>
<thead>
<tr>
<th>General sample location</th>
<th>Specific sample location</th>
<th>n</th>
<th>Range</th>
<th>Mean</th>
<th>Standard deviation</th>
<th>Range</th>
<th>Mean</th>
<th>Standard deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endozone</td>
<td>Diagenetic infilled cements</td>
<td>7</td>
<td>3.4 to 4.1</td>
<td>3.7</td>
<td>0.23</td>
<td>-8.1 to -5.4</td>
<td>-7.3</td>
<td>0.95</td>
</tr>
<tr>
<td></td>
<td>Zooecial skeletal walls</td>
<td>4</td>
<td>3.7 to 3.8</td>
<td>3.8</td>
<td>0.03</td>
<td>-7.2 to -6.9</td>
<td>-7.1</td>
<td>0.18</td>
</tr>
<tr>
<td>Exozone</td>
<td>Diagenetic infilled cements</td>
<td>9</td>
<td>3.4 to 4.1</td>
<td>3.7</td>
<td>0.24</td>
<td>-8.2 to -5.5</td>
<td>-7.1</td>
<td>1.22</td>
</tr>
<tr>
<td></td>
<td>Zooecial skeletal walls</td>
<td>5</td>
<td>3.4 to 3.7</td>
<td>3.6</td>
<td>0.09</td>
<td>-8.2 to -7.1</td>
<td>-7.9</td>
<td>0.44</td>
</tr>
</tbody>
</table>

n = number of samples.
whole, the zooecial skeletal walls (mean $\delta^{13}C = 3.9\%_o$ VPDB, mean $\delta^{18}O = -6.5\%_o$ VPDB) displayed significantly higher values than the diagenetic infilled cements (mean $\delta^{13}C = 3.6\%_o$ VPDB, mean $\delta^{18}O = -7.6\%_o$ VPDB) (t-Tests, $P < 0.019$). For the exozone in particular, zooecial skeletal walls also had significantly higher $\delta^{13}C$ and $\delta^{18}O$ values than diagenetic infilled cements (mean $\delta^{13}C = 3.6\%_o$ VPDB, mean $\delta^{18}O = -7.6\%_o$ VPDB) (t-Tests, $P < 0.025$). In contrast, endozonal cement and skeletal wall samples were not significantly different in either $\delta^{13}C$ or $\delta^{18}O$ mean values (t-Tests, $P > 0.05$). This probably reflects mixing of the zooecial skeletal wall carbonate and the diagenetic infilled cement carbonate in the thin-walled endozone. This could happen if the targeted cement was relatively thin and the drill penetrated the underlying zooecial wall. This mixing can be seen in Figure 4 where the arrow in the upper right corner may reflect inclusion of some skeletal carbonate in the cement.

6 DISCUSSION

In order to interpret these results, the original isotope values of the contemporaneous seawater must be known. The global mean isotope value of Early Permian (Kungurian stage) seas has been inferred from various sources such as LMC brachiopod skeletons. In the early Permian $\delta^{13}C$ values are consistently estimated at between $+4$ and $+6\%_o$ VPDB, and $\delta^{18}O$ values are estimated at between $-4$ and $-6\%_o$ VSMOW (Gruszczynski et al. 1989, Scholle 1995, Mii et al. 1997, Veizer et al. 1999). Using an intermediate value for the mean isotope values of the Early Permian seawater of $\delta^{13}C = +5\%_o$ VPDB and $\delta^{18}O = -5\%_o$ VSMOW (Gruszczynski et al. 1989, Scholle 1995, Mii et al. 1997, Veizer et al. 1999), our least diagenetically altered samples (i.e. exozone skeletal walls) display $\delta^{13}C$ values and $\delta^{18}O$ values that are 1.0% lower (i.e. 5.0—4.0% and $-5.0$ to $-6.0\%_o$, respectively). $\delta^{13}C$ and $\delta^{18}O$ values are significantly, positively correlated ($m = 0.20$, $R^2 = 0.88$, $P< 0.01$; Fig. 4).

Isotope values do not reveal an obvious signal of photosynthesizing endosymbionts. The lack of higher $\delta^{13}C$ and a positive correlation between $\delta^{13}C$ and $\delta^{18}O$ values argue for their absence. The only isotopic evidence for their presence are lower $\delta^{18}O$ values, but these could simply represent a minor diagenetic signal.

Our data agree well with those of Håkansson & Madsen (1991) giving confidence to the analyses made many years apart in different laboratories (Fig. 5). Their mean $\delta^{13}C$ value was 3.6% compared to our mean of 4.0% VPDB, and their mean $\delta^{18}O$ value was $-6.4\%_o$ VPDB compared to our mean of $-6.0\%_o$ VPDB. Our interpretations based on the newest literature reviewed in section 4 differ as Håkansson & Madsen (1991) interpreted lower $\delta^{13}C$ values as indicative of photosynthesizing endosymbionts.

Figure 5. Plot of $\delta^{13}C$ and $\delta^{18}O$ values from colony of Tabulipora sp. from this study (GI 90635-1) compared to original data from Håkansson & Madsen (1991) (GGU-220665-3, GGU-220675-53, and miscellaneous colonies).
Due to the lack of direct evidence of photosynthesizing endosymbiotic algae in the fossil record (i.e., discovery of the endosymbionts themselves), indirect evidence such as isotopes must be used. Are there other independent characters that can be used to test the algal symbiosis hypothesis? Based on Cowen (1983) and Stanley & Swart (1995), 17 characteristics of hosts with photosynthesizing endosymbiotic algae were identified (Table 1). Some were morphological, others were environmental, while others were geochemical. The Permian *Tabulipora* sp. from Greenland was examined for each of these (Table 1).

### 7 CONCLUSIONS

Weighing equally each of the 17 characteristics of indirect evidence for the presence of photosynthesizing endosymbiotic algae in the host bryozoans, the count is nine in support, six in opposition, and two unresolved (Table 2). Of the nine supporting characteristics, six are qualified with some doubt leaving three definite lines of supporting evidence. These are large size (the original impetus for the paper), thin tissue layers for light to pass through, and a high level of colonial integration. Of the six in opposition, three

<table>
<thead>
<tr>
<th>Indirect evidence of photosynthesizing endosymbiotic algae in host</th>
<th>Is this true for the bryozoan in this study?</th>
<th>Qualifications</th>
</tr>
</thead>
<tbody>
<tr>
<td>- Large size</td>
<td>Yes</td>
<td>See Figure 1.</td>
</tr>
<tr>
<td>- Rapid growth</td>
<td>?</td>
<td>No evidence.</td>
</tr>
<tr>
<td>- Restricted to simple phyla</td>
<td>No</td>
<td>But other hosts with photosynthesizing endosymbiotic algae (e.g. bivalves, nudibranchs, and ascidians and possibly even brachiopods as well) are not simple.</td>
</tr>
<tr>
<td>- Most commonly are filter feeders</td>
<td>Yes</td>
<td>But foraminiferans and nudibranchs with photosynthesizing endosymbiotic algae are exceptions.</td>
</tr>
<tr>
<td>- High surface area-to-volume ratios</td>
<td>Yes</td>
<td>But the robust branch sizes reduce the ratios compared to other less robust ramose species. But bivalves with photosynthesizing endosymbiotic algae fail this test as well.</td>
</tr>
<tr>
<td>- High skeleton-to-body ratios</td>
<td>Yes</td>
<td>But flatworms and nudibranchs with photosynthesizing endosymbiotic algae are exceptions.</td>
</tr>
<tr>
<td>- Soft tissue layers on the photic side</td>
<td>Yes</td>
<td>But the undersides of branches would have been shaded, but bivalves with photosynthesizing endosymbiotic algae partly fail this test as well. In general, the confluent outer membrane of trepostomes is thin. Specifically, <em>Tabulipora</em> ’s growing tip has been interpreted as a greenhouse (Håkansson &amp; Madsen 1991, Text-Fig. 3)</td>
</tr>
<tr>
<td>- Thin tissue layers for light to pass through</td>
<td>Yes</td>
<td>But the ramose growth habit could also be in response to growth toward plankton which is the same general direction as light.</td>
</tr>
<tr>
<td>- Grow toward light</td>
<td>Yes</td>
<td>This species has giant macular feeding structures (Key et al. 2002). The closest contemporaneous reefs are found further south in the Norwegian-Greenland Sea Basin of East Greenland (Stemmerik 1995). Stemmerik (1997) correlated this facies with modem, shelf edge, cool-water carbonates deposited in 140-250 m depth.</td>
</tr>
<tr>
<td>- High level of colonial integration</td>
<td>Yes</td>
<td>35-40°N paleolatitude.</td>
</tr>
<tr>
<td>- Most common in oligotrophic reef environments</td>
<td>No</td>
<td>No evidence.</td>
</tr>
<tr>
<td>- Restricted to shallow water in photic zone</td>
<td>No</td>
<td>35-40°N paleolatitude.</td>
</tr>
<tr>
<td>- Restricted to low turbidity water</td>
<td>?</td>
<td>But see Discussion.</td>
</tr>
<tr>
<td>- Restricted to tropics with minimal fluctuations in seasonal light intensity</td>
<td>No</td>
<td>But see Discussion.</td>
</tr>
<tr>
<td>- Higher $\delta^{13}C$</td>
<td>No</td>
<td>But see Discussion as this could be due to diagenesis.</td>
</tr>
<tr>
<td>- Lower $\delta^{18}O$</td>
<td>Yes</td>
<td>But see Discussion.</td>
</tr>
<tr>
<td>- Lack of positive correlation between $5^{13}C$ and $8^{18}O$ values</td>
<td>No</td>
<td>But see Discussion.</td>
</tr>
</tbody>
</table>

Table 2. List of 17 characteristics that can be used to infer the presence of photosynthesizing endosymbiotic algae in fossil hosts and how each was scored for the bryozoans in this study. Modified from Cowen (1983) and Stanley & Swart (1995).
are qualified with some doubt leaving three definite pieces of contradictory evidence. These are most common in oligotrophic reef environments, restricted to shallow water in photic zone, and restricted to tropics with minimal fluctuations in seasonal light intensity. The morphological evidence was largely in favor of endosymbiosis (8 in support, 1 in opposition, and 1 equivocal). The paleoenvironmental evidence was largely against endosymbiosis (0 in support, 3 in opposition, and 1 equivocal). The isotopic evidence was also largely against endosymbiosis (1 in support, 2 in opposition, and 0 equivocal). Thus the evidence for the presence of photosynthesizing endosymbiotic algae in these bryozoans is at best equivocal.

In the absence of direct evidence for endosymbionts, Cowen (1983) reasoned for the most conservative approach to testing this hypothesis in fossils by arguing that any single piece of negative evidence requires the rejection of the algal symbiosis hypothesis. Based on the presence of three qualified negative pieces of evidence and three unqualified negative pieces of evidence, the algal symbiosis hypothesis for gigantism in these bryozoans is rejected.

The gigantism in Tabulipora sp. may have simply been a function of exposure to ideal growing conditions. Gigantism has been long known from other Permian faunas (e.g. Hayasaka & Hayasaka 1953), so perhaps it was simply an environmental effect. This is supported by the fact that these bryozoans are not the only large elements of their fauna, as there are also large productid and spiriferid brachiopods (Håkansson & Stemmerik 1995) and giant colonies of the bryozoan Amphiporella sp. (Madsen 1994, Stemmerik 1997).

This lack of an endosymbiotic vital effect is good news for those using bryozoan skeletons for stable isotope-based temperature calculations. It is generally assumed that bryozoan skeletons are secreted in isotopic equilibrium with their surrounding water. The data on which this is based is limited but growing and indicates the majority of bryozoans secrete their skeletons in isotopic equilibrium (Forester et al. 1973, Pätzold et al. 1987, Wefer & Berger 1991, Rao & Nelson 1992, Rao 1993, Bone & James 1997, Rahimpour-Bonab et al. 1997, Crowley & Taylor 2000, Machiyama et al. 2002, Smith & Key 2004, Smith et al. in press). The most notable exceptions are documented in Crowley & Taylor (2000) and Smith et al. (in press).

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ABSTRACT: The aim of the study was to investigate the adaptations of bryozoans to life in dynamic environment of inner parts of Arctic fjords. The study was carried in four West Spitsbergen fjords: Homsund, Van Mijen, Isfjorden and Kongsfjorden. The majority of the coastline in the inner parts of the West Spitsbergen fjords is occupied by tidal glaciers or influenced by glacier-fed river outflows. The considered areas are characterized by high rate of sedimentation (up to 600g/m²/24h), high concentrations of total suspended matter (up to 800g/dm³=) in water, fine unstable bottom sediments, fresh water discharge from glaciers and rivers, cold stagnant waters at the bottom. SCUBA diving, grab sampling and dredging were used to obtain the samples. Four main types of adaptation to the dynamic fjord environment were observed: free-living, colonization of dropstones, colonization of algae, and anchoring to the fine sediment by rootlike structure. Free living bryozoans are only represented by one species - *Alcyonidium disciforme* Smitt, 1871. This species by its shape (disc-like) and encapsulation of sand particles within the zooarium (acting as ballast) is very much adapted to life on unstable fine sediments and high rate of sedimentation. ‘Faunistic islands’ created by dropstones act as oasis for the rocky fauna in an otherwise soft sediment unfriendly for suspension feeders. *Eucratea loricata* (Linnaeus, 1758) and *Dendrobeania murrayana* (Johnston, 1847) are dominant here. Very often algae, which grow on the dropstones, are the substrate for bryozoans. During this study three species of algae were investigated: *Desmarestia aculeata* (L.) Lamouroux, 1813, *Laminaria saccharina* (L.) Lamouroux, 1813 and *Ptilota plumosa* (L.) Agardh, 1817. *Harmeria scutulata* (Busk, 1855) and *Celleporella hyalina* (Linnaeus, 1767) are the most numerous species present on that kind of substrate. Root-creating bryozoans were recorded very rarely. *Kinetoskias arborescens* Danielssen, 1868 was the only species observed.

1 INTRODUCTION

Many studies have indicated the importance of substrate for bryozoan distribution (Hayward, 1978, Hayward & Ryland, 1978, Cook, 1981) Bryozoan occurrence is restricted in most cases to firm substrate. When we start to think about the substrate colonized by Bryozoa, boulders and algae probably first come into our mind. And in majority we are right. But there are exceptions. Lunulitiforms are the perfect example of such exceptionality (e.g. Cadée et al., 1989, Cook & Chimonides, 1994). Through their morphology and life history they adapted to live on soft sediment. Lunulitiforms are free-living bryozoans, which at the beginning of their growth need small sand particles to develop the colony. Reaching a certain stage of development they continue to live free in sediment interstices or on the surface of the sea floor (Cook & Chimonides, 1994). A striking example from the Arctic is the soft bottom ctenostomate bryozoan *Alcyonidium disciforme* Smitt, 1871, its distribution being driven by the occurrence of substrate dominated by clay and mud (Kuklinski & Porter 2004). Both taxa have around shape. In general, the bryozoan’ morphotype is strongly related to nature of the habitat it occupies (Cook, 1981). Not much attention has been paid to bryozoan ecology in soft-bottom environment, except for the Lunulitiforms (some exceptional examples Cook, 1979, 1981, Cadée, 1987).

Most previous benthic studies of the Arctic proximal to tidal glaciers lack bryozoan records (e.g. Wlodarska-Kowalczyk et al., 1998, Sejr et al., 2000). Probably the sampling efforts were too low to record these patchily distributed organisms. Even if some fjordic research mentions the presence of bryozoans on soft grounds, the data are limited to phylum occurrence or density (Dale et al., 1989). The present investigation deals with Arctic fjord glacial bays bryozoans. Fjords are transition between the land and open oceans, regions of strong physical and chemical gradients where fresh and salt waters mix and react (Suvitski et al., 1987). Therefore, they are very dynamic systems. The sea
floor is covered by fine sediments and only ice-rafted cobbles can act as faunal islands where species requiring hard substrates can colonize (Dale et al., 1989, Syvitski et al., 1989). This study took six years of observation of bryozoan adaptation to life in highly disturbed Svalbard inner fjordic area.

2 MATERIAL AND METHODS

2.1 Study area

Inner fjordic area are defined in this study as basins in the vicinity of glaciers which range in size from 0.5 to 10 km in width and from 1 to 10 km in length, with depth range from 5 to 240 m depth. This study covers four such areas including Kongsfjorden, Isfjorden, Van Mijen Fjord and Homsund (Fig. 1).

The hydrology of the Spitsbergen glacial bays is very complex (Fig. 2). In Kongsfjorden, water masses are distinguished. The include from top to bottom Surface Waters originating from glacier melt-water outflows, Transformed Atlantic Waters originating on the Spitsbergen shelf. Local Fjordic Waters and Winter Bottom Waters formed by a process of deep convection in winter (Svendsen et al. 2002). The bottom water layers of the fjords are influenced by Local Fjordic Waters of salinity >34.4 and temperature <1°C, the remains of the autumn-winter convection and the cooling of fjordic waters in contact with glaciers. In the deepest depressions of the inner basin Winter Waters of temperature < -0.5°C and salinity >34.4 might be present. Transformed Atlantic waters of salinity >34.7 and temperature >1°C is rather characteristic for the central basin and may occur down to the bottom.

Suspension concentrations, close to glaciers can reach 200-800 mg/dm³, decreasing in the central and outer parts of the fjord in summer. In the inner basin concentrations in intermediate water layer may reach...
20-25 mg/dm$^3$ and 2-3 mg/dm$^3$ in the central parts, while relatively clear water in the outer parts of the fjord contains 0.5 mg/dm$^3$ (Elverhoi et al., 1983, Zajaczkowski, 2000). For the schematic sketch of sedimentation processes, dropstone release see Figure 3.

Icebergs and growlers are observed all over the fjord the whole year round. Their influence on the bottom was recorded to be down to 40 m depth. They are the source of the dropstones which are very often the only hard substrata present in the glacial bays (Dowdeswell & Forsberg, 1992).

Muds dominate the subtidal sediments of all glacial bays (e.g. Wlodarska-Kowalczuk et al., 1998, Zaborska, 2001, Wlodarska-Kowalczyk & Pearson, 2004). Here, intensive sedimentation of mineral material results in the formation of unconsolidated, labile sediments (Syvitski et al., 1987). Deposited material is not compacted, water trapped between flocks cannot escape and a layer of very condensed suspension overlying the bottom is formed (Dyer, 1989). Bottom sediment has low organic material content which is the result of dilution due to high sediment accumulation rates. The glacial bays are characterized by fast-ice formation during winter, which lasts longer in comparison to the other parts of the fjord. Long periods of fast ice result in suppression of primary production and flux of organic matter to the bottom (Görlich et al., 1987). Fresh water discharge from the melting glaciers during the summer causes strong water mass stratification with a maximum gradient at 5-20 m depth. This effect restricts to some extend the vertical exchange of energy and matter between the water masses layers (Görlich et al. 1987).

The faunal composition of glacial bays is dominated by small, detritus feeders, thyasirid and nuculanid bivalves and cirratulid and sabellid polychaetes (Wlodarska-Kowalczuk et al., 1998, Wlodarska-Kowalczyk & Pearson 2004).

Processes and patterns described above take place in most of the sites covered by this study. Van Mijen Fjord differs in hydrological regimes due to its limited contact with the sea (there is a large island at the mouth of the fjord). In this particular fjord, the presence of icebergs is reduced due to the lower number of tidal glaciers. The inner part of this fjord is feed by a land-ended glacier.

2.2 Methods

The material was collected in four fjords (Kongsfjorden, Isfjorden, Van Mijen Fjord and Homsund - see Fig. 1) during r/v Oceania and r/v Jan Mayen cruises in the years 1997 and 2002, and during land-based expedition in 2001. There were three techniques used to collect the samples: Van Veen grab, dredge and SCUBA diving. Of the 78 sites investigated 5 were sampled by

![Figure 3. Schematic sketch of suspension distribution mechanisms and rates of sedimentation of inorganic material in Kongsfjorden (data obtained from Zajaczkowski, 2000).](image-url)
Within collected samples bryozoans were present on dropstones colonized by bryozoans that individual cobbles. The sediment around dropstones was analyzed. Samples were taken by divers at Kongsfjorden using small cores at three shallow stations - 10m depth (no 1: 78°58.9’N and 12°13.3’E, no 2: 78°53.5’N and 12°15.0’E, no 3: 78°56.5’N and 12°25.9’E). These stations were selected on the basis of bryozoans presence. Sediment fractions were categorized as clay (<4 μm), silt (4—63 μm), sand (63—2000 μm), pebbles (2—64 mm) and cobbles (64—256 mm). Grain size measurements were made using a combination of the hydro meter method and sieving. Subsequently, all sediments were suspended in a solution of hexametaphosphate (5 g/1), which has the effect of reducing the links between clay particles due to flocculation. The density variation of the solution was measured at different time intervals and, finally, Stokes’ law was used to compute the mean diameter of the sediment particles from their settling speed and the changing density of the solution with time. This method is described in detail by e.g. Kaddah (1974) and Gee & Bauder (1979).

3 RESULTS

Within collected samples bryozoans were present on dropstones, sand, algae and as free living forms. The free living mode of life is represented only by one species: Alcyonidium disciforme Smitt, 1871. The general distribution of the species obtained during course of this study together with historical data are presented on the Figure 1. Among 78 sampled sites A. disciforme was present at 28 stations. The species occurred in all four investigated fjords. Depth distribution ranged 8 to 240 m. It was restricted to the areas, which were under direct influence of tidal glacier.

Colonization of dropstones creating ‘faunistic islands’ were represented by Dendrobeania murrayana (Johnson, 1847) and Eucratea loricata (Linnaeus, 1758). The species are characterized by their erect flexible colony growth forms. They were found only in Kongsfjorden (D. murrayana: 78°58.9’N and 12°13.3’E - depth 13 m; E. loricata: 78°53.5’N and 12°15.0’E - depth 10m). The sediment around dropstones colonized by D. murrayana is mostly clay (clay 54%, silt 27%, sand 10%, gravel 9%), while the sediment around boulders with E. loricata was dominated by silt (clay 29%, silt 66%, sand 5%, gravel 0%).

Eight algae individuals growing on the dropstones were collected and the associated fauna analyzed. Three species of algae hosting bryozoans were found: Desmarestia aculeata (L.) Lamouroux, 1813 (Phaeophyta), Laminaria saccharina (L.) Lamouroux, 1813 (Phaeophyta) and Pilota plumosa (L.) Agardh, 1817 (Rhodophyta). Of the 20 taxa inhabiting the algae 1 was determined to phylum level, 2 to family, 4 to genus and 13 to species level. The most specious assemblage was present on D. aculeata with 16 taxa present; only one species (Harmeria scutulata Busk, (1855)) was present on P. plumosa. The dominating species on the algae were Celleporella hyalina (Linneaus, 1767), Alcyoni­dium gelatinosum (Linneaus, 1767) and Harmeria scutulata (Busk, 1855) (Table 1). All the material was collected in Kongsfjorden. Of the 47 stations investigated in Kongsfjorden only at 2 of them algae were found. Depth range of the samples was from 6 to 10 m. The surroundings of the dropstone on which the algae with bryozoans occur was dominated by clay at the station no. 1 (clay 54%, silt 27%, sand 10%, gravel 9%) and by silt at the station no. 2 (clay 29%, silt 66%, sand 5%, gravel 0%) - see the method chapter for the station coordinates.

Kinetoskias arborescens Danielssen, 1868 was only one species found with root- like structures which enable the bryozoan to attach to the small stones. The species was recorded only at Van Mijen Fjord (Fig. 4). Of the 11 stations investigated the species was present in only two stations (in one grab at station 1 and in two grabs at station 2 - see Fig. 4). The size of the colony was not exceeding 2 cm in length, what can be considered as a juvenile stage (P.J. Hayward - pers.comm.).

4 DISCUSSION

Bryozoan distribution and diversity is strongly related to the type of sea bottom (Cook, 1981). The more diverse is the substrate studied the more diverse is the bryozoan fauna occurring in it (Kuklinski & Barnes in press). The studied area is characterized by a rather homogenous soft sediment (Zaborska, 2001, Wlodarska-Kowalczyk & Pearson, 2004). Substrate type is related to water depth and distance from the sediment source. It is one of the major controls on faunal communities both in Canadian Arctic and Svalbard fjords (Dale et al., 1989, Wlodarska-Kowalczyk & Pearson, 2004). Dale et al. (1989) report from Canadian Arctic fjords that individual cobbles...
Table 1. Abundance of the bryozoans colonies number on the different algae species - mean ± SD/400ml of algae - in brackets: range of abundance (N indicates the number of given algae individuals collected).

<table>
<thead>
<tr>
<th></th>
<th>Laminaria saccharina</th>
<th>Ptilota plumosa</th>
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<tr>
<td></td>
<td>Desmarestia aculeata</td>
<td></td>
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<td>N</td>
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<td>4</td>
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<td>3</td>
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<tr>
<td>Alcyonidium gelatinosum (Linnaeus, 1767)</td>
<td>124.2 ± 107.24</td>
<td>0.4 ± 0.79</td>
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<tr>
<td>(0-257)</td>
<td></td>
<td>(0-1)</td>
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<tr>
<td>Alcyonidium mamillatum Alder, 1857</td>
<td>—</td>
<td>10.4 ± 2.94</td>
</tr>
<tr>
<td>Desmarestia aculeata</td>
<td></td>
<td>(4-12)</td>
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<td>(0-327)</td>
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</tr>
<tr>
<td>Alcyonidium mýlili Dalyell, 1847</td>
<td>—</td>
<td>4.9 ± 6.22</td>
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<td>(0-12)</td>
<td></td>
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<tr>
<td>Celleporella hyalina (Linnaeus, 1767)</td>
<td>122.5 ± 142.11</td>
<td>19.0 ± 13.09</td>
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<td>(0-284)</td>
<td>45.8 ± 5.89</td>
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<td>(4-29)</td>
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<td>Harmeria scutulata (Busk, 1855)</td>
<td>92.0 ± 157.85</td>
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<tr>
<td>(0-327)</td>
<td>352.0 ± 332.92</td>
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<td>(116-587)</td>
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<tr>
<td>Lichenopora sp.</td>
<td>36.1 ± 64.42</td>
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<td>(0-132)</td>
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<tr>
<td>Bowerbankia sp.</td>
<td>1.5 ± 3.08</td>
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<td>(0-6)</td>
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<tr>
<td>Alcyonidium loricata (Linnaeus, 1758)</td>
<td>1.5 ± 3.08</td>
<td>0.1 ± 0.26</td>
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<td>Scrupocellariidae indet.</td>
<td>1.5 ± 3.08</td>
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<tr>
<td>Tricellaria ternata (Ellis &amp; Solander, 1786)</td>
<td>1.5 ± 3.08</td>
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<td>(0-6)</td>
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<tr>
<td>Callopora ineate (Linnaeus, 1767)</td>
<td>0.5 ± 1.02</td>
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<td>(0-6)</td>
<td>4.1 ± 5.89</td>
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<tr>
<td>Callopora sp.</td>
<td>3.8 ± 6.48</td>
<td>0.7 ± 1.21</td>
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<td>(0-13)</td>
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<tr>
<td>Cribrilina annulata (Fabricius, 1780)</td>
<td>0.5 ± 1.02</td>
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<tr>
<td>(0-6)</td>
<td>33.3 ± 11.78</td>
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<td>(25-42)</td>
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<tr>
<td>Tegella arctica (d'Orbigny, 1850)</td>
<td>0.5 ± 1.02</td>
<td>4.1 ± 5.89</td>
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<tr>
<td>Tegella armifera (Hincks, 1880)</td>
<td>—</td>
<td>2.4 ± 4.25</td>
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<tr>
<td>Scrupocellaria arctica (Busk, 1855)</td>
<td>6.7 ± 13.51</td>
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<tr>
<td>Dendrobeania sp.</td>
<td>2.0 ± 4.05</td>
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<td>(0-6)</td>
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<tr>
<td>Tubuliporidae indet.</td>
<td>1.3 ± 2.70</td>
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<td>(0-5)</td>
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<tr>
<td>Tegella armifera (Hincks, 1880)</td>
<td>0.7 ± 1.35</td>
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<tr>
<td>Bryozoa indet.</td>
<td>—</td>
<td>4.1 ± 5.89</td>
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</table>

form the ‘faunal islands’ when isolated in softground environment. They also state a correlation between the number of ice-rafted debris and density of the organisms inhabiting the faunal islands. The bryozoan fauna in glacial bays is noticeably reduced compared to other parts of the fjord. Kuklinski (2002) found 143 taxa of bryozoan all over Kongsfjorden, being almost six times more than in all investigated inner areas of the fjords. Bryozoans in glacial bays are very patchily distributed and the frequency of their occurrence is very low. For the soft bottom macrofauna a decrease in species richness towards the inner parts of Arctic glacier-influenced fjords has also been reported (Wlodarska-Kowalczyk & Pearson, 2004).

The reason for the low diversity of the bryozoan fauna in glacial bays might be the distance that the larvae of non-indigenous species must travel to get to inner parts of the fjords. Most of the Arctic bryozoan species produce lecithotrophic larvae (Kluge, 1975).
being able to stay in the water column for hours rather than days (Ryland, 1974). Thus, the observed low biodiversity to some extend might be the result of viability of the larvae.

Seasonally heavy sedimentation in glacial bays occurs in summer and, thus, might coincide with the period of reproduction of the bryozoans. As a result, the sea bottom covered by fine sediment tends to be unpopulated. Because of the largely inhospitable silt covered sea bottom surfaces no larvae will settle in the inner part of the fjord.

As shown by Kvitek (1989) and Kuklinski & Porter (2004) _Alcyonidium disciforme_ is perfectly adapted to the conditions present in the inner part of Arctic fjords, characterized by a soft bottom and the presence of a seasonally high rate of sedimentation (Svendsen et al., 2002). Its adaptation is evident in the shape of the colony, since its flat ring shape of colony with hole inside is hydrodynamically prepared to lie on the top of unstable soft substrate (Kvitek, 1989). The species has capacity to sequester sand particles from its immediate environment. This phenomenon is suspected to act as ballast for the colony allowing it to move to places with more favourable conditions (Kuklinski & Porter, 2004).

The presence of erect flexible species, such as _Dendroebania murrayana_ and _Eucratea loricata_ is determined by the occurrence of firm substrate such as dropstones. There are two features, which help the species to survive times of very intensive sediment load lasting for at least 3 summer months annually (Svendsen et al. 2002). Firstly species occur in rather shallow water (10-13 m depth) still under the influence of tidal currents. In the Svalbard area the tidal amplitude reaches more than 1 m (Svendsen et al., 2002). Thus, colonies temporally covered with sediment through their flexibility and bending within the tidal currents most likely can clean their colonies. Secondly this species possessed large and numerous avicularias which might be able to sweep the sediment out of the colony (Kluge, 1975). This feature may play a crucial role for survival in habitats with high sedimentation rates.

_Harmeria scutulata_ is a dominating species on shallow boulder communities (Barnes & Kuklinski, 2003). Its occurrence in other areas on the algal substrate is not as numerous as in inner fjordic areas. It is suspected that the species possesses a planktotrophic larvae (high abundance of colonies and lack of ovicell would suggested it) which in many cases are able to remain in the water column for weeks. This could be of great importance for dispersal since it would allow larvae to be transported over longer distances. The larvae taken by the current from the areas with greater density of maternal colonies to the inner part of the fjord may colonize any firm substrate available - in this case algae. Using algae as a substrate in area experiencing seasonally high rate of inorganic sedimentation might be beneficial for a sheet like colony. It might happen that the species during the time of highest concentrations of suspended matter in summer stop feeding by the use of the tentacles and instead start to use the exudates of algae. Why does _Harmeria_
**Kinetoskias arborescens** was found only at two stations in Van Mijen Fjord among 78 stations investigated. There is only one former record of the species from Svalbard waters done by Nordgaard (1918). He found the specimen in Bellsund (area at the entrance of the Van Mijen Fjord) at 30-40 m depth. No habitat description was included so any comparison is impossible to conduct. Van Mijen Fjord differs in many ways from the three other fjords studied. It is isolated by an island at the entrance and has contact with the open sea just by two narrow passages (Fig. 4). This influences the hydrology of the fjord, which is driven more by local environmental forces (e.g. glaciers, fresh water discharge).

Occurrence of *Kinetoskias arborescens* only at two stations with low densities in a juvenile state seems accidental and suggest that this habitat is not the most favourable for the species. Yet adaptation of the species of the genus *Kinetoskias* to fjordic environments and in general to soft bottoms was recorded as early as 1893 by Norman. The species of this genus develop root-fibers by which they anchor themselves in the mud (Norman, 1893). Norman (1893) stated T do not remember any other Polyzoa which have rootlets of this character, though different species have very varied modes of attachment’. Norman’s statement together with low abundance in Svalbard fjords suggest that the species of this genus are very habitat selective.

Rooted cheilostome Bryozoa do successfully inhabit soft sea bottoms from the tropics to the polar regions (Klug 1975, Cook 1981, Cook & Chimonides 1981, Cadée 1987). In Svalbard area rooted cheilostomes are very rare. Recent research of soft bottom fauna is rather extensive (e.g. Gulliksen et al., 1985, Holte et al., 1996, Wlodarska et al., 1996, Wlodarska-Kowalczuk et al., 1998, Kendall et al. 2003, Wlodarska-Kowalczuk & Pearson 2004), thus, the sampling effort can not be blamed for low record numbers.

The present study shows that the harsh environment of inner Arctic fjord basins influences the composition of bryozoan faunas, and only some morphotypes can survive there. The flat, ring-shaped *Alcyonidium disciforme* is able to survive free living on the sediment, while encrusting or erect flexible colonies need a firm substrate to survive. These observation correlates with the one done by Cook (1981) for deep sea sediments. Erect colonies by their flexibility and life in any sort of current are cleaned from sediment. Encrusters by living on flexible algae use the same mechanism.

Inner fjordic environments have many features in common with deep sea bottom and shallower sandy areas (Cook, 1981): small grain-size of the sediment, instability, lack of firm substrata and high inorganic sedimentation and resuspension. In all mentioned habitats similar adaptations of bryozoan were observed: free-living forms, usage of any firm substrate available (shells, stones, algae), root-like structure for anchoring to the substrate, etc.

The present study indicates the importance of substrate for bryozoan colonization, particularly in areas close to the glacial environment. It suggests that dispersal over the sea floor of the bryozoan larvae is substrate selective.

### ACKNOWLEDGEMENTS

I thank very much Dr Maria Wlodarska-Kowalczuk for valuable comments on the manuscript. I am very grateful to Agata Zaborska for granulometry analyses. Land base expedition to Ny Alesund - LSF in 2001 was supported by a grant (NP-51/2001) from the European Commission. The study has been completed thanks to the funds provided by grant from the European Commission’s programme ‘Transnational Access to Major Research Infrastructures’ to the Trondheim Marine Systems Research Infrastructure and grant 3 P04F 081 24 from Polish State Committee for Scientific Research.

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Bryodiversity on coastal boulders at Spitsbergen

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ABSTRACT: Boulder scree is the most common form of subtidal hard substratum in West Spitsbergen fjords and elsewhere in the high arctic. The communities on such shallow substrata seem likely to give the earliest signals of organism response to change in the high arctic marine environment, yet virtually nothing is known about them. We examined boulders at three stations at each of two fjords, Kongsfjorden (79°N, 12°E) and Homsund (77°N, 16°E). Homsund is influenced by Arctic water masses whilst Kongsfjorden is more influenced by Atlantic warmer waters. We examined 2752 boulders (total surface area: 254,681 cm\(^2\)) across the intertidal, 6 m and 12 m. Species richness was patchy, but locally high, though dominance by a single species resulted in low diversity levels (Shannon Weiner \(H < 2.8\)). 73 taxa of Bryozoa were determined; 5 to higher taxa, 16 to genus and 52 to species level. Cluster and multidimensional scaling analyses showed intertidal samples to differ substantially from those in the subtidal. Thirteen taxa (8 species) occurred in the intertidal zone compared to 73 taxa (52 species) in the subtidal. All the intertidal taxa were also present in the subtidal samples. All communities were dominated by *Harmeria scutulata* Busk (57% of colonies in the intertidal and 54% in the subtidal). The next most abundant species, *Cauloramphus intermedius* Kluge and *Cribrilina annulata* Fabricius represented just 5% of colonies. Despite the distance between Kongsfjorden and Homsund (over 200 km) and differences in hydrological features between the fjords, no difference between their boulder communities were found.

1 INTRODUCTION

Boulder shores are common to coastlines across the globe at any latitude or longitude, and as such they potentially provide an important source of multiple scale comparison. At high latitudes, north and south, they are dominated by two remarkably similar sorts of organisms either side of the high water mark: encrusting bryozoans under water and encrusting bryophytes above it. Being easier to reach mosses received earlier attention and have remained important in Arctic and Antarctic terrestrial study. Their marine counterparts on shallow hard substrata at the high Arctic latitude of Spitsbergen started over a century ago and was conducted mostly by Nordic scientists. Among the first faunistic records published were works by Smitt (1868), Bidenkap (1897, 1900) and Nordgaard (1900, 1918). Necessarily, pioneer studies were mainly taxonomic investigations. Even though west Spitsbergen is probably the best investigated of high Arctic sites, even in shallow water new species are still being added (Kuklinski & Hayward 2004). In the last five decades there has been little follow up of the early studies. Though some studies mention bryozoans, few papers have focussed on bryozoans *per se* (see Rozycki & Gruszczynski 1986, Gulliksen et al. 1999, Pipenburg et al. 1996, Lippert et al. 2001). Ecological data from the Spitsbergen area and from the Arctic in general are very scarce. In our study we concentrate on coastal West Spitsbergen as a part of broad investigation of the ecology of high Arctic bryozoans (Kuklinski 2002a, b).

Studies of boulder epifaunal communities have shown a broad range of factors to influence species diversity, composition and community structure. Seasonal and annual changes in the physical environment were shown to cause changes in species composition (Sebens 1986). Osman (1977) has shown that physical disturbance of the rock has an influence on species diversity and composition. Intermediate levels of disturbance enhance diversity on rocks primary by allowing a certain level of colonization but limiting the spatial extent of the dominant space competitor (Wilson 1987). Large boulders thus have more organisms through the level of stability as well as species-area relationships (Osman 1977, Barnes et al. 1996, Barnes & Kuklinski 2003). Among biotic factors predation and competition for space seem to be
important forces in structuring the assemblages (Dayton 1971, Jackson 1977, Witman 1985). Even on high Arctic boulders in which only a small proportion of space is occupied, interactions between organisms are still common and important (Barnes & Kuklinski 2003). In the current study we investigate patterns of distribution and diversity in boulder communities in the intertidal and shallow subtidal in two Arctic fjords. Our sites were chosen to cover scales from metres to hundreds of kilometres, different hydrological regimes and depths from the intertidal to 12 m.

2 MATERIAL AND METHODS

2.1 Study area and sampling protocol

The study region was the west of Spitsbergen (in the Svalbard Archipelago) (Fig. 1). Within this, two study localities situated approximately 250 km apart were selected; Kongsfjorden (79°N) and Homsund (77°N). Three sites, 3 km apart, were then selected in each fjord. We denoted these as K1 (79°01'.8"N, 11°49.8'E), K2 (78°59.5"N, 11°58.9'E) and K3 (78°58.5"N, 11°29.8'E) at Kongsfjorden and H1 (77°00.8"N, 15°33.3'E), H2 (76°56.8"N, 15°48.4'E) and H3 (76°57.4"N, 15°55.6'E) at Homsund (Fig. 1). At each of these sites boulders were collected at three levels: the intertidal, at 6 m depth and at 12 m depth. In all cases samples were collected from two spots approximately 10 m apart i.e K2-a-IT, K2-b-IT, K2-a-6, K2-b-6, K2-a-12, K2-b-12. Boulders collected ranged in surface area from 1-1850 cm².

Samples were collected during July 2002 emise of t/y Oceania using SCUBA. The coastal shallow benthic environment in the area is subjected to ice scour from floating ice during summer months. Inner fjords areas are characteristically covered by winter fast ice, which occurs less often and extensively in the central and outer parts of the fjord (Weslawski et al. 1988, Svendsen et al. 2002). Like temperature, the salinity of near bottom waters is stable, varying from just 33 to 34. Surface layer salinity does change rapidly around June (32-25 see Swerpel 1985, Weslawski et al. 1988, Svendsen et al. 2002). Both fjords are influenced by two water masses: the warmer West Spitsbergen Current and colder Sørkap Current originating from Arctic Ocean (Swerpel 1985, Loeng 1991, Svendsen et al. 2002). Kongsfjorden is more influenced by the warmer Atlantic water bodies and Homsund by the colder Arctic water masses (Swerpel 1985, Svendsen et al. 2002).

2.2 Data analyses

Most taxa were identified to species level using a stereomicroscope. The surface area of stones was estimated using an inelastic net marked with a cm² grid (see Barnes et al. 1996 for a discussion of this methodology).

Several diversity measures were calculated: number of taxa, Margalef species richness index, Pielou evenness index and Shannon-Wiener H index (log base e). Number of individuals per sample was counted. All the calculations were done with use of data standardized to 4000 cm² of the rocks surface at each site.

One-way analyses of similarities (ANOSIM; Clarke & Green 1988) and multiple pairwise comparisons were used to test a priori differences in communities between the sites. ANOSIM uses the test statistic R, which is calculated using average rank similarities among pairs of replicates within each of 2 groups, minus the average rank similarity of replicates between groups, and is scaled to give a value between -1 and 1 (Clarke 1993). Thus, R = 1 when all similarities within groups are less than any similarity between groups, R > 0.75 when there is big difference with the groups either well separated, R > 0.5 when overlapping but clearly different, R < 0.25 when groups are barely distinguishable at all, and R = 0 when replicates within and between groups are equally similar. If R = — 1, then pairs consisting of 1 replicate from each group is more similar to each other than are pairs of replicates from the same group (Clarke 1993).
Table 1. Taxa recorded during the course of the investigation (*new records to Svalbard area, in the first row: stations abbreviation with their depth [IT - intertidal] according to Fig. 1)

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### Cribrilinidae

*Cribrilina annulata*  
(Fabricius, 1780)

### Hippothoidae

*Hippolhoa arctica* Kluge, 1906  
*Celleporella hyalina*  
(Linnaeus, 1767)  
*Harmeria scutulata*  
(Busk, 1855)

### Escharellidae

*Escharella klugei* (Hayward, 1979)  
*Escharella ventricosa*  
(Hassall, 1842)  
*Escharella sp.*

### Smittinidae indet.

*Smittina betla* (Dawson, 1859)  
*Smittina minuscula*  
(Smitt, 1868)  
*Smittina majuscula*  
(Smitt, 1868)  
*PoreUa minuta* (Norman, 1869)

### Umbonulidae

*Umbonula arctica* (Sars, 1851)

### Bitectiporidae

*Pentapora boreale*  
(Kuklinski & Hayward, 2004)

### Schizoporellidae

*Schizoporella lineata*  
(Nordgaard, 1896)  
*Schizoporella Crustacea*  
(Smitt, 1868)  
*Schizoporella pachystega*  
(Kluge, 1929)  
*Schizoporella porifera*  
(Smitt, 1868)  
*Schizoporella sp.*  
*Hippodiplosia obesa*  
(Waters, 1900)

*Hippodiplosia murdochi*  
(Kluge, 1962)

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<tr>
<td>Cheilopora sp.</td>
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<tr>
<td>Bryozoa indet.</td>
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</table>
The multivariate analysis was applied to species square root transformed data using the PRIMER package. The Bray-Curtis similarities were calculated. Ordination (non-metric multidimensional scaling (MDS)) and classification (using group average linking) of samples were performed. Groups of samples were distinguished based on the resultant cluster and MDS plot.

3 RESULTS

On the 2752 boulders (total surface area = 254,681 cm²) collected, encrusting fauna was rare on the 912 boulders collected from the intertidal, but abundant on the 861 boulders from 6 m, and on the 979 boulders from 12 m. Bryozoans, which comprise 73 taxa, largely cheilostomes, dominated (>90%) the fauna in terms of the number of taxa present (Table 1). There were 3 species which were recorded for the first time in Svalbard: Calliopora whiteavesi Norman, 1903, Rhaphomostomella bilaminata var. sibirica Kluge, 1929, Cheilopora praelucida Hincks, 1888. The intertidal samples were depauperate, though we found 13 taxa (8 species). 73 taxa (52 species) were present in the subtidal samples, which included all the intertidal taxa. There were 43 taxa (31 species) present in both fjords - 13 taxa were present only in Hornsund and 17 taxa were present only in Kongsfjorden (see Table 1). Maximum intertidal bryo-

zoan richness was 6 taxa at any one site (at H1) and minimum was 0 (at H2-b and H3-b). Total subtidal richness differed little between Kongsfjorden (60 taxa - highest site value 36 taxa) and Hornsund fjord (56 taxa - highest site value 40 taxa). The highest rich-

ness was in the subtidal at the site H3 (6 m) where 40 taxa were found and the lowest (in the subtidal) was at site H2 (12 m) in which there were 16 taxa. There were no significant differences in sample richness levels between the two fjords. There was no signifi-
cant correlation between the taxa number and depth (r = -0.0849, p = 0.693).

As with similarities in richness, the highest values of Shannon-Wiener H index were ~2.7 in both fjords. We summarise variability in richness, diversity and evenness in Table 2. No significant correlation between depth and value of Shannon-Wiener index was found (r = 0.1418, p = 0.509). There was signifi-
cant negative correlation between densities of indi-
viduals and depth (r = -0.4083, p = 0.048). There was no significant negative correlation between densities of individuals and depth (r = -0.0849, p = 0.693). There were more individuals at 6 m depth than at 12 m. Communities were strongly dominated by the abundance of just one species (Fig. 2). Harmeria scutalata Busk 1855 (Fig. 3) a pioneer species comprised 57% of colonies in the intertidal and 54% in the subtidal. Colonies of this species dominated the pioneer communities on the boulder surfaces. We judged these colonies to be nearly all less than a year old; they rarely exceeded 1 cm² in area. The next most abundant species.

Table 2. Biodiversity measures for all the sampling sites including: S - species number, N - number of individuals, d - species richness (Margalef index), J' - Pielou's evenness index, H' - diversity Shannon-Wiener index, 1-X' - Simpson index; (sites symbols according to Fig. 1; abbreviations: IT - intertidal; 1-12 - depth in metres; a, b - subsample within the site; all the calculation are done on 4000 cm² of surface of the boulders).

<table>
<thead>
<tr>
<th>S</th>
<th>N</th>
<th>d</th>
<th>J'</th>
<th>H'</th>
<th>1-X'</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kl-a-IT 4</td>
<td>2.9</td>
<td>2.79</td>
<td>0.83</td>
<td>1.15</td>
<td>0.93</td>
</tr>
<tr>
<td>Kl-b-IT 3</td>
<td>1.5</td>
<td>2.44</td>
<td>0.92</td>
<td>0.64</td>
<td>1.32</td>
</tr>
<tr>
<td>Kl-a-6 36</td>
<td>2438.9</td>
<td>4.49</td>
<td>0.64</td>
<td>2.29</td>
<td>0.81</td>
</tr>
<tr>
<td>Kl-b-6 33</td>
<td>1627.3</td>
<td>4.33</td>
<td>0.71</td>
<td>2.49</td>
<td>0.87</td>
</tr>
<tr>
<td>Kl-a-12 33</td>
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<td>5.22</td>
<td>0.78</td>
<td>2.74</td>
<td>0.92</td>
</tr>
<tr>
<td>Kl-b-12 34</td>
<td>485.6</td>
<td>5.34</td>
<td>0.79</td>
<td>2.79</td>
<td>0.92</td>
</tr>
<tr>
<td>K2-a-IT 4</td>
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<td>1.73</td>
<td>0.49</td>
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<td>K2-b-IT 4</td>
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<td>1.53</td>
<td>0.38</td>
<td>1.22</td>
<td>0.80</td>
</tr>
<tr>
<td>K2-a-6 30</td>
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<td>0.42</td>
<td>1.42</td>
<td>0.53</td>
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<tr>
<td>K2-b-6 30</td>
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<td>0.54</td>
</tr>
<tr>
<td>K2-a-12 36</td>
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<td>K2-b-12 28</td>
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<td>0.53</td>
<td>1.76</td>
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<tr>
<td>K3-a-IT 2</td>
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<td>1.00</td>
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<tr>
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<td>K3-a-6 20</td>
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<td>K3-a-12 22</td>
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<td>0.78</td>
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<td>K3-M2 21</td>
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<td>0.83</td>
<td>2.52</td>
<td>0.90</td>
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<tr>
<td>H1-a-IT 5</td>
<td>5.4</td>
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<td>0.93</td>
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<td>H1-b-IT 10</td>
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<td>0.70</td>
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<td>0.82</td>
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<td>0.37</td>
<td>0.41</td>
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<td>0.23</td>
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<td>H2-b-6 19</td>
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<td>0.99</td>
<td>0.41</td>
</tr>
<tr>
<td>H3-a-IT 4</td>
<td>3.7</td>
<td>2.29</td>
<td>0.90</td>
<td>1.24</td>
<td>0.91</td>
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<tr>
<td>H3-a-6 40</td>
<td>1135.9</td>
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<td>0.72</td>
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<td>H3-b-6 38</td>
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<td>1019.24</td>
<td>0.48</td>
<td>0.40</td>
<td>1.38</td>
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Figure 2. Dominance curve including all the samples.
Figure 3. *Harmeria scutulata* (Busk, 1855) - a dominant species on both intertidal and subtidal Spitsbergen coastal boulders.

Cauloramphus intermedius Kluge, 1955 and Cribrilina annulata Fabricius, 1780 represented just 5% of colonies each. Dominance values for other taxa were all below 5% (Table 3).

ANOSIM a priori statistic (Global R = 0.141, p = 0.016) revealed no difference between the communities at our study sites. Pair-wise ANOSIM statistic for all the sites is presented in the Table 4. Cluster (Fig. 4) and MDS (Fig. 5) divided samples into two major groups: intertidal samples and subtidal samples. Similarity between these two groups was below 20%. Within the subtidal group samples from the site K3 had a low affinity to other sites (40% of similarity). This site showed striking macroscopic differences as it was densely inhabited by the sea urchin *Strongylocentrotus droebachiensis* Muller, 1776.

### Table 3. Dominance (%) of selected taxa for two major associations revealed by multivariate analyses.

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<tr>
<th>Taxon</th>
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<th>Subtidal</th>
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<tr>
<td><em>Harmeria scutulata</em></td>
<td>57.4</td>
<td>53.8</td>
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<tr>
<td><em>Callopora</em> sp.</td>
<td>8.3</td>
<td>3.0</td>
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<tr>
<td><em>Tricellaria témata</em></td>
<td>8.3</td>
<td>0.4</td>
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<td><em>Eucratea loricata</em></td>
<td>7.7</td>
<td>0.4</td>
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<tr>
<td><em>Cristidae</em> indet.</td>
<td>4.5</td>
<td>3.9</td>
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<tr>
<td><em>Celleporella</em> hyalina*</td>
<td>3.1</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Cribrilina annulata</em></td>
<td>2.8</td>
<td>5.5</td>
</tr>
<tr>
<td><em>Tegella arctica</em></td>
<td>2.3</td>
<td>3.6</td>
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<tr>
<td><em>Callopora</em> craticula*</td>
<td>1.4</td>
<td>0.2</td>
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<tr>
<td><em>Tubuliporidae</em> indet.</td>
<td>1.4</td>
<td>0.7</td>
</tr>
<tr>
<td><em>Callopora lineata</em></td>
<td>1.0</td>
<td>0.1</td>
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<td><em>Cauloramphus intermedius</em></td>
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<td>5.4</td>
</tr>
<tr>
<td><em>Cylindroporella</em> tubulosa*</td>
<td>-</td>
<td>3.0</td>
</tr>
<tr>
<td><em>Tegella</em> retraversa*</td>
<td>-</td>
<td>2.9</td>
</tr>
<tr>
<td><em>Electro arctica</em></td>
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<td>2.3</td>
</tr>
<tr>
<td><em>Tegella</em> armifera*</td>
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</table>

### Table 4. ANOSIM pair-wise statistic between sites.

<table>
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<th></th>
<th>HI</th>
<th>H2</th>
<th>H3</th>
<th>K1</th>
<th>K2</th>
<th>K3</th>
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<tr>
<td>H2</td>
<td>R = 0.115</td>
<td>R = 0.061</td>
<td>R = -0.007</td>
<td>R = 0.069</td>
<td>R = 0.141</td>
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<tr>
<td></td>
<td>p = 0.143</td>
<td>p = 0.223</td>
<td>p = 0.374</td>
<td>p = 0.188</td>
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<tr>
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<td>R = 0.115</td>
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<td>R = 0.117</td>
<td>R = 0.179</td>
<td>R = 0.340</td>
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<tr>
<td></td>
<td>p = 0.143</td>
<td>p = 0.016</td>
<td>p = 0.186</td>
<td>p = 0.095</td>
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<tr>
<td>K1</td>
<td>R = -0.007</td>
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<td>R = 0.072</td>
<td>R = 0.149</td>
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<tr>
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<td>p = 0.374</td>
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<td>p = 0.197</td>
<td>p = 0.087</td>
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<td>R = 0.141</td>
<td>R = 0.340</td>
<td>R = 0.279</td>
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4 DISCUSSION

In general regional and local taxonomy and biodiversity have been more intensively studied in the northern hemisphere, and considerably more in the north Atlantic compared to the south Atlantic. This trend is reversed now, with a moderate level of Antarctic research and a paucity of Arctic studies. Despite the proximity of North American and European research centers, we know comparatively little about high Arctic littoral and sublittoral ecology. North Atlantic patterns of bryodiversity from the tropics to high polar regions do, however, offer one of the only strong pieces of evidence in support of the global latitudinal cline in richness (Clarke & Lidgard 2000). The northern polar habitat is, geologically, a young one and is still in the process of being invaded (Dunton 1992). In small scale space and time, though, the same is true - the boulder fields we examine here are colonized almost entirely by young ‘individuals’ of pioneer taxa. The few studies of Arctic boulder faunas in the

168
littoral and sublittoral have revealed communities comprising many species but dominated by just a few (Osburn 1955, Kluge 1962, 1975, Dick & Ross 1988) and governed by extreme hierarchies (Barnes & Dick 2000, Barnes & Kuklinski 2003).

Our shallow boulder study recorded 52 bryozoan species, about one third of the total bryozoans known from the Svalbard area (Gulliksen et al. 1999). The non-recorded species occur mainly in the deeper habitats and those specific to certain substrata such as algae or bivalve shells (Lippert et al. 2001, Kuklinski 2002b). Deeper habitats are suspected to have higher richness than those in the shallow subtidal (Kuklinski 2002a). We found very low community variability within the intertidal or within the subtidal sites (see Fig. 4). Such uniformity may be a feature of polar sites owing to the similar and very high levels of energy and disturbance they experience (Barnes 2000). Although great distance and hydrological differences occur between the fjords they display only small differences in species composition. Only at the K3 subtidal site, with high abundance of sea urchins (sea urchin barren), were there moderate community differences (Fig. 4). Even here, differences with other sites by most community measures were small (Table 2). Had we included mobile macrofauna or algae in our analyses we suspect that this site would have been found to be less similar (due to the abundance of echinoids, hermit crabs and calcareous algae). At lower latitude, Witman (1985), Sebens (1986), Kitching (1987) and others have found that the presence of sea urchins has a profound effect on benthic communities (including those on boulders) such as that considerable decrease in the local diversity. Both echinoids and calcareous algae (which are typically abundant in sea urchin barrens) can have a marked impact on benthos; by grazing and by superior overgrowth performance respectively.

Shallow polar benthos typically experiences one of the most frequent and intense levels of disturbance in nature, from wave action, salinity changes (Dayton 1990), scraping by floating ice (Peck & Bullough 1993, Conlan et al. 1998, Gutt & Pipenburg 2003), being ripped by anchor ice (Dayton et al. 1974, Dowdeswell & Forsberg 1992) or pit digging by megafauna. The intertidal zone, where disturbance is most extreme, can have daily temperature and salinity variations greatly exceeding the annual subtidal variation (e.g. Barnes et al. 1996) as is the case in the Spitsbergen area (Svendsen et al. 2002). Low species numbers in the intertidal zone thus are explained by ecological (rather than evolutionary) factors; the older Antarctic environment also has depauperate littoral zones at the 60°+ latitudes. On southern Atlantic shores Barnes & Lehane (2001) recorded 85-97% mortality per annum among intertidal bryozoans; higher than in subtidal communities (65-92%). We would
suggest that ice scour and wave action affects Spitsbergen shores in the same way and that similarly extreme mortality levels occur in the intertidal zone and to a lesser extent the subtidal zone of our study sites. No stable or developed communities were visible in the Spitsbergen intertidal zone, either at our study sites or those investigated earlier (Weslawski et al. 1993, Szymelfening et al. 1995). Even on the most stable or protected substrata the development of communities in Arctic or Antarctic intertidal zones is very limited - it is not surprising that for decades polar biologists thought that the zone was devoid of life.

At very few places the species composition of encrusting communities of the intertidal and the subtidal zones resemble to each other. Our study, like equivalent investigations in the Antarctic (Barnes et al. 1996, Barnes & Arnold 1999), does illustrate, however, that high latitude intertidal communities are composed entirely of a subset of subtidal species. The intertidal assemblages are very much impoverished forms of the subtidal community: unlike at other latitudes, there are no intertidal specialists. Another similarity between our sites and those in the southern polar region examined by Barnes & Arnold (1999) is that some (e.g. HI) were ice disturbed during summer but overlain by considerable ice cover during the winter. Our study encompassed sites covered by ice in winter and those, which are not. Therefore they experience different durations and frequencies of ice scour. Despite this we did found no obvious differences between the fauna in such areas.

When the frequency of catastrophic disturbance is high, the most abundant species are generally those with fast growth rates, early sexual reproductive capabilities, and good powers of dispersal. This has proved evident in the Antarctic (Barnes 1996, Gutt & Pipenburg 2003), the Arctic (Conlan et al. 1998, Barnes & Kuklinski 2003) as well as elsewhere in the world (Paine 1979, Karlson 1983). At our study sites, this seems particularly extreme with just one species (cheilostome: Harmeria scutulata Busk, 1855) constituting over 50% of the fauna present across the littoral and sublittoral and from local to regional scales. Its life history is unknown. A recent panel colonization investigation undertaken by us, has indicated that it has, for a polar species, fast growth. Considering the abundance and ubiquity of this species on the Spitsbergen coast, it would seem of some importance to establish the life history strategy and ecology of this species. This would help both to interpret the context of environmental change and understand the strategies employed in successful colonization of such a highly disturbed habitat.

The levels of diversity we found on Spitsbergen boulders were, overall, similar or in some cases higher than those described from similar Antarctic habitats (e.g. Barnes et al. 1996, Barnes & Arnold 1999). Barnes et al. (1996) recorded 5 and 21 bryozoan species (in the intertidal and subtidal respectively) at Signy Island, and fewer at Antarctic Peninsula sites. Thus values of 57 species in Alaska (Barnes & Dick 2000) and 73 taxa in our study, found using similar methods and effort, are high. Even in a temperate (50°N) Atlantic location Maughan & Barnes (2000) found only 61 species. Such high Arctic richness is perhaps a surprise given the historical context of a youthful Arctic still in the process of invasion (Dunton 1992), the isolation of the archipelago, and the fact that most of our study sites are free from winter ice or covered for relatively short time during the year (thus are potentially more disturbed). Scale may be an important issue here, as we found a high proportion of the described species for the whole of the Spitsbergen region, whereas the Antarctic studies found but a small proportion of the species known in the Scotia Arc or Antarctic Peninsula. Furthermore the West Spitsbergen coast has a milder climate than other Arctic sites at the same latitude (Gammelsrod & Rudels 1983), because of the effects of the warm West Spitsbergen Current so it may not be typical, for the Arctic.

5 CONCLUSION

We have found high richness, low diversity, domination by a single species and surprising uniformity of bryozoans along the west Spitsbergen coast, compared with other similar Arctic or Antarctic habitats. As these values come from a young, isolated and highly disturbed environment they stand out as anomalies for Bryozoa - one of the few taxa for which a strong latitudinal signal exists (Barnes 2000, Clarke & Lidgard 2000). We suggest local factors as causal. Predation seems likely to be minor and competition of only real influence in protected habitats though to identify factors of major importance requires more study. The uniformity of assemblages suggests little role for broader processes (such as hydrological conditions) on shallow boulders in the Spitsbergen area.

ACKNOWLEDGEMENTS

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Cheilostomate Bryozoa of the Bellingshausen Sea (Western Antarctica): a preliminary report of the results of the ‘Bentart 2003’ Spanish Expedition

C.M. López-Fé
Labomtorio de Biologia Marina, Departamento de Fisiologiu y Zoologia, Facultad de Biologia, Universidad de Sevilla, Sevilla. Spain

ABSTRACT: A preliminary report on the Bryozoa from the Spanish Antarctic Expedition ‘Bentart 2003’ is presented. A total of 107 species have been identified and are listed here, collected by Agassiz trawl and box corer in 22 stations along the Bellingshausen Sea and the Antarctic Peninsula. The samples from the Bellingshausen Sea are less diverse than those from the Antarctic Peninsula. Some observations about the colour of living bryozoans were made during the cruise. Twenty species have been found in areas where they were not previously reported.

1 INTRODUCTION

The Spanish Expedition ‘Bentart 2003’ collected benthic samples along the Bellingshausen Sea and the Antarctic Peninsula in February 2003. Most stations yielded cheilostome Bryozoa. The benthic communities of the Bellingshausen Sea in general were found to be quite poor. Most bryozoans consisted in small colonies on rocks on a bottom of iceberg debris.

The results presented here are still preliminary. Only the unequivocally identified species are included. A low number of examples, not listed, require further examination, and some new species may have to be erected.

The Bellingshausen Sea remains as one of the lesser-known areas of the Antarctic Ocean. The Belgian Antarctic Expedition of 1897-1899 (Waters 1904) still remains the main sampling programme in the area, with more than 70 collecting stations. Maybe the lack of research bases along its coasts is a reason of this absence of studies. On the contrary, the Antarctic Peninsula, easily accessible and with many bases is one of the best known areas. Complete sets of references to bryozoan studies there may be found in Moyano (1991) and Hayward (1995). More recently, some studies have been achieved on the epibenthic communities of the Antarctic Peninsula and nearby archipelagos (Barnes 1995a, b, Arnaud et al. 1998, Barnes & Brockington 2003). Bryozoa are a major component of the Antarctic epibenthos (Barnes & De Grave 2000, Bader 2002, and references therein).

2 MATERIAL AND METHODS

The samples were collected from the Spanish oceanographic ship B.I.O. Flespérides in 22 stations from 63°53’S 61°48’W (Gerlache Strait, easternmost and northernmost station) to 70°55’S 98°26’W (near Thurston Island, westernmost and southernmost station), including two stations at Peter I Island (Fig. 1). The depths ranged between 46 and 2043 m. An Agassiz trawl two metres wide and a box corer were used at all stations. Most Bryozoa were collected by the trawl. Additionally, some SCUBA dives were done when possible at Peter I Island and Paradise Bay. For reasons of homogeneity, they have not been included in the results, and only one species (Inversiula nutrix Jullien, 1888) was found by diving but not by trawl. Trawlings were of five minutes duration at a speed of two knots. Some observations, mainly the colour of living colonies, were made on fresh material, but most samples were stored in alcohol for further examination.

3 RESULTS

A total of 107 species were identified, most of them previously known in the area (Table 1). It is remarkable that 41 species were present in only one station. It is evident that the sampling effort at each station was not enough to give complete or even approximate information of the bryozoan fauna of the area. Furthermore, the possible patchiness of the distribution causes a single station be uninformative.
However, stations can be grouped in three sets that cover distinctive areas. Stations 1 to 8 are in the western part of the Bellingshausen Sea. Stations 9 to 17 are offshore in the center of the Bellingshausen Sea, and 18 to 25 are near the coast of the eastern part of the Bellingshausen Sea and the Antarctic Peninsula. Forty-one species were recorded in each one of the former two regions, while 73 were found in the coastal eastern part of the sampled area. Species richness clearly falls away from the continental shelf. In addition, the faunistic composition of the stations situated in the Bellingshausen Sea (1 to 17) is different from that of the stations placed in the Antarctic Peninsula (18 to 25). Only 41 species of 107 were found in both areas, while 19 species were collected only in the Bellingshausen Sea, and 47 species were found only in the Antarctic Peninsula, despite the geographical proximity of both areas.

All the stations near to or deeper than 1000 m show low species richness (always less than 10 species) (Fig. 2). Stations 3, 11, 12, 15 and 17 are in the continental slope, as can be observed by the great difference in depth with neighbouring stations that are not much more southern (Fig. 1, Table 1).

The species richness seen in Bellingshausen Sea is actually even poorer than appears from the figures. A solely qualitative analysis does not show that in the Antarctic Peninsula the colonies are larger and better developed. Many erect species are present in this area.

On the contrary, the stations of the Bellingshausen Sea, even those with a comparative high species richness, yielded mostly encrusting species represented by colonies smaller than 1 cm². A total of 21 species have been found in areas where they were not previously reported, but it is probably a consequence of the lack of studies, because many of them are known in more or less neighbouring areas, like the Weddell Sea or the Ross Sea.
Table 1. List of species and stations. Abbreviations: Mar. B.: Marguerite Bay. No. St.: number of stations in which the species has been found. N.: New record for this area. West. Bellings. Sea: Western Bellingshausen Sea.

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Some specimens showed, when alive, colours that are very different to that of preserved material. Antarctic Bryozoa have been studied mostly from preserved material collected some time ago, and the actual colour of most species is unknown. The change is very noticeable in some instances. Bader (2001) reported on the colour of some species. As is common among Bryozoa, most species are beige, light orange or light yellow. *Austroflustra vulgaris* (Kluge, 1914). This species shows the most surprising change observed. Reputed to be deeply brown (Hayward, 1995), almost black, the living colonies are light yellow. Bader (2001) reported it as beige. The change of colour occurs slowly, taking some hours. It does not depend on the mode of preservation: colonies preserved in formaline, alcohol or simply as untreated fragments turn the same dark colour. *Isoseculiflustra rubefacta* (Moyano, 1996). Preserved material of this species has a very noticeable red or dark pink colour, which together with features of the colony form, allow to distinguish it from *I. tenuis* (Kluge, 1914) (Moyano, 1996). However, living specimens are light brown. This change in colour occurs quickly after death or preservation. As in the previous case, it does not depend on the mode of preservation. *Carbasea curva* (Kluge, 1914). The dark red colour of living specimens becomes brown when preserved. *Smittinella rubrilingulata* (Rogick, 1956). This species is dark red when alive. The colour is very slowly lost. Colonies collected in February 2003 were still a pinkish colour in December 2003. *Trilochites biformatus* (Waters, 1904). Living colonies of this species exhibit a very remarkable yellowish green colour (similar to some fluorescent markers), quickly lost after death or preservation. Other species exhibit colours that are quite common among bryozoa. *Isoschizoporella tricuspis* (Calvet, 1909), *I. secunda* Hayward & Taylor, 1984 and *Pemmatozoporella marginata* (Calvet, 1909) are orange. *Reteporella frigida* (Waters, 1904) is light yellow.

5 DISCUSSION

The richness of the bryozoan fauna of the Antarctic Peninsula and its adjacent archipelagos is well known (Moyano 1991, Hayward 1995, López de la Cuadra & García Gómez 2000, Barnes & Grave 2000, Barnes & Brockington 2003), but the Bellingshausen Sea still remains poorly known. The continental shelf in this area is very deep, and the ice shelf extends far offshore. During the ‘Bentart 2003’ cruise the limit of the ice shelf extends to water deeper than 400 m. Studies on primary productivity were carried out during the cruise. They are still unpublished, but the overall impression was that this is an area of a very low productivity. All this may explain the low number of species and the small size of the colonies.

Important faunistic differences seem to exist between the Antarctic Peninsula and the Bellingshausen Sea. The former region is clearly richer, and many species found in it (up to 47 in our samples) were not collected in the Bellingshausen Sea. This supports the suggestion made by Barnes & De Grave (2000) that the Antarctic Peninsula may be considered a biogeographical subzone of the Antarctic Ocean, differentiated from West Antarctica.

No relationship with depth has been seen in the shelf stations, although all the deepest ones show a very low species richness. This pattern is similar to that found by Zabala et al. (1997) for the Weddell Sea. Barnes (1995b) found that, at Signy Island, many of the species studied occurred over much of the depth range of the study, from 0 to 290 m. He also suggested that massive/foliaceous species were more abundant in shallower locations while erect species were predominant at deeper stations. This trend is not observed in the data of the present study, but probably we lack enough shallow stations to compare. Erect species in general were found at rich areas, mainly in the Antarctic Peninsula and, less abundant, at Peter I Island while the offshore stations of the Bellingshausen Sea mostly yielded small encrusting colonies. Bryozoa were the most abundant component of many of the stations, considering both number of species and number of colonies, specially in the remarkably poor stations located in the Bellingshausen Sea. The ability of Bryozoa to colonize and complete their development on small substrata (Winston & Hakanson 1986) and the low energetic requirements of small colonies probably explain this abundance, as the bottom of most offshore stations was composed of mud and small rocks, usually smaller than 50 mm.

Most of the 21 species found outside of their previously known area simply complete a gap that was present due to lack of earlier studies. This is the case of species that were previously known in the Antarctic Peninsula or the Scotia Arc and also in the Ross Sea and are here reported for the first time in the central Bellingshausen Sea. Moyano (1991) and Hayward (1995) may be consulted for the previous known range of most species. Other species actually extend their known ranges. *Crassimarginatella inconstuntia* (Kluge, 1914) and *Smittina anecdata* Hayward & Thorpe, 1990 were not known in Western Antarctica (Hayward 1995). *Fenestralina cervicornis* Hayward & Ryland, 1990, *Figularia discors* Hayward & Taylor, 1984 and *Thrypticocirrus rogickae* Hayward & Thorpe, 1988 were previously reported only from the Ross Sea. *Isoseculiflustra rubefacta* is reported for the first time out of the Antarctic Peninsula, but its previous confusion with *I. tenuis* (see Moyano 1996) make it possible...
that some previous citations of *I. tenuis* correspond to *I. rubefacta*, but anyway none of them were previously reported from the western Bellingshausen Sea. *Lacerna eatoni* (Busk, 1876) and *Micropora notialis* Hayward & Ryland, 1993, previously known in the Antarctic Peninsula, also extend their known limits to the western Bellingshausen Sea.

ACKNOWLEDGEMENTS

The ‘Bentart 2003’ cruise was supported by the project REN2001-1074/ANT of the Spanish ‘Ministerio de Ciencia y Tecnologia’. I am grateful for the assistance of scientific staff of the cruise and to the crew of the BIO Hespérides. I am also thankful to D.K.A. Barnes and P.N. Wyse Jackson for the revision of the manuscript and their valuable suggestions.

REFERENCES


The potential role of microbial activity and mineralization in exoskeletal development in Microporellidae

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ABSTRACT: The relationship of microbes and bryozoans has not been investigated extensively. Studies have been limited to the role of microbes as potential symbionts, producers of films on marine surfaces and their effect on bryozoan substrate selection, or antibiotic roles. The role of microbes and their intimate association with calcium carbonate skeletal features has been largely ignored. Within the family Microporellidae many of the microbes incrusting the frontal wall or frontal shield structure initially appear to be associated with ascopores and pores. Microbial mats encompassing large areas of the colonies appear to be secondary developments. The microbes precipitate minerals which can ultimately lead to microbial fossilization and alteration of the skeletal mineralogy. The minerals can also serve as biosignatures for identifying microbial activity.

1 INTRODUCTION
Most bryozoologists consider epibionts such as diatoms, coccoliths, and microbes as a nuisance or hindrance for their studies as the epibionts can occlude taxonomically important features. These epibionts may affect survival strategies by either impeding colony development or by preventing overgrowth by other bryozoans (Scholz 1995, Morris et al. 2002). The microbes forming mats can attract, precipitate, and nucleate minerals by either passive or enzyme mediated methods (Southam & Donald 1999). In addition, many microbes form biofilms that are also subject to mineralization and subsequent fossilization. Mineralization optimally occurs upon microbial death, and in laboratory experiments the process can occur within one week (Westall et al. 1995). Common cations associated with this process include iron, calcium, and magnesium (Gerdes et al. 1986, Ferris et al. 1994, Southam & Donald 1999). In this paper we will investigate the role of microbial precipitates, microbial fossilization and their impact on living bryozoan skeletal mineralogy, along with their probable role in skeletal repair and the paleontological implications.

2 MATERIALS AND METHODS
The bryozoans used in this study were from the Hancock Institute for Marine Studies collections (AHF). All of the material, except Microporelloides planata from Loma Point, were presumably alive when they were collected as there are remains of the outermost soft tissue membrane. Most of the specimens in the collection were initially preserved in formalin, and later rinsed in 70% ethanol and air-dried. Later collections were not initially preserved in formalin, but allowed to air dry. The list of slides are: Microporelloides hawaiensis D.F. Soule, H.W. Chaney, P.A. Morris 2003, Cocoanut Island, Oahu, Hawaii, on coral (AHF Station 500-66); Microporelloides hawaiensis, Au Au Channel, Hawaii, depth 87-95 m, on black coral (AHF Station 606-67); Fenestruoides morrisiae D.F. Soule, J.D. Soule, H.W. Chaney 1995, Miramar Beach, Santa Barbara, California, on kelp holdfast; Microporelloides planata (D.F. Soule, J.D. Soule & H.W. Chaney 1995); D.F. Soule, H.W. Chaney, P.A. Morris 2003, Loma Pt., California (AHF Station 28A19); Microporelloides planata, MAT holotype 212, AHF Station 1234-48, off Santa Catalina Island, 1.25 miles east of White Cove, California, depth 65.48 m; Fenestruina farnsworthi D.F. Soule, J.D. Soule, H.W. Chaney 1995, Bird Rock, Catalina Island, California, depth 8 m; Microporelloides cribrosa (Osbum 1952) D.F. Soule, H.W. Chaney, P.A. Morris 2003, off San Pedro breakwater, California, depth 18 m; Microporelloides cribrosa, Carmel, California, intertidal, AHF Station M14-84; Microporelloides infundibulipora (Osbum 1952) D.F. Soule, J.D. Soule, H.W. Chaney 1995,
Figure 1. **A-Fenestrulina farnsworthi**, Bird Rock, Santa Catalina Island, California. Scale bar is 1 mm. Zooidal frontal wall is covered by diatoms (D) and various microbes. Some of the microbes are flaccid (F). Other microbes, particularly the filaments, appear to be attracting additional minerals, either actively or passively, as indicated by the spherical particles on their surfaces (M). **B - Fenestruoides morrisae**, Miramar Beach, Santa Barbara, California. Scale bar is 2 mm, presumptive mineralized microbes are incorporated in the zooidal frontal wall (M). **C - Microporelloides cribrosa**, San Pedro breakwater, California. Bar line is 10 mm. Collapsed filaments (F) and an example of a coccolith (Co) is indicated. **D - Fenestrulina farnsworthi**, Bird Rock, Santa Catalina Island, California. Scale bar is 50 mm. Operculum, oral spine and other areas of the zooidal frontal wall are covered with diatoms (D), **E - Fenestrulina farnsworthi**, Bird Rock, Santa Catalina Island, California. Scale bar is 20 mm. Internal surface of zooidal frontal wall. Biofilm (B) and diatoms (D) are indicated near the ascopore. **F - Microporelloides cribrosa**, San Pedro breakwater, California. Scale bar is 2 mm. Zooidal frontal wall covered with presumptive fossilized microbes (M) and extensive biofilms (F).

AHF holotype 211.3 miles NW Anacapa Island, AHF Station 1267-41, depth 86 m. The bryozoans were coated for 15 seconds (approximately 5 nm) with platinum; carbon tape was used to establish a conductive surface between the bryozoans mounted on glass slides and the electron microscope stub. The colonies were analyzed with a Philips XL40 scanning electron microscope (SEM). An Oxford Link Isis IXRF energy
Figure 2. A - *Microporelloides hawaiiensis*, Cocoanut Island, Oahu, Hawaii. Scale bar is 5mm. The developing edge of an ascopore is microbe free (S). Microbes are found within a few microns of the developing ascopore margin (M). B - *Microporelloides hawaiiensis*, fossilized microbes Cocoanut Island, Oahu, Hawaii, Scale bar is 5 mm. Avicularium is covered by probable (M). C - *Microporelloides planata*, Loma Point, California. Optical microscopy indicates a poorly preserved bryozoan, but with SEM, the poor preservation can be attributed to precipitated minerals and probable alteration of original mineralogy forming the colony. There is no evidence of biofilms, diatoms, coccoliths, or other microbes observed on colonies that were probably alive when they were collected. Aperture of the zooid is indicated (A).

dispersive x-ray spectroscopy (EDS) system was used to determine qualitative elemental composition.

3 RESULTS: MICROBIAL DESCRIPTION

3.1 Microbial forms and shape; areas inhabited by microbes

A variety of microbial epibionts, including their biological products, i.e. biofilms, trapped particulate matter and precipitated minerals, are associated with Microporellidae from the northeastern Pacific. The taxa and morphologies include coccoliths, diatoms, filaments, coccoids and rod-shaped morphologies (Figs la-f). The coccoid forms have a smooth surface, varying in size. The microbial epibionts and their biological products form mats varying in development. Microbes and biofilms can also be identified on the internal surfaces of the zooid frontal wall, but we do not know which, if any, of these microbes were present prior to death (Fig. le, Fig. 13 of Soule et al., this volume). Other than the external and internal zooid frontal wall, microbes and their biological products, including biofilms and agglutinated particles, can form heavy mats on other areas. These areas include the operculum covering, the aperture, pore sieve plates, and avicularia (Figs Id, 2a & b, Figs 8-10 of Soule et al., this volume).

There are areas on the Microporellidae colonies that are either relatively or entirely free of epibionts. The edges of developing ascoepores are usually free of microbes, but colonization can occur within a few microns (Fig. 2a). Younger or peripheral areas of the colony are relatively free of epibionts while the older areas are more heavily settled (younger area Figs 1-4, 15-18 of Soule et al., this volume, older areas Figs la-d. Fig. 2a).

3.2 Microbial fossilization, cation, bryozoan preservation

Most of the bryozoan material found in the AHF collections was initially preserved in formalin, which has
helped preserve microbial remains. Energy dispersive x-ray spectroscopy (EDS) analysis indicates that most of the morphologies, with the exception of diatoms and coccoliths, vary in their degree of mineralization or fossilization. For instance, some rod-shaped morphologies appear to be relatively unfossilized as their surfaces are flaccid and do not appear rough (Figs 1a, c), while others appear to be highly mineralized as indicated by their rougher surfaces containing precipitated minerals (Fig. 1f, Fig. 2a). In some instances the mineralization has proceeded to a point that the microbes appear to be either partially or entirely incorporated into the mineralized frontal wall of the zooid (Figs 1b, f). EDS analysis of the exoskeleton covered by epibionts indicates varying levels of silicon (Si), even in the apparent absence of diatoms, varying levels of sulfur (S) and magnesium (Mg), and consistently elevated levels of calcium (Ca). Occasionally iron (Fe) is present; aluminum (Al) is either present at low levels or entirely absent (Fig. 3b). Very few areas of the colony are characterized by only Ca (as calcium carbonate) with no other identifiable elements present (Fig. 3a). One of these areas is the developing edges of ascopores (Fig. 2a).

Some or all of the coccoid forms may not be microbial, but a product of carbonate precipitation within biofilms instead (Gerdes et al. 1994). Their size variation, including forms at the lower size limit for viability, may also support an inorganic origin.

Colonies appearing to be poorly preserved using light microscopy indicate significant alteration, including excessive mineral precipitation when viewed with SEM. There is also an absence of microbes and their products, including biofilms in these specimens (Fig. 2c).

4 DISCUSSION

The role of microbes has evolved through time. Initially microbes survived by inhabiting the extreme environments of a young Earth, and they utilized various minerals associated with rocks as an energy source. With the evolution of metazoans their role changed and they were able to adapt to different life strategies, which included an intimate association with bryozoans. The study of microbes and bryozoans has been generally directed towards the role of microbes as potential symbionts, as producers of films on marine surfaces that could serve as a substrate, as producers of biofilms and their affect on bryozoan substrate selection, or as antibiotics in bryozoan colonies (Crisp & Ryland 1960, Cuffey 1970, Brancato & Woollacott 1982, Pettit et al. 1983, Maki et al. 1989, Colon-Urbán 1991, Gordon & Mawatari 1992, McKinney & McKinney 1993, Scholz & Hillmer 1995). The association of microbes with bryozoan skeletons has received limited attention. Microbes may increase the ability of the colony to prevent overgrowth by other bryozoans; in some types of stressed environments the microbes could conversely, overgrow the colony and prevent colony development (Scholz 1995, Morris et al. 2002).

In our limited studies, the microbes associated with Microporellidae initially appear to prefer to incrust openings on the colony skeleton. This initial attachment may indicate a preference for points where there may be opportunities for deriving nutrients from organic debris. For instance, the everted lophophore creates currents that carry nutrients to the bryozoan orifice. These currents and the dissolved organic materials that they carry could provide microbial nourishment. Microbial association with pore plates, ascopores, avicularia, and ultimately the colony, may be variable, particularly with the avicularia (Winston 1984, 1986). For instance, if some of the microbes were responsible for antimicrobial or general defensive activity, they would protect the colony from overgrowth by other bryozoans (Scholz 1995) or from other carnivorous invertebrates such as pycnogonids and juvenile gastropods (Soule unpublished), or extensive overgrowth by microbes that would significantly hinder the ability of colonies to survive (Morris et al. 2002).
The skeletal compositions of the Microporellidae colonies we investigated appears to be variable. Pure calcium carbonate was restricted to exoskeletal layers lacking microbes (Figs 2a, 3a). The identified cations, Mg, Fe, S, sodium (Na), chlorine (Cl), Al, Si, potassium (K) were found in varying concentrations (Fig. 3b). Na and Cl are residues of the marine water and were found associated with halite crystals. The presence of S could be associated with sulfur reducing bacteria or indicative of colony organic remains. Si was identified when there was no evidence of diatoms. The source may be from the activities of other microbes (Southam & Donald 1999). Al is not generally associated with microbial precipitation, but with the apparent absence of both diatoms visible clay minerals on the skeletal surfaces, this may be the source. K is occasionally found, but is likely to be indicative of organic activity.

The fossilization of microbes and the precipitation of a variety of minerals may result in the incorporation of the microbes in the exoskeleton (Figs 1b, f). This activity appears to be primarily restricted to living or possibly recently deceased colonies. If the colony continues to be exposed to the marine waters after its demise, skeletal alteration may occur that is not a direct result of microbial processes. The surface may be subject to erosion and precipitation as a result of chemical processes associated with marine waters (Fig. 2c). Optical microscopy of bryozoans with no living components would indicate a poorly preserved or abraded colony. Such processes probably affect the fossil record significantly, limiting the number of colonies preserved within the sedimentary record.

Extensive remains, mostly intact, of the outermost soft tissue membrane were found on all of the materials studied. These remains indicate that the colonies were probably alive when they were collected. Possible exceptions were Microporelloides planata (Fig. 2c), and possibly Fenestrolina famsworthi (Fig. 1e). The former is in poor condition as there is evidence of erosion and possibly mineral precipitation caused by chemical processes in marine waters. The latter image is of the internal surface of the zooidal frontal wall. There is no evidence found in the literature of diatoms inhabiting the interior surfaces of living bryozoans. These microbes may have moved to the internal surfaces for the purpose of ‘dining’ on the dead and decaying soft-bodied remains.

5 CONCLUSIONS

We argue that microbes, as concluded by other investigators, are an important factor in bryozoan survival. We propose that their remains can be identified either through their fossilized remains or the by the identification of signatures such as possibly Fe and Mg. We further propose that there may initially be preferential sites for microbial settlement on bryozoan colony surfaces, but subsequent to the establishment of a small microbial colony, the microbes may form extensive mats.

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REFERENCES


Bryozoa of the CIMAR-7 Expedition to the Aysenian fjords and channels, southern Chile

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ABSTRACT: Bryozoans collected between 20 and 247 m depth by the Chilean CIMAR-7 Expedition to channels and fjords north of the Penas gulf, v. gr. Estera Elefantes near Laguna San Rafael National Park, yielded 30 typically Magellan species. Among these stand out Chondriovelum angustilobatum, Beania maxilla, B. fragilis, Cellaria malvinensis, Callopora deseadensis, Aspidostoma giganteum, Nevianipora milneana, Smittina undulimargo and Romancheina labiosa. The presence of the genera Chondriovelum and Adeonella reveals both vicariant relationships with Antarctica, South Africa and Australia and also a bryozoan similarity among external and internal fjords, islands and channels of the Magellan Madre de Dios area and the interior sea of the Aysenian region. These results were complemented through comparison with results obtained from two stations of the German Sonne Expedition, one off Cucao Bay (Chiloé Island) at 503 m depth and the other at 538 m depth off Concepción Bay. Seven out of eight species in this collection were typical Magellan species such as Ogivalia elegans. As a general conclusion the bryozoans collected by the CIMAR-7 Expedition indicate the existence of a typical Magellanic fauna in the inner Aysenian sea.

1 INTRODUCTION

Although studies on the bryozoans of the southern region of South America date back more than 150 years and have documented in more than 200 species so far (Moyano 1982, 1999), little is actually known of the bryozoans inhabiting the interior seas of Chiloé, Aysén and Magallanes. However, in the last two decades more information has become available following the collecting activities of Chilean, German and Italian cruises and expeditions to the Magellan Strait and to channels and fjords situated north and south of it (Moyano 1991, 1997, 1999). The results of these activities have allowed us to extend the geographical distributions of many species, initially described from the Falkland and Burdwood Bank areas, up to Cape Horn and Magellan Strait. What has also become apparent is that there is a similarity of bryozoan marine faunas on either side of the southern-most part of South America.

The Aysenian region is situated between the Magellanian and Chiloecan regions which lie to the south and north respectively and some zoogeographers have suggested that this region has an intermediary zoogeographical role between the southernmost Magellanic province and the northernmost Peruvian-Chilean zoogeographical region which reaches Chiloecan fjords and channels (Brattström & Johanssen 1983).

Information on the bryozoans of the Aysenian inner sea is almost non-existent because there have been no national or international collecting expeditions made to the area. The Chilean Navy CIMAR-7 Expedition help overturn, at least in part, this lack of information and partially helped answer the following questions: (1) Are there two different bryozoan faunas, one to north of Gulf of Penas (Aysenian fauna) and another to south of it (Magellanian fauna)? (2) Are bryozoans of the inner archipelagos different from those facing the open sea? This paper gives the primary faunistic results of the CIMAR-7 Expedition which begin to answer these elementary questions.

2 MATERIALS AND METHODS

The first part of the CIMAR-7 Cruise was carried out on board of the AGOR 60 Vidal Gormaz of the Chilean Navy, from the mouth of the Guafo, 43°45.20'S. (Station 1) to Elefantes fjord 46°28.5'S. (Station 27). The expedition started from Puerto Montt on 7th July 2001 and ended on 21st July 2001.

32 stations were sampled in the fjords and channels of the area, but only six yielded bryozoans. Details of these stations and sampling methods are given in Table 1.

In order to augment the information obtained from the CIMAR-7 Expedition, bryozoan samples obtained
Table 1. Chilean CIMAR-7 (2001) stations yielding Bryozoa.

<table>
<thead>
<tr>
<th>Station</th>
<th>Location</th>
<th>Date (m)</th>
<th>Depth</th>
<th>Sampling method</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>Moraleda channel</td>
<td>9/7/2001</td>
<td>9/7/2001 186</td>
<td>trawl</td>
</tr>
<tr>
<td>13</td>
<td>Moraleda channel</td>
<td>9/7/2001 76</td>
<td>trawl</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>Moraleda channel</td>
<td>9/7/2001 160</td>
<td>trawl</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>Elefantes fjord</td>
<td>14/7/2001 60</td>
<td>trawl</td>
<td></td>
</tr>
<tr>
<td>26</td>
<td>Elefantes fjord</td>
<td>14/7/2001 20</td>
<td>trawl</td>
<td></td>
</tr>
<tr>
<td>30</td>
<td>Quitralco fjord</td>
<td>16/7/2001 247</td>
<td>trawl</td>
<td></td>
</tr>
</tbody>
</table>

Table 2. German PUCK Sonne Cruise (2001) stations yielding Bryozoa. GC-6 = Gravity core; AGT = Agassiz trawl.

<table>
<thead>
<tr>
<th>Station</th>
<th>Location</th>
<th>Date (m)</th>
<th>Depth</th>
<th>Sampling method</th>
</tr>
</thead>
<tbody>
<tr>
<td>7163-9</td>
<td>Off Concepción Bay</td>
<td>24/4/2001</td>
<td>538 GC-6</td>
<td></td>
</tr>
<tr>
<td>7176-5</td>
<td>Off Cucao Bay</td>
<td>2/5/2001</td>
<td>502 AGT</td>
<td></td>
</tr>
</tbody>
</table>

3 RESULTS

The whole CIMAR-7 bryozoan collection is shown in Table 3 and bryozoan species recovered by the Sonne Expedition are listed in Table 4. Both expeditions were essentially oceanographical, and the bryozoans formed only a side element of the expedition; this explains why the bryozoan collections obtained were small and of low diversity. The CIMAR-7 bryozoan collection is dominated by encrusting species found growing on the few rock fragments obtained; these account for more than 50% of the colonies obtained and are followed by cellariiform species which make up 17% of the bryozoans recovered. If the whole collection is analyzed in terms of encrusting versus erect species, the former predominate totalling 18 species (60.3%) against only 11 species (36.7%) of the latter, but if flexible as against rigid colonies are compared, the former comprise only 9 species (5 cellariiform, the two flexible encrusting Beania, one catenicelliform and one unclassified ctenostome) whereas the latter total 21 species. The results given in Table 4 which list the bryozoans obtained during the Sonne Expedition, reveal a very different situation when compared with Table 3. The number of species is only 8, seven of which are erect (87.5%). Most of the species are rigid and erect (5 vinculariiform, 62.5%). Two species, the cheilostome Cellaria tenuis and the cyclostome Nevianipora milneana are present in both collections.

4 REMARKS ON SELECTED SPECIES

4.1 CIMAR R-7 Expedition

Adeonella patagonica (Hayward, 1988) (Fig. 1D-E)

This is one of three Magellan species belonging to a tropical or subtropical genus comprising 48 species (Hayward 1988). Its presence in sub-Antarctic cold waters seems to be relictual. This new record extends its known distribution to the north by 5° (of latitude) and includes in its range the Aysenian inner sea.

Beania fragilis (Ridley, 1881)

A rare Patagonian species found for just the second time in Chilean waters since it was first described in 1881 by Ridley. It has also been collected in the southern Argentinian coasts (López-Gappa & Lichtschein 1990).

Callopora deseadensis (López-Gappa, 1981)

Species described from Port Deseado, Argentina (López-Gappa & Lichtschein 1988), also present in Tierra del Fuego (Hayward & Thorpe 1989). Now discovered in the Aysenian inner sea, its distribution is extended 8° northwards along the Chilean Pacific coast.

Cellaria malvinensis (Busk, 1852)

One of most common cellariids in the Magellan region both in the south western Atlantic and in the south eastern Pacific. Apparently the first to see and describe this species was Alcide d’Orbigny (1847) and later it was fully described and illustrated by
Table 3. Bryozoa collected during the CIMAR-7 cruise in the inner sea of Aysén, Southern Chile, during July 2001

<table>
<thead>
<tr>
<th>Species</th>
<th>Stations/depths (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>6 13 14 25 26 30</td>
</tr>
<tr>
<td>CHEILOSTOMATIDA (22 spp.)</td>
<td></td>
</tr>
<tr>
<td>Adeonella patagonica</td>
<td>x</td>
</tr>
<tr>
<td>Amastigia sp.</td>
<td>x</td>
</tr>
<tr>
<td>Aspidostoma giganteum</td>
<td>x</td>
</tr>
<tr>
<td>Beania fragilis</td>
<td>x</td>
</tr>
<tr>
<td>Beania maxilla</td>
<td>x</td>
</tr>
<tr>
<td>Callopora deseadensis</td>
<td>x</td>
</tr>
<tr>
<td>Cellaria malvinensis</td>
<td>x</td>
</tr>
<tr>
<td>Cellaria tenuirostris</td>
<td>x</td>
</tr>
<tr>
<td>Cellaria variabilis?</td>
<td>Ce</td>
</tr>
<tr>
<td>Celleporella discreta</td>
<td>x</td>
</tr>
<tr>
<td>Chondriovelum angustilobatum</td>
<td>I</td>
</tr>
<tr>
<td>Ellisina sp.</td>
<td>x</td>
</tr>
<tr>
<td>Fenestrulina sp.</td>
<td>I</td>
</tr>
<tr>
<td>Micropora notialis</td>
<td>I</td>
</tr>
<tr>
<td>Microporella sp.</td>
<td>I</td>
</tr>
<tr>
<td>Osthenosia sp.</td>
<td>I</td>
</tr>
<tr>
<td>Porella sp.</td>
<td>I</td>
</tr>
<tr>
<td>Romancheina labiosa</td>
<td>I</td>
</tr>
<tr>
<td>Smittina monacha</td>
<td>I</td>
</tr>
<tr>
<td>Smittina undulimargo</td>
<td>I</td>
</tr>
<tr>
<td>Smittina sp.</td>
<td>I</td>
</tr>
<tr>
<td>Tricellaria aculeata</td>
<td>Ca</td>
</tr>
<tr>
<td>CYCLOSTOMATIDA (7 spp.)</td>
<td></td>
</tr>
<tr>
<td>Crisia sp.</td>
<td>x</td>
</tr>
<tr>
<td>Diastopora sp. 1</td>
<td>x</td>
</tr>
<tr>
<td>Diastopora sp. 2</td>
<td>x</td>
</tr>
<tr>
<td>Entalophora sp.</td>
<td>x</td>
</tr>
<tr>
<td>Homera sp.</td>
<td>x</td>
</tr>
<tr>
<td>Nevianipora milneana</td>
<td>x</td>
</tr>
<tr>
<td>Stomatopora sp.</td>
<td>x</td>
</tr>
<tr>
<td>CTENOSTOMATIDA (1 indeterm., sp.)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>1 8 6 7 12 3</td>
</tr>
</tbody>
</table>

Fz = Zoarial forms: I = encrusting: 17 ssp. (57%); V = vinculariiform: 3 (10%); A = adeoniform: 1 (3.3 %); Ca = catenicelliform: 1 (3.3%); Ce = cellariiform: 5 (17%); Cel = celleporiform: 1 (3.3%); E = eschariform: 1 (3.3%); 0 = unclassified: 1 (3.3%).

George Busk (1884) in his report on the bryozoans collected during the Challenger Expedition.

Cellaria tenuirostris (Busk, 1852)
Another common cellariid having a sub-Antarctic circumaustral distribution. It is present both in the Magellanic regions and in the Australian-New Zealand realm (Gordon 1984).

Chondriovelum angustilobatum (Moyano, 1974) (Fig. 1A-C)
Uncommon encrusting species, described originally from Madre de Dios archipelago, it is closely related to the vicariant eschariform Antarctic species, C. adeliense (Livingstone 1928). This record extends its known distribution northwards by 5° and to the inner Aysenian sea (See Moyano 1974 and Hayward 1995). A third fossil species of the genus, C.fossilis was discovered by Gordon & Taylor (1999) from Chatham Island close to New Zealand. Gordon & Taylor’s report extends the distribution of this Magellan-Antarctic genus to the western south Pacific.

Romancheina labiosa (Busk, 1854) (Fig. 3A-F)
Described from the Cape Horn area. Common in both sides of the southern tip of South America and
Table 4. Bryozoa from two stations of the Sonne Expedition.

<table>
<thead>
<tr>
<th>Species</th>
<th>Concénpcion Bay</th>
<th>Cucao Bay</th>
<th>Fz</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amastigia sp.</td>
<td>x</td>
<td>Ce</td>
<td></td>
</tr>
<tr>
<td>Andreella megapora</td>
<td></td>
<td>I</td>
<td></td>
</tr>
<tr>
<td>Cellaria tenuis</td>
<td></td>
<td>Ce</td>
<td></td>
</tr>
<tr>
<td>Foveolaria elliptica</td>
<td></td>
<td>V</td>
<td></td>
</tr>
<tr>
<td>Hornera sp.</td>
<td></td>
<td>V</td>
<td></td>
</tr>
<tr>
<td>Nevianipora milneana</td>
<td></td>
<td>V</td>
<td></td>
</tr>
<tr>
<td>Ogivalia elegans</td>
<td></td>
<td>V</td>
<td></td>
</tr>
<tr>
<td>Orthoporidroides erectus</td>
<td></td>
<td>V</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>2</td>
<td>7</td>
<td></td>
</tr>
</tbody>
</table>

Fz = Zoarial forms: I = encrusting: 1 (12.5%); V = vinculariform: 5 (62.5%); Ce = cellariiform: 2 (25%).

associated with areas of upwelling in central Chile. This explain its presence below depths of 15 m in Arauco Gulf (37°S).

Smittina undulimargo (Moyano, 1983)
This species described by Moyano (1983) from the continental slope facing central Chile seems to be present in sub-Antarctic waters bathing the continental slope and the shelf from central Chile to Magellan zone. This present record shows it is also present in the inner Patagonian Pacific seas and also present in Magellanic samples to be described elsewhere.

4.2 Sonne Expedition

Andreella megapora (Moyano & Melgarejo, 1978)
The northernmost species of the sub-Antarctic genus Andreella is eurybathic, living from the upper subtidal zone to more than 500 m depth.

Foveolaria elliptica (Busk, 1884) (Fig. 3D-F)
This is a sub-Antarctic and apparently circumaustral species. This present report extends its distribution 5° northwards along the Chilean coasts.

Nevianipora milneana (d’Orbigny, 1847) (Fig. 4A-F)
A typical Magellanic cyclostome species that inhabits the deepest waters on the shelf and also in the continental slope. It forms dense aggregations on hard substrates.

Ogivalia elegans (d’Orbigny, 1847) (Fig. 2A-C)
A common sub-Antarctic species of the south eastern Pacific and southwestern Atlantic. Material was collected from 538 m depth on the continental slope off Concepción Bay (36°24.44’S); this extends its known distribution 13° further north.

Orthoporidroides erectus (Waters, 1888)
This range of this species which was described by Waters (1888) from Cape Horn vicinity, now extends from Tierra del Fuego area to Chiloé Island, that is more than 10° further north than before.

5 DISCUSSION AND CONCLUSION

The total number of bryozoan species known in the Magellanic zoogeographical province is close to 220. The 36 species collected during the CIMAR-7 emise and the Sonne cruise represent only 16.4% of that total, and are typically those inhabiting the sub-Antarctic waters that bath the coasts of the southern tip of South America. Thus, the Aysenian bryozoan fauna reported in the present study based the CIMAR-7 collection, is typically Magellan. This is complemented and reinforced by the seven species collected off Cucao Bay, Chiloé Island, by the Sonne Expedition; two of these species are shared by both collections.

The few rock fragments collected and examined, show a high diversity of species on only a small area of few squared centimetres. It is highly suspected that many species that might be expected from the study area were not collected due to the small number of those fragments recovered by trawling. It is probable that other species growing on living or inert substrata colonized also by other animals were sent to other zoologists, and these have not seen by the author. Only new cruises to the area will reveal the actual bryozoan diversity of the Aysén inner sea.

Typical species of the Chilean-Peruvian province were not found in the samples studied although two species typical of cold waters in central Chile were found: Smittina undulimargo and Romancheina labiosa. The first is typically from the continental slope and the second from upwelling areas. Both are also present in Tierra del Fuego coasts. The presence of Ogivalia elegans on the slope off Concepción Bay extends further north the distribution range of, at least, part of the Magellanic bryozoan fauna. It is highly probable that many other species be present. However, samples from the slope between 300 and more than 1000 m depth studied by Moyano (1991) led him to propose a Bathyal bryozoogeographical province on the base of a very characteristic and apparently endemic fauna.

Adeonella patagonica, common in external archipelagos like Madre de Dios, is now reported from the Aysenian inner sea. Moreover this species belonging to a tropical or subtropical genus, probably represents a relict in the Magellanic area. This position is probably similar for other taxa such as a species of Chiastosella (to be described elsewhere) and Sinupetraliella formidabilis Moyano 1999, both discovered in the vicinity of Cape Horn (Moyano 1999).
Figure 1. A-C. Chondriovelum angustilobatum. A. Frontal view of an encrusting zoarium, x30. B. Three autozooids and one interzooidal avicularium, x71. C. Interzooidal avicularium, x90. D-F. Adeoneüa paragon ica. D. Zoarial frontal view, x30. E. Two zooids and one kenozooid, all showing an acute frontal dependent avicularium, xl05. F. Two zooids: a smaller autozooid and a larger biaviculariate gonozooid, x90.
Figure 2. A-C. *Ogivalia elegans*. A. View of a zoarial twig next to a bifurcation, x15. B. Zooids lacking the proximal small avicularium, x30. C. Zooid in a bifurcation also lacking avicularium, x41. D-F. *Foveohria elliptica*. D. Bifurcation of a highly calcified zoarium, x17. E. Opesium and proximo-lateral avicularium, x90. F. Frontal avicularium almost embedded and wrapped by the increasing calcification, x180.
Figure 3. A-F. *Romancheina labiosa*. A. General view of a reproductive colony. x15. B. Frontal view of an ovicellate zooid. x49. C. Oral area of a fertile zooid. Note the distal ovicell and the two lateral avicularian chambers limiting the central proximal oral sinus, x98. D. Two ovicellate zooids seen from the proximal side, x41. E. Oral complex: aperture, lateral avicularia and ovicell, x79. F. Latero-oral avicularium. Note the complete oral bar and the frontal pores of its chamber, x195.
Figure 4. A-F. *Nevianipora milneana*. A. Reproductive branch with a post-axilar gonozooid, x15. B. Reproductive branch with an axilar gonozooid, x15. C. Gonozooidal area of A, x30. D. Gonozooidal area of B, x34. E. Central zone of C with ooeciostorae, x49. F. Central zone of C with ooeciostome, x139.
Apparently bryozoans from the inner sea are not different from those occurring in the external archipelagos facing the open ocean. Although the number of species included in the present study is less than a fifth of the known Magellanic bryozoan fauna, the species gathered are typically Magellan, sub-Antarctic or circumaustral. This is the case of *Cellaria malvinensis* and *Aspidostoma giganteum* (typically Magellan), *Cellaria tenuirostris* (circumaustral). Within the collection obtained by the CIMAR-7 expedition, the ranges of species such as *Callopora deseadensis*, *Adeonella patagonica* and *Chondriovelum angustilobatum* have been expanded to include the inner Aysenian sea and extended to the north, since they were previously known from places south of 50°S. Some of the species collected during the *Sonne* Expedition show a greater extent of their known distribution: in the case of *Ogivalia elegans* this species was found off Concepción Bay 13° further north than before.

ACKNOWLEDGEMENTS

The Chilean Navy and especially people on board of R/V AGOR 60 *Vidal Gormaz* are deeply thanked for undertaking the CIMAR-7 Expedition. The author also thanks Marco Antonio Rétamai, Department of Oceanography, Universidad de Concepción, who sorted and kept the bryozoans of the CIMAR-7 Expedition, and Margarita Marchant, Zoology Department, Universidad de Concepción for collecting and fixing the bryozoans of the *Sonne* Expedition.

REFERENCES


Some middle Permian bryozoans from Svalbard, Arctic Norway

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Natural History Museums (Geology), University of Oslo, Blindem, Oslo, Norway

ABSTRACT: The middle to upper Permian (Ufimian-Kazanian) succession of Svalbard comprises the upper part of the Kapp Starostin Formation (above the Voringen Member) in western and central Spitsbergen, and the Miseryfjellet Formation of Bjamoya both units within the Tempelfjorden Group. The Ufimian-Kazanian part of the Kapp Starostin Formation consists of silicified spiculitic shales (‘cherts’), partly silicified limestones and locally developed glauconitic sandstones in the uppermost part. The Miseryfjellet Formation is made up of partly silicified sandy limestones and more sandy units. The fossils in the investigated sections are typical middle to late Permian cold water forms - sponges, brachiopods, echinoderms and bryozoans. Corals and trilobites are rare, ammonoids are extremely rare and other temperate to warm-water forms, such as fusulinid foraminiferans are absent. The shaley parts of the Kapp Starostin Formation are dominated by abundant delicate trepostomids, rhabdomesids, cryptostomids and fenestellids. The partly silicified limestone units are dominated by more robust trepostomids, and robust species of Polypora, Acanthocladia and Reteporidra. This division may reflect the recurrent changing depositional environments (quiet/rough waters), sea level changes or a selection through transport. The identified faunas resemble Ufimian-Kazanian faunas described from adjacent Boreal (Arctic) regions, and are significantly different from Tethys (equatorial) faunas.

1 INTRODUCTION - GEOLOGICAL SETTING

The Svalbard Archipelago comprises all islands in the area 74° to 81°N and 10° to 35°E, situated at the northwestern part of the Barents Shelf (Fig. 1). The middle to upper Permian succession here comprises the Tempelfjorden Group totalling some 380 m thickness in the area covered by the present study.

Figure 1. Map of the Arctic with localities mentioned in the text.
Spitsbergen is the largest island, and Bjornoya lies on a southerly continuation of the Sorkapp-Homsund High on the western margins of the Svalbard platform. Thicker and more contiguous Permian sequences occur in a series of basins lying between the Svalbard platform and northern Norway. The lithological descriptions and interpretations below are in part based on Worsley et al. (1986), Stemmerik (1997), Dallmann (1999) and Worsley et al. (2002).

Thickness and facies patterns of Permian sequences on Svalbard are related to a series of NNW-SSE trending lineaments which were active as a result of tensional stress in the Carboniferous. A relatively stable platform developed throughout Svalbard during the Permian, while intracratonic rift systems developed to the west forming the Zechstein seaway. A marked change in both litho- and biofacies types occurs at the base of the Tempelfjorden Group. The fossils in the investigated sections are typical middle to late Permian cold water forms - sponges, brachiopods, echinoderms and bryozoans. Corals and trilobites are rare, ammonoids are extremely rare and other temperate to warm-water forms, such as fusulinid foraminifers are absent. Carbonates throughout the underlying Gipsdalen Group contain biotic associations with chlorozoan or warm water affinities, including fusulinids and abundant algae (Stemmerik 1997). All observations suggest a climatic shift around the boundary between the Gipsdalen and Tempelfjorden groups (Fig. 2) - this reflects both northwards plate movement and changing palaeogeographic regimes and change in oceanic current systems related to rifting and development of the Zechstein seaway.

1.1 Stratigraphy

The Tempelfjorden Group contains shales, siltstones and cherts, silicious sandstones and limestones, as well as sandy bioclastic limestones. Throughout Svalbard the Tempelfjorden Group is laterally divided into several formations (see Fig. 2) - bryozoans in the current study have been collected from the Kapp Starostin Formation of Spitsbergen and adjacent smaller islands (mainly Akseloya), and the Miseryfjellet Formation of Bjornoya, see Figure 1.

The Kapp Starostin Formation is 380 m thick in its type section in the Festningen profile of outer Isfjorden (Fig. 3). The formation is here dominated by spiculitic shales, cherts and siltstones, with minor siliceous sandstones and sandy limestone intervals, and is in the sampled localities divided into three members. The basal Voringen Member (up to 20 m thick) is a sandy bioclastic limestone with a rich brachiopod and bryozoan fauna (Nakrem 1995). The middle unit, the Svenskegga Member is composed of alternating shales, siltstones and cherts and siliceous limestones. Rich bryozoan faunas occur in the siliceous limestones whereas mainly delicate forms, especially rhabdomesids and fenestellids are locally abundant in the shales (Nakrem 1994a). The uppermost unit, the Hovtinden Member is shale and siltstone dominated and contains few fossils. It is approximately 50 m thick in the Festningen area. The age of the Voringen Member is late Artinskian to early Kungurian based on conodonts (Szaniawski & Malkowski 1979), non-fusulinid foraminifers in the underlying units (Sosipatrova 1972) and bryozoans (Nakrem 1995). Correlation of the upper part of the formation is problematic, but Nakrem et al. (1992) conclude with a Kazanian age for this part (see also Fig. 2).

The Miseryfjellet Formation consists of 115 m partially silicified biosparites directly overlying Devonian Carboniferous and lower Permian units on Bjornoya (Fig. 2). Basal sandstones and conglomerates also

---

<table>
<thead>
<tr>
<th>(Jamaya)</th>
<th>Southern Spitsbergen</th>
<th>Central-Western Spitsbergen</th>
<th>Nordaustlandet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Voringen</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Svenskegga</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hovtinden</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kapp Starostin Fm.</td>
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</tr>
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<td>Miseryfjellet Formation</td>
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</tr>
<tr>
<td>Gipshuken Fm. (Gipsdalen Grp.)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 2. Stratigraphic division of the middle Permian units of Svalbard.
Spiculitic shales and cherts form the single most abundant lithofacies of the Kapp Starostin Formation at Festningen (Flellem 1981) and Akseloya (Fredriksen 1988, Henriksen 1988) where most bryozoans discussed in the present study derive from. Abundant trace fossils, such as Zoophycos and Chondrites, clearly indicate low energy, but oxygenated bottom environments well below normal wave base. Bryozoans and other fossils, especially brachiopods, are occasionally present as coquinal lags within this facies type, and they may represent periodic storm reworking. Sponges, usually of the genus Haplistion, are abundant in these beds, some sponges are encrusted by trepostomids, bryozoans like Neoeridotrypella preserved in position, and are thus believed to be fossilized in situ. In some cases, colonial sponges form moundlike buildups with encrusting bryozoans.

Typical bryozoans in the spiculitic shales and cherts comprise delicate colonies of Ramipora hochstetteri Toula, 1875; Permoholecmera merum Ozhgibesov, 1983; Primorellapolita Romanchuk & Kiseleva, 1968; Clausotrypa spinosa Fritz, 1932; delicate fenestellids (Rectifenestella pseudoretiformis (Morozova, 1970); R. compacta Morozova, 1986; Fabifenestella compléta (Nikiforova, 1936); Altemifenestella greenharbourensis (Nikiforova, 1936); A. spitzbergenensis (Nikiforova, 1936); Lyrocladia vera Morozova, 1986); and finely branched trepostomids like Dyscritella spingera (Bassler, 1929). Laterally persistent beds of silicious limestones occur repeatedly throughout the Kapp Starostin Formation. These beds predominantly consist of interbedded packstones and shales, and their boundaries are gradual from spiculitic cherts. These limestone beds were formed on an open marine platform situated below normal wave base, as is indicated by the presence of lime mud and interbedded shales. Grain supported textures in some units may be due to reworking by currents or waves. More massive coquinas dominated by transported bryozoans and less abundant bryozoans are believed to have been formed as platform edge bars above normal wave base, perhaps during periods of lower sea level.

Typical bryozoans in the silicious bioclastic limestones include robust trepostomids like multilamellar Neoeridotrypella sp., Anisotrypella sp., Tabulipora aberrans Morozova, 1986; Tabulipora arcticensis Ross & Ross, 1962; Rhombotritypa insolita Morozova, 1986; Rhombotritypa alfredensis Morozova, 1986; Stenopora timanensis Morozova, 1970; Dyscritella parallela Morozova, 1970; Dyscritella savinaensis Morozova, 1986 and Dyscritella arctica Morozova,
2.2 Miseryfjellet Formation

The Miseryfjellet Formation of Bjornoya shows an atypical development of sandy limestones, silicious limestones and well-sorted sandstones. Both fauna and sedimentary structures suggest shallow, well-agitated depositional environments, probably above normal wave base.

The basal sandstones and conglomerates are usually 1 to 3 m thick, and few thick trepostomids (Tabulipora) have been found in this unit. Faunal elements, including bryozoans are short-distance transported as they show little wear in otherwise rough depositional conditions. Apart from a middle sandstone unit, the remaining part of the formation is dominated by sandy limestones with a prolific brachiopod and bryozoan fauna. Typical bryozoans in the sandy limestones comprise Rhombotrypella alfredensis Morozova, 1986; Tabulipora greenlandensis Ross & Ross, 1962; Tabulipora aberrans Morozova, 1986; Dyscritella bogatensis Morozova, 1970; D. insolita Morozova, 1986; D. lucida Morozova, 1986; D. arctica Morozova, 1986; D. savinaensis Morozova, 1986; Dyscritellina fuglensis Morozova, 1986; Rectifenestella retiformis (Schlotheim, 1816); Septopora syncladiaformis Nikiforova, 1936; Polyoporea optima Morozova, 1986; Kingopora microopora (Stuckenberg, 1895); Timanodictya nikiforovae Morozova, 1966 and Gilmoropora heintzi (Malecki, 1977).

Other species are introduced in the upper part, among them Ramipora hochstetteri Toula, 1875; Stenopora grandis Morozova, 1970; Permoheloclema merum Ozhgibesov, 1983; Rectifenestella cf. gijigensis (Nekhoroshev, 1959); Lyrocladia cf. vera Morozova, 1986; Polypora kossjensis Ravikovich, 1948; Anisotrypella certa Morozova, 1986; Wjatkella assuet Morozova, 1986 and Reteporidra tuncheimensis Morozova, 1986.

It should be noted that Hinganella is so far not recorded from the middle Permian of Svalbard, because Hinganella heintzi Malecki, 1977 was reassigned to Gilmoropora heintzi (Malecki, 1977) in Nakrem (1988). Reference to Malecki’s work (1977) is made both in Morozova & Kruchinina (1986) and in Ross (1995), but Hinganella still remains unknown from Svalbard.

3 BRYOZOAN BIOSTRATIGRAPHY AND PALAEOBIOGEOGRAPHY

The completion of Pangaea during the late Permian saw the formation of several sedimentary provinces and regions. The most conspicuous differences in faunal composition can be seen when comparing northern Boreal faunas with equatorial Tethys faunas. The sea-way between these regions was closed off in Ufimian-Kazanian times, and endemic taxa evolved. Svalbard together with the Canadian Arctic Islands (Sverdrup Basin), North Greenland (Wandel Sea Basin) and Novaya Zemlya (Russia) is part of the Franklinian province, and the faunas are compared with those published from the Cordilleran province (western North America), the Kazanian province (Russia), Timan-Pechora (Russia) and East-Siberian arctic provinces (Mongolia, Russia) (Morozova & Kruchinina 1986, Gilmour & Morozova 1999 and references therein).

Middle to late Permian bryozoans are reported from North Greenland, Wandel Sea Basin in several papers, for example Madsen & Håkansson (1989) and Madsen (1994). Bryozoans in the Station Nord and Ingeborg Formations are only identified to genus level, and the fauna contains Ramipora, Tabulipora, Dyscritella, Fenestella, Penniretepora, Polypora. Ascopora and Clausotrypa. These faunas, except for Ascopora, are very similar to those from the middle Permian of Svalbard.

Novaya Zemlya marks the continuation of the Urals and the Permian lithologies resemble closely those found in Svalbard. The bryozoan faunas are quite similar on a generic level, but many species from Novaya Zemlya are not reported from Svalbard. The youngest Permian deposits (and faunas) of Novaya Zemlya may be younger than those found in Svalbard.

Late Palaeozoic bryozoans from the Canadian Arctic Islands - the Sverdrup Basin, are described in Morozova & Kruchinina (1986), but faunas identified in that work were taken from samples collected for other purposes, and bryozoans were not collected systematically through the units. Bryozoans are common in most of the Permian formations of the Sverdrup Basin, but these require systematic treatment and description. The collections of middle to upper Permian bryozoans published by Morozova & Kruchinina (1986) are, however, clearly similar to the middle Permian faunas from Svalbard.

Middle Permian bryozoans from the Cordilleran province of Nevada, Idaho and Washington (western North America) (Gilmour & Snyder 1986, Gilmour & Walker 1986, Gilmour & Morozova 1999 and references therein) have many taxa in common with the Kazanian province, as well as Svalbard. Stellahezaformis (Gilmour & Snyder, 1986) has been considered as endemic for the Cordilleran province,
but is also found in the middle Permian of Svalbard in the current study.

The Russian Platform and northern Urals (the Kazanian province) (Morozova 1970, Lisitsyn & Morozova 1998) have many genera in common with the Boreal regions. Many taxa first believed to be endemic of this region have later proved to have a distribution through the rest of the Boreal seas and also westwards to the Cordilleran province. The Boreal sea thus was no barrier for fauna migration in middle to late Permian times.

Zechstein deposits with bryozoans are known from Great Britain, Germany and Poland (data compiled in Morozova (1970) with additions in Ernst (2001)). According to palaeogeographic reconstructions the Zechstein seaway provided a connection to the Boreal seas, but the Svalbard faunas are rather different from the more temperate Zechstein faunas.

A database containing 253 taxa, mainly species, extracted from references mentioned above has been used in a simple multivariate statistical analysis of 15 middle to upper Permian stratigraphic units of present day Northern to Arctic areas. Only 67 taxa are present in more than one unit, - this indicates the strong endemism on species level. A cluster analysis using MVSP (Kovach 2002) based on these 67 taxa reveals two distinct clusters (Fig. 3), - one consisting of middle to upper Permian units from Svalbard and Novaya Zemlya and one consisting of Cordilleran and Kazanian units. These two clusters, which also have the richest faunas, also form a cluster separating them from the other units. East Arctic units (Mongolia) with very high degree of endemism are clearly different from these, as is the Zechstein fauna and the Ufimian of Northern Urals.

4 CONCLUSIONS

The distribution of bryozoans in the middle Permian Templefjorden Group of Svalbard may be utilized as biostratigraphical and biogeographical tools. A total of 31 taxa are identified in the Kapp Starostin Formation (Spitsbergen) and 20 in the Miseryjellet Formation (Bjomoya). Some genera and species of Anisotreypella, Neoeridotreypella, Kinopora and Ramipora have distinct stratigraphic and geographic distribution, whereas many others have a more global distribution.

Some genera common in the Lower Permian Gipsdalen Formation of Svalbard (Nakrem 1994b) are absent in the middle Permian units, among them Ascopya and Rhabdomeson. These genera are otherwise well known from middle Permian units elsewhere, especially in the Tethys realm (Ross 1978, Ross & Ross 1990, Gilmour & Morozova 1999). It may be deduced from this that the mentioned genera did not adapt to the shift towards cooler depositional settings in the Boreal sea that Svalbard was part of during middle Permian time.

On a generic level the middle Permian bryozoan fauna of the Tethys Realm was distinctly different from the Boreal faunas, and many Tethyan genera, for example Epiactinotrypa, Ruzhenceviana, Tavayzopora, Dybowskiella, Hayasakapora, and A rax opora have still not been found in the middle Permian Boreal deposits (see also Gilmour & Morozova 1999). More studies need to be done to reveal bryozoan distributions in rather large areas, for example the Canadian Arctic, where bryozoans still are only known from scattered collections.

ACKNOWLEDGEMENTS

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Morphological differentiation in the *Celleporella hyalina* (Linnaeus, 1767) complex (Bryozoa: Cheilostomata) along the Chilean coast

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**ABSTRACT:** *Celleporella hyalina* (L.) is an encrusting bryozoan, which has been reported to have a cosmopolitan distribution and a wide occurrence along the Chilean coast. Such distribution is incongruent with what is known of the species’ larval biology, since *C. hyalina* has a larva with a pelagic stage lasting 1.5—4.0 h, which is likely to facilitate reproductive isolation between populations, leading into speciation, with or without inter-population morphological differentiation. To assess whether the so-called ‘*C. hyalina*’ from five different localities ranging 30° of latitude along the Chilean coast are morphologically homogeneous, in the present study we determined: a) whether morphological differences in the number of pseudopores present in the ovicell and/or in the early astogeny exist in colonies from different localities, and b) the comparative plasticity of pseudopore production in response to experimental environmental conditions, in colonies from two localities in central Chile. Although along the Chilean coast the early astogeny of ‘*C. hyalina*’ conforms to the general pattern described for the species, significant differences among localities were found in both the lateral position of the first zooid budded from the ancestrula and in the angle at which the first two zooids are budded from the ancestrula. Furthermore, the number of pseudopores per unit surface area of the ovicell showed highly significant differences among localities, while the total number of pseudopores per ovicell significantly decreased from the northern to the southern populations. The experimental study with *C. hyalina* from two localities circa 400 km apart (Las Cruces and Ramuntcho) showed that the number of pseudopores in the ovicell is a plastic character modulated by water temperature and dissolved oxygen concentration. As in colonies collected in the natural environment, under experimental laboratory conditions colonies from Las Cruces generated a significantly higher number of pseudopores per ovicell than those from Ramuntcho. In spite of the within-population plasticity in pseudopore number, significant differences remained between colonies from the two populations when exposed to identical environmental conditions in the laboratory. These results, added to the reproductive incompatibility among localities (unpublished results), strongly suggest that cryptic species exist along the Chilean coast under the single name of ‘*Celleporella hyalina*’.

1 INTRODUCTION

Most bryozoans produce lecithotrophic larvae with a short planktonic life. Among marine invertebrates distance of larval dispersal is partially correlated with time spent in the plankton (Crisp 1976), and this in turn may strongly influence geographical range and genetic structure of populations (Crisp 1978, Jackson 1986, Scheltema 1989). *Celleporella hyalina* (Linnaeus, 1767) is an encrusting bryozoan that on the base of morphologic characters has been regarded as a cosmopolitan species (Hayward & Ryland 1979, Moyano 1983, 1986, Cancino 1986, Orellana & Cancino 1991). Such cosmopolitan distribution is incongruent with what is known of the species’ larval biology, since *C. hyalina* has a larva with a pelagic stage lasting 1.5—4.0 h (Cancino & Hughes 1988). Furthermore, spermatozoid dispersal is also limited, since sperm half-life in *C. hyalina* does not exceed 2 hours after liberation (Manriquez 2000, Manriquez et al. 2001). This is likely to facilitate reproductive isolation between populations, leading to speciation, with or without inter-population morphological differentiation.
Cosmopolitan species that produce larvae with a short planktonic life and which are identified only on morphological characters (morphospecies), are likely to represent a suit of cryptic species, especially when variation of the characters used for taxonomic classification is unknown. As a morphospecies, *C. hyalina* can be identified from its schizoporelloid ancestrula, its unilateral budding pattern, its spiral early astogeny, and its small adventitious male and female zooids (Moyano 1986, Cancino & Hughes 1988, Cáceres & Moyano 1992).

Variation on one or more of these morphological characters, however, can be detected along the Chilean coast, both within local populations and along geographical gradients. Analysis of scanning electron micrographs of this species (Moyano 1986) shows that the number of pseudopores per ovicell varies along the Chilean coast, increasing from the Magellanic area towards central and northern Chile. The ovicell functions as an incubation chamber and its pseudopores have been thought to facilitate gaseous exchange for the developing larva. Water temperature is a major environmental gradient along the Chilean coast, with lower temperature characterising the Magellanic region. Since both lower metabolic rate in poikilotherms and higher gas solubility in seawater correlate with lower temperature, the lower number of pseudopores in southern Chilean populations of *C. hyalina* can be explained as the expression of a morphological character controlled by larval oxygen requirements. A higher number of pseudopores would be required for the northern populations given likely higher metabolic rates and lower oxygen solubility at higher water temperatures. It is unknown, however, whether such difference in the number of pseudopores is due to physiological plasticity in response to oxygen requirements or due to genetically fixed morphological differences facilitated by a low genetic flux among such populations.

The objective of the present study was to compare morphological attributes of *C. hyalina* from different populations along the Chilean coast. The number of pseudopores in the ovicell and early astogeny of the colonies was studied in natural populations in order to determine if the previously observed differences in pseudopore numbers (Moyano 1986) are statistically significant along the Chilean shore. To establish if the number of pseudopores in the ovicell is a morphological character modulated by environmental variables such as temperature and/or dissolved oxygen concentrations the number of pseudopores formed in the ovicells was studied under laboratory conditions.

2 MATERIALS AND METHODS

Reproductive colonies of *C. hyalina* from 5 localities along the Chilean coast were collected (Antofagasta 23°39'S; 70°25'W; Coquimbo 29°57'S; 71°22'W; Las Cruces 33°31'S; 71°38'W; Ramuntcho 36°44'S; 73°11'W and Punta Arenas 52°56'S; 71°12'W).

2.1 Number of pseudopores per ovicell in natural populations along the Chilean coast

The number of pseudopores per ovicell was measured from the parental colonies obtained at each locality. At least a 100 ovicells per locality were observed under the stereomicroscope at a 100 X magnification and the total number of pseudopores per ovicell was counted. A one-way Analysis of Variance (ANOVA) was used to determine if pseudopore number differed significantly among localities. To determine if pseudopore number was correlated with ovicell size, the surface area of the ovicell was measured and the respective number of pseudopore counted for four populations (Antofagasta, Las Cruces, Ramuntcho and Punta Arenas). Ovicell surface was determined by regarding the ovicell as a hemisphere whose size was determined as the average of two diameters, one taken from the aperture to the distal edge of the ovicell and the other at right angles to the previous one.

2.2 Early astogeny in *C. hyalina* from different populations along the Chilean coast

The side, at which the first zooid is budded from the ancestrula, either right or left in the unilateral budding pattern, was determined in small colonies from the 5 localities studied and differences in frequencies among localities were tested by x² goodness-of-fit (Cancino & Hughes 1988). The absolute value of the angle at which the two first zooids are budded from the ancestrula was also determined (Fig. 1).

For testing if the budding angle differs between populations, the Watson’s F test for circular means was used for each angle measured, applying Bonferroni correction for multiple comparisons, which in this case reduced the critical value a to 0.005 (Sokal & Rohlf 1995, Zar 1996).

2.3 Number of pseudopores per ovicell in response to experimental conditions of temperature and dissolved oxygen concentration

Four colonies from Ramuntcho and 4 from Las Cruces were cloned following the method used for Manriquez (2000). A clonemate was assigned to each of the four treatments generated by combining two experimental water temperatures (9°C and 15°C) with two oxygen concentrations (normoxia 100% and hypoxia 50% of oxygen saturation). The number of pseudopores was counted, as above, in ovicells generated under the experimental conditions. In order to induce the formation of ovicells, focal ramets were reared in the presence of ramets from another clone.
Figure 1. Schematic representation of a colony of *Celleporella hyalina* with 2 zooids budded from the ancestrula, following the unilateral budding pattern. Three angles were measured as indicated: A-B = angle formed between the distal-proximal axis of the ancestrula with the respective axis of the first zooid (hereafter angle at which the first zooid is budded from the ancestrula). B-C = angle formed between the distal-proximal axes of the first and second zooid to be budded (hereafter angle between the first two zooids), and A-C = angle formed between the distal-proximal axis of the ancestrula with the respective axis of the second zooid (hereafter angle at which the second zooid is budded from the ancestrula). Data were registered as absolute value of the angle, regardless of the left or right position of the zooids with respect to the ancestrula.

but from the same population (Manriquez 2000). A two-way ANOVA was used to determine if significant differences among the combined treatments of oxygen concentration and seawater temperature existed for each locality. A one-way ANOVA was used to determine if significant differences between localities existed for each combined condition of oxygen concentration and seawater temperature.

3 RESULTS

3.1 Ovicell surface and number of pseudopores per ovicell in natural conditions

Mean surface area of the ovicell varied between 57.73 X10^3 pm², for Antofagasta and 51.59 X10^3 pm² for Las Cruces. Locality was a significant main effect (ANOVA: F(3, 116) = 4.60; p < 0.005), but the a posteriori Tukey test for paired comparisons revealed significant differences in mean ovicell area only for Antofagasta - Las Cruces (p = 0.007) and Antofagasta - Punta Arenas (p = 0.018). There was no significant correlation (R = 0.69; p = 0.31) between surface area of the ovicell and latitude of the localities (Fig. 2A).

The number of pseudopores per unit of surface area (pm²) of the ovicell showed highly significant differences among localities (ANOVA: F(4, 548) = 73.34; p < 0.0001). The a posteriori Tukey test confirmed the existence of significant differences (p < 0.05) for all paired combinations, with Antofagasta - Las Cruces being the only pairwise comparison with marginal values of significance (p = 0.053). The number of pseudopores per unit area of ovicell was negatively correlated with latitude (R = 0.95; p = 0.046) (Fig. 2B).

In agreement with the above results, number of pseudopores per ovicell showed clinal variation along the Chilean shore, decreasing from north to south (Fig. 3), with significant differences between all 5 localities (ANOVA: F(4, 548) = 570.60; p < 0.0001; a posteriori Tukey test: p < 0.005 for all paired comparisons).

3.2 Early astogeny

The early astogeny of *C. hyalina* from Chile agrees in general with that of *C. hyalina* from Britain (Cancino & Hughes 1988). In four out of the five localities studied the first zooid of the unilateral budding pattern was generated in similar proportions towards the right or left side of the ancestrula (x² p > 0.05; Table 1). In Coquimbo, however, left-sided budding was significantly more frequent that right-sided (y² = 4.9; 1 df; p < 0.026).
Figure 3. Frequency distribution of the number of pseudopores in ovicells of *Celleporella hyalina* from natural populations from Antofagasta (A), Coquimbo (B), Las Cruces (C), Ramuntcho (D) and Punta Arenas (E). The average (x), standard deviation (S.D.) and number of observations are given for each locality.

Table 1. Early astogeny in *Celleporella hyalina* (L.) from 5 localities along the Chilean coast. The numbers represent the frequencies of the different positions of the first zooid relative to the ancestrula.

<table>
<thead>
<tr>
<th></th>
<th>Unilateral</th>
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<td>Right</td>
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<td>35</td>
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<td>76</td>
<td>4</td>
<td>2</td>
<td>171</td>
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</tbody>
</table>

The angle at which the first zooid was budded from the ancestrula, pooling left-sided and right-sided budding, showed significant differences between Punta Arenas and all the other localities (<p < 0.005), with the exception of Antofagasta (Table 2). Similarly, significant differences were observed, mainly between Punta Arenas and the other localities and between Coquimbo and the other populations, regarding (a) the angle between the first and the second zooid, and (b) the angle at which the second zooid was budded from the ancestrula (Table 2).

3.3 Number of pseudopores per ovicell in response to experimental conditions of temperature and dissolved oxygen concentration

The average number of pseudopores per ovicell, obtained in the laboratory, varied according to treatment (Fig. 4). Two-way ANOVA for colonies from Las Cruces showed that both temperature and dissolved oxygen concentration had significant effects on pseudopore number (F(i, 760) = 433.51, p < 0.0001 and F(i, 760) = 62.09, p < 0.001, respectively). There was also a significant temperature - oxygen interaction, (F(i, 760) = 10.79, p < 0.01). Two-way ANOVA on the number of pseudopores per ovicell of experimental colonies from Ramuntcho showed significant effects of temperature but not of dissolved oxygen concentration (F(i, 891) = 251.60, p < 0.0001 and F(i, 891) = 1.47, p = 0.22, respectively). A significant temperature - oxygen interaction was also detected (F(i, 891) = 168.58, p < 0.0001).

Pairwise comparison revealed significant differences in the number of pseudopores per ovicell between colonies from Ramuntcho and Las Cruces in all four treatments (one-way ANOVA: 15°C - 100% 0₂: F(12,382) = 23.6, p < 0.0001; 15°C - 50% 0₂: F(12,345) = 9.22, p < 0.01; 9°C - 100% 0₂: F(12,382) = 116.18, p < 0.0001; 9°C - 50% 0₂: F(12,474) = 14.19, p < 0.001) (Fig. 4). This is a highly significant result, demonstrating that each population shows a characteristically restricted range of variation in pseudopore number in response to variation in water temperature and oxygen concentration.

4 DISCUSSION

The natural populations of *Celleporella hyalina* (L.) from along the Chilean coast showed significant morphological differences in (a) the early pattern of astogeny, (b) ovicell surface area and number of pseudopores. The significance of these findings is discussed below.

4.1 Early astogeny

Early astogeny in colonies of all the studied populations agrees with the general pattern known for
Table 2. Budding angles in early astogeny of *C. hyalina*: Probability values (p) of the Watson’s F test for circular means, followed by Bonferroni correction (α = 0.005), in pairwise comparisons of Antofagasta (ANT), Coquimbo (COQ), Las Cruces (L C), Ramuntcho (RAM) and Punta Arenas (PA). The values compared are angle at which the first zooid is budded from the ancestrula (ANC-1st), angle between the first and the second zooid budded from the ancestrula (lst-2nd), and angle at which the second zooid if budded from the ancestrula (ANC-2nd).

<table>
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<th>ANC-1st</th>
<th>1st-2nd</th>
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<td>58</td>
<td>10.63</td>
<td>&lt;0.0001</td>
<td>24.13</td>
</tr>
</tbody>
</table>

Figure 4. Average number of pseudopores per ovicell in colonies of *Celleporella hyalina* reared under four experimental treatments in the laboratory (9°C and 15°C, combined with two dissolved oxygen concentrations, 50% and 100% saturation). The colonies originated from Ramuntcho (A, B) and Las Cruces (C and D). Data are means (Circles), standard errors (Boxes) and standard deviations (Lines). N = 3 colonies per treatment and 7-100 ovicells observed per colony.

*C. hyalina* in British waters (Cancino & Hughes 1988). Significant differences, however, exist between some of the studied populations regarding both the position and the angle at which the first zooid is budded from the ancestrula. In colonies from Coquimbo the first zooid was budded preferentially towards the left side of the ancestrula, while in the other populations there were no significant differences in the frequency of budding towards left or right side of the ancestrula. In Ramuntcho the simultaneous bilateral budding and the distomedial budding of a single zooid were respectively between twelve and four times more frequent than in the British population of *C. hyalina* (Cancino & Hughes 1988). Neither of these two budding patterns was found in any other of the Chilean populations.

Differences in the angle at which the first two zooids are budded from the ancestrula provide further evidence of morphological differentiation between populations of *C. hyalina* along the Chilean coast, with Coquimbo and Punta Arenas showing the largest discrepancy from other populations.

The budding pattern in early astogeny has generally been regarded as a character of high taxonomic value for the genera and species of Hippothoidae (Moyano 1986). Our results showed that the early pattern of budding differs significantly among populations along the Chilean shore and from that described as typical for *C. hyalina* (Cancino & Hughes 1988, Cáceres & Moyano 1992), suggesting that several species could be included under the name of *Celleporella hyalina*.

4.2 Ovicell surface area and number of pseudopores

Ovicell surface area varied between localities, but was not significantly correlated with latitude. In contrast, the number of pseudopores per ovicell was negatively correlated with latitude, confirming the reports by Moyano (1986) that pseudopore number decreases towards southern, hence cooler and more oxygenated waters. According to our results, this pattern is partly
the result of a plastic phenotypic response to temperature and dissolved oxygen concentration and partly due to genetically determined character variation underpinning morphological differentiation of populations along the Chilean Coast.

Our experimental study of *C. hyalina* from both Las Cruces and Ramuntcho showed that the number of pseudopores in the ovicell is a plastic character modulated by water temperature and dissolved oxygen concentration. Phenotypic plasticity, however, differed between localities since the colonies from Las Cruces showed significant effects of Temperature and dissolved Oxygen concentration, as well as a significant Temperature-Oxygen interaction; while for Ramuntcho only the Temperature and Temperature-Oxygen interaction had a significant effect. Moreover, in all four treatments the colonies from Las Cruces and Ramuntcho showed significant differences in pseudopore number. As with material collected from the natural environment, colonies from Las Cruces reared under experimental conditions displayed more pseudopores per ovicell than those from Ramuntcho. This is a highly relevant result since in spite of the within-population plasticity in ovicell pseudopore number, significant differences remain between the colonies of the two populations when exposed to identical environmental conditions. Such phenotypic differences between this two localities circa 400 km apart are likely to be the result of the process of local adaptation, generated through reproductive isolation enhanced by the low larval dispersion associated with the short larval pelagic stage of *C. hyalina*. (Cancino & Hughes 1988, Ramirez & Cancino 1991). It is well known that low larval dispersion and/or geographic isolation restrict genetic flux between populations, affecting their genetic structure (Goldson et al. 2001).

4.3 *Is there a ‘C. hyalina’ complex along the Chilean coast or a single species?*

The results of the present study provide evidence of phenotypic differentiation along the Chilean coast, suggesting that we could be dealing with a cryptic species complex. Moreover, unpublished results of mating trials have shown reproductive incompatibility between colonies from Antofagasta, Las Cruces, and Ramuntcho, confirming that such populations represent different biological species and rendering the reported "cosmopolitan" distribution of *C. hyalina* (Hayward & Ryland 1979, Moyano 1983, Ramirez & Cancino 1991) as still more unlikely. Further studies are required to determine and describe the members of this species complex, for in doing so the underestimation of the species diversity in a given locality would be avoided, which is of great importance for both the marine diversity debate (May 1994) and the management of coastal marine ecosystems (Underwood & Fairweather 1989).

5 **CONCLUSIONS**

The study of both the early astogeny pattern and the number of pseudopores in the ovicell of *Celleporella hyalina* provide evidences of phenotypic differentiation between populations along the Chilean coast.

The experimental study showed that the number of pseudopores in the ovicell is a plastic character modulated by water temperature and dissolved oxygen concentration. However, in spite of the within population plasticity in ovicell pseudopore number, significant differences remained between colonies of two populations from central Chile, even when exposed to identical environmental conditions.

Our results strongly suggest that along the Chilean coast a cryptic species complex under the name of ‘*Celleporella hyalina*’ exist.

**ACKNOWLEDGEMENTS**

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**REFERENCES**


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Submarine freshwater springs in the Adriatic Sea: a unique habitat for the bryozoan Pentapora fascialis

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ABSTRACT: Large colonies of the bryozoan Pentapora fascialis (Pallas, 1766) growing inside the plume of submarine freshwater springs (vruljas) have been surveyed. In the Velebit Channel, P. fascialis grows only under the influence of a vrulja’s outflow, at depths from 1 m to 35 m. We have investigated the water chemical composition and temperature of each vrulja’s plume. The amount of nutrients, carbonates, and temperature of the vruljas’ plumes were measured during three different seasons in 2002 and 2003. All measured nutrients had considerably higher concentrations inside the vruljas than in the seawater (9.185 ± 7.111 mmol/m³ NO³ in vruljas and 1.109 ± 0.949 mmol/m³ NO³ in the seawater; 7.911 ± 8.316 mmol/m³ SiO₄ in vruljas and 1.643 ± 1.330 mmol/m³ SiO₄ in the seawater; 1.757 ± 1.496 mmol/m³ NH₄ in vruljas and 1.141 ± 1.299 mmol/m³ NH₄ in the seawater; 0.116 ± 0.119 mmol/m³ NO² in vruljas and 0.105 ± 0.106 mmol/m³ NO² in the seawater and 0.044 ± 0.034 mmol/l dissolved C0₂ in vruljas and 0.017 ± 0.012 mmol/l dissolved C0₂ in the seawater), while C0³ had lower values inside vruljas’ plumes than in the seawater (0.098 ± 0.075 mmol/l C0³ in vruljas and 0.202 ± 0.081 mmol/l C0³ in the seawater). The temperature of the vruljas’ outflow was low and constant throughout the year and varied between 9.76 and 14.02°C, while the seawater temperature at 23 m varied between 8.22 and 23.52°C. The period of vruljas’ inactivity was only 5.6 days per year which means that Pentapora fascialis must be permanently adapted to grow in the conditions of fluctuating, lower salinity.

1 INTRODUCTION

Submarine freshwater springs or vruljas are karst phenomena developed by geomorphological processes under the influence of recent sea-level changes (Fritz 1992). They are rather common features along the eastern Adriatic Sea coast and the most remarkable ones are located in the areas where intensively Karstified mountain ranges (Mt Velebit, Mt Biokovo) rise directly from the sea, canalising groundwater from the hinterland (Suric 2002). The total number of vruljas in the Adriatic Sea is unknown (Kuhta & Novosel 2000). Pentapora fascialis (Pallas, 1766) is the largest and most conspicuous calcified bryozoan in the Adriatic Sea. In the vicinity of Rovinj in the northern Adriatic Sea, P. fascialis was found growing on rock walls and more commonly on cobbles or on gorgonian stalks (Hayward & McKinney 2002). The colonies are attached to the substratum by means of an encrusting base. From this they grow upwards in bilaminar sheets, which from time to time fuse. The sheets are composed of two layers of large zooids, which are quincunically arranged. Adult colonies may be a dominant and important part of the sessile benthos and colony size may be substantial (Hayward & Ryland, 1999). Stirn et al. (1969) mentioned P. fascialis as a euryhaline species. They reported the presence of large colonies in the vicinity of vruljas in the Velebit Channel, growing...
almost year-round in salinities ranging from 8 to 20 PSU, in a particular facies of coralligenous biocoenosis where submarine freshwater springs causes strong bottom currents and low sedimentation rate. Within this facies, *P. fascialis* provides a substratum for numerous encrusting and mobile species.

But why does *P. fascialis* grow only in the vicinity of vruljas along the surveyed coast of the Velebit Channel? Here we investigate vruljas’ activity as well as vruljas’ and seawater temperature, nutrients and carbonates in conjunction with distribution of *P. fascialis*.

2 STUDY SITE AND METHODS

*Pentapora fascialis* colonies were observed *in situ* by SCUBA diving along the coast of the Velebit Channel, in the North Adriatic Sea (Fig. 1). Numerous vruljas were present along the surveyed coast, some with large colonies of *P. fascialis* growing only within reach of the freshwater plume. Surveys were made between 1995 and 2004 along the north Velebit Channel coast (from Sv. Juraj town to Lukovo Otočko in more than 50 dives) and along the coast of the nearby Prvic Island (Rt Silo, Rt Samonjin and Rt Strazica during 20 dives). However, large colonies of *P. fascialis* were observed at only four locations: Grmac, Zdralova, Zmovnica and Kola coves (Fig. 1). Vruljas with *P. fascialis* colonies were found between 1 m and 35 m depth, on rocky bottom or sandy bottom mixed with rocks and boulders.

Kola cove is in the town of Sv. Juraj and is characterized by mixed rock and sediment bottom down to 20 m depth. Zmovnica cove is 2 km south of Sv. Juraj with a sandy floor. Only one pier, built in the center of Zmovnica, and the bottom in the vicinity of pier is

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**Figure 1.** Map of the northern part of the Adriatic Sea with a detailed map of the study locations. 1 - Kola; 2 - Zmovnica; 3 - Zdralova; 4 - Grmac.
hard rocky substrate. In contrast, Zdralova and Grmac, located 4.5 and 5 km south of Sv. Juraj, are mainly hard bottom coves to about 20 m depth, while the sediment bottom appeared deeper.

From each location one small *P. fascialis* colony (about 20 cm in diameter) was sampled as well as subsamples of five bigger colonies in order to determine the epibiotic bryozoan fauna. At each location the outlet of vruljas found in the rocky fractures was sampled for other bryozoan species in addition to *P. fascialis*.

Vruljas water were sampled *in situ* with 51 Nansen bottles. Outflow of the vruljas was tested for carbonates (total CO$_2$, HC$_3$O$_3^-$, CO$_2^{\text{aq}}$ and dissolved CO$_2$) in March, June and November 2003, and for nutrients (nitrate, nitrite, phosphate, ammonia and silicate) in July 2002 and March, June and November 2003. Chemical parameters were analyzed by standard oceanographic methods (Strickland & Parsons 1972, Ivanicic & Degobbis 1984).

In Grmac, one-year temperature conditions of three vruljas outflow in the sediment bottom were surveyed using three small Stow Away TidbiT temperature loggers. Three loggers were fixed 50 cm deep in each vrulja’s outlet with a stainless steel-wedge, while one referential logger was fixed on rock 20 m away from the nearest vrulja and 1 m above the sea bottom. Data were measured from 27th May 2002 to 21st May 2003, with ±0.2°C accuracy, and a 16-minute sampling interval. The surveyed vruljas were located at 22, 23 and 24 m depth, while the referential logger was placed in ‘normal’ seawater at 23 m depth. The logger fixed in the first vrulja at 22 m depth could not be found at the end of the study.

3 RESULTS

3.1 Temperature

The temperature of seawater at 23 m depth varied between 8.22°C and 23.52°C during the one-year period (Fig. 2). At the same depth and in the same period, the temperature of vrulja 1 outflow varied between 9.76°C and 11.16°C and of vrulja 2 at 24 m between 10.00°C and 14.02°C (Fig. 2). The largest temperature oscillations of the seawater was recorded in 12-13 September 2002 when temperature jumped from 16.64°C to 22°C in less than 10 hours. In contrast, the temperature of the vrulja’s outflow was steady throughout the year which indicates constant activity of the vruljas except for short intermittent periods between 24th February 2003 and 25th March 2003 (Fig. 3). During that period of inactivity the temperature recorded by the vruljas’ outflow loggers was equal to the seawater temperature. Altogether both surveyed vruljas were inactive only 96, 9 hours, while vrulja 1 was inactive for 36 more hours.

![Figure 2. One-year temperature time series of seawater and vruljas outflow recorded in Grmac at 23 m depth from 27/5/2002 to 21/5/2003.](image-url)
3.2 Vruljas’ outflow composition

The nutrients and carbonates within the vruljas’ outflow were measured in spring, summer and winter conditions (Tables 1, 2). All measured nutrients (nitrate, silicate, ammonia, nitrite and phosphate) had considerably higher concentrations inside the vruljas than in the seawater, especially nitrate, silicate and ammonia: $9.185 \pm 7.111 \text{ mmol/m}^3$ NO$_3$ in vruljas and $1.109 \pm 0.949 \text{ mmol/m}^3$ NOT in the seawater; $7.911 \pm 8.316 \text{ mmol/m}^3$ SiO$_4$ in vruljas and $1.643 \pm 1.330 \text{ mmol/m}^3$ SiO$_4$ in the seawater; $1.757 \pm 1.496 \text{ mmol/m}^3$ NH$_4^+$ in vruljas and $1.141 \pm 1.299 \text{ mmol/m}^3$ NH$_4^+$ in the seawater; $0.116 \pm 0.119 \text{ mmol/m}^3$ NO$_3$ in vruljas and

Table 1. Nutrient measurements of the seawater (at 3 m depth) and three vruljas outflow placed in Grmac at 23 m (Vrulja 1), 21 m (Vrulja 2) and 19 m (Vrulja 3) of depth in July 2002 and March, June and November 2003.

<table>
<thead>
<tr>
<th>Period</th>
<th>Locality</th>
<th>NO$_3^-$ (mmol/m$^3$)</th>
<th>SiO$_4$ (mmol/m$^3$)</th>
<th>NH$_4^+$ (mmol/m$^3$)</th>
<th>NO$_2^-$ (mmol/m$^3$)</th>
<th>PO$_4^{3-}$ (mmol/m$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>July 2002</td>
<td>Vrulja 1</td>
<td>3.424</td>
<td>2.195</td>
<td>0.366</td>
<td>0.050</td>
<td>0.036</td>
</tr>
<tr>
<td></td>
<td>Vrulja 2</td>
<td>5.164</td>
<td>3.720</td>
<td>0.527</td>
<td>0.046</td>
<td>0.056</td>
</tr>
<tr>
<td></td>
<td>Vrulja 3</td>
<td>1.943</td>
<td>0.917</td>
<td>0.322</td>
<td>0.029</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Seawater</td>
<td>0.201</td>
<td>0.103</td>
<td>0.347</td>
<td>0.046</td>
<td>0.015</td>
</tr>
<tr>
<td>March 2003</td>
<td>Vrulja 1</td>
<td>14.786</td>
<td>5.370</td>
<td>1.469</td>
<td>0.314</td>
<td>0.699</td>
</tr>
<tr>
<td></td>
<td>Vrulja 2</td>
<td>8.533</td>
<td>3.504</td>
<td>3.366</td>
<td>0.313</td>
<td>0.043</td>
</tr>
<tr>
<td></td>
<td>Vrulja 3</td>
<td>4.980</td>
<td>3.180</td>
<td>0.725</td>
<td>0.307</td>
<td>0.078</td>
</tr>
<tr>
<td></td>
<td>Seawater</td>
<td>1.005</td>
<td>3.098</td>
<td>0.319</td>
<td>0.253</td>
<td>0.043</td>
</tr>
<tr>
<td>June 2003</td>
<td>Vrulja 1</td>
<td>5.974</td>
<td>22.522</td>
<td>0.818</td>
<td>0.027</td>
<td>0.055</td>
</tr>
<tr>
<td></td>
<td>Vrulja 2</td>
<td>5.911</td>
<td>22.612</td>
<td>0.784</td>
<td>0.059</td>
<td>0.057</td>
</tr>
<tr>
<td></td>
<td>Vrulja 3</td>
<td>5.911</td>
<td>19.314</td>
<td>1.167</td>
<td>0.025</td>
<td>0.039</td>
</tr>
<tr>
<td></td>
<td>Seawater</td>
<td>0.791</td>
<td>2.325</td>
<td>0.842</td>
<td>0.013</td>
<td>0.025</td>
</tr>
<tr>
<td>November 2003</td>
<td>Vrulja 1</td>
<td>25.993</td>
<td>5.281</td>
<td>4.012</td>
<td>0.062</td>
<td>0.055</td>
</tr>
<tr>
<td></td>
<td>Vrulja 2</td>
<td>18.707</td>
<td>4.026</td>
<td>3.602</td>
<td>0.088</td>
<td>0.072</td>
</tr>
<tr>
<td></td>
<td>Vrulja 3</td>
<td>8.894</td>
<td>2.294</td>
<td>3.929</td>
<td>0.078</td>
<td>0.026</td>
</tr>
<tr>
<td></td>
<td>Seawater</td>
<td>2.437</td>
<td>1.048</td>
<td>3.057</td>
<td>0.109</td>
<td>0.016</td>
</tr>
</tbody>
</table>

Table 2. Carbonate measurements of the seawater (at 3 m depth) and three vruljas outflow placed in Grmac at 23 m (Vrulja 1), 21 m (Vrulja 2) and 19 m (Vrulja 3) of depth in March, June and November 2003.

<table>
<thead>
<tr>
<th>Period</th>
<th>Locality</th>
<th>Salinity (PSU)</th>
<th>Temp. (&lt;°C)</th>
<th>PH</th>
<th>Total C$_0$ (mmol/l)</th>
<th>HCO$_3$ (mmol/l)</th>
<th>CO$_2^{2-}$ (mmol/l)</th>
<th>Dissolved CO$_2$ (mmol/l)</th>
<th>Total alkalinity</th>
<th>Carbonate alkalinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>March 2003</td>
<td>Vrulja 1</td>
<td>27.95</td>
<td>10.0</td>
<td>7.87</td>
<td>2.73</td>
<td>2.585</td>
<td>0.086</td>
<td>0.040</td>
<td>2.79</td>
<td>2.76</td>
</tr>
<tr>
<td></td>
<td>Vrulja 2</td>
<td>31.26</td>
<td>10.5</td>
<td>8.14</td>
<td>2.38</td>
<td>2.076</td>
<td>0.215</td>
<td>0.021</td>
<td>2.57</td>
<td>2.51</td>
</tr>
<tr>
<td></td>
<td>Vrulja 3</td>
<td>35.25</td>
<td>10.5</td>
<td>8.17</td>
<td>2.04</td>
<td>1.735</td>
<td>0.218</td>
<td>0.013</td>
<td>2.25</td>
<td>2.17</td>
</tr>
<tr>
<td></td>
<td>Seawater</td>
<td>37.61</td>
<td>11.5</td>
<td>8.29</td>
<td>1.81</td>
<td>1.443</td>
<td>0.273</td>
<td>0.008</td>
<td>2.10</td>
<td>1.99</td>
</tr>
<tr>
<td>June 2003</td>
<td>Vrulja 1</td>
<td>25.00</td>
<td>11.5</td>
<td>7.57</td>
<td>2.88</td>
<td>2.740</td>
<td>0.033</td>
<td>0.105</td>
<td>2.83</td>
<td>2.82</td>
</tr>
<tr>
<td></td>
<td>Vrulja 2</td>
<td>26.41</td>
<td>11.0</td>
<td>7.76</td>
<td>3.17</td>
<td>3.010</td>
<td>0.054</td>
<td>0.091</td>
<td>3.16</td>
<td>3.14</td>
</tr>
<tr>
<td></td>
<td>Vrulja 3</td>
<td>27.77</td>
<td>10.5</td>
<td>7.69</td>
<td>2.28</td>
<td>2.190</td>
<td>0.045</td>
<td>0.053</td>
<td>2.30</td>
<td>2.28</td>
</tr>
<tr>
<td></td>
<td>Seawater</td>
<td>37.79</td>
<td>15.0</td>
<td>7.95</td>
<td>2.69</td>
<td>2.540</td>
<td>0.114</td>
<td>0.031</td>
<td>2.83</td>
<td>2.77</td>
</tr>
<tr>
<td>November 2003</td>
<td>Vrulja 1</td>
<td>26.21</td>
<td>10.1</td>
<td>7.96</td>
<td>3.08</td>
<td>2.974</td>
<td>0.115</td>
<td>0.026</td>
<td>3.25</td>
<td>3.20</td>
</tr>
<tr>
<td></td>
<td>Vrulja 2</td>
<td>30.25</td>
<td>10.2</td>
<td>8.00</td>
<td>2.59</td>
<td>2.716</td>
<td>0.013</td>
<td>0.028</td>
<td>1.80</td>
<td>5.74</td>
</tr>
<tr>
<td></td>
<td>Vrulja 3</td>
<td>34.79</td>
<td>10.4</td>
<td>8.02</td>
<td>1.95</td>
<td>1.851</td>
<td>0.101</td>
<td>0.015</td>
<td>2.12</td>
<td>3.20</td>
</tr>
<tr>
<td></td>
<td>Seawater</td>
<td>38.09</td>
<td>12.0</td>
<td>8.05</td>
<td>2.30</td>
<td>2.027</td>
<td>0.220</td>
<td>0.013</td>
<td>2.57</td>
<td>2.47</td>
</tr>
</tbody>
</table>
0.105 ± 0.106 mmol/m^3 NO_3 in the seawater and 0.102 ± 0.189 mmol/m^3 PO_4 in vruljas and 0.025 ± 0.013 mmol/m^3 PO_4 in the seawater (Fig. 4). Measurements showed that there is 10 to 50 times more nitrate in the vruljas’ outflow then in the seawater. Furthermore, the amount of total CO_2, HCO_3 and dissolved CO_2 was higher inside the plume: 2.570 ± 0.436 mmol/l total CO_2 in vruljas and 2.270 ± 0.441 mmol/l total CO_2 in the seawater; 2.431 ± 0.479 mmol/l HCO_3 in vruljas and 2.003 ± 0.549 mmol/l HCO_3 in the seawater and 0.044 ± 0.034 mmol/l dissolved CO_2 in vruljas and 0.017 ± 0.017 mmol/l dissolved CO_2 in the seawater. In contrast, CO_3 had lower values inside vruljas’ plumes than in the seawater: 0.098 ± 0.075 mmol/l CO_3 in vruljas and 0.202 ± 0.081 mmol/l CO_3 in the seawater (Fig. 5).

3.3 Bryozoans and other fauna in plumes of the vruljas

In the surveyed area, along the Velebit Channel coast, Pentapora fascialis colonies were found only on the locations where vruljas were present. In Kola cove numerous colonies were found even at only 1 m depth. There, colonies about 20 cm in diameter were observed on the rocky bottom, growing in visually blurred water coming from the vrulja’s outlet. (Blurring occurs because of continually shifting, light-refracting boundaries between the low-density water from the vrulja and the high-density sea water.) In Zmovnica, Pentapora fascialis colonies were mainly present around the rocky pier, where one colony of 150 cm in diameter was observed as well as numerous smaller colonies. Pentapora fascialis was most abundant in the Zdralova and Grmac localities, growing on rocks and boulders where the vrulja’s opening was about 20-50 cm away and outflow circulated directly through colonies. The mean diameter of six measured colonies in Grmac was 43 cm and the diameter ranged between 15 cm and 70 cm.

Some bryozoan species were found as epibionts on Pentapora fascialis colonies. All were unilaminar species; four were encrusting: Beania magellanica (Busk, 1852), B. mirabilis Johnston, 1840, Diplosolen obelia (Johnston, 1838) and Patinella radiata (Audouin, 1826), and two were small erect species: Aetea truncata (Landsborough, 1852) and Bugula fulva Ryland, 1960. Beside Pentapora fascialis, only four other bryozoan species were found growing on the rocks inside the vrulja outlets. These were mostly multiserial and encrusting species: Schizomavella cornuta (Heller, 1867), Celleporina tubulosa (Hincks, 1880) and Schizobrachiella sanguinea (Norman, 1868) while only one species was small flexible erect: Bugula fulva.

Other sessile colonial organisms recorded growing inside the vruljas’ plumes were the anthozoan Eunicella cavolinii (Koch, 1887) and the serpulid Salmacina dysteri (Huxley, 1855). S. dysteri was always only found growing as an epibiont of Pentapora fascialis. Beside this, a very abundant mobile species often observed inside vruljas outflow was the crinoid Antedon mediterranea (Lamarck, 1816).

4 DISCUSSION

One of the main features of the marine environment where numerous vruljas are present is strong water circulation, providing abundant food for filter-feeding animals as well as low sedimentation rate. But why does Pentapora fascialis grow only inside the vrulja’s outflow, in the conditions of lower salinity? The most probable reasons are injections of nutrient-rich and bicarbonate-rich water. Through numerous underground channels and crevices, ground water brings
high concentration of nutrients into the sea thereby stimulate a higher phytoplankton concentration in the area. Ground water also bring freshwater phytoplankton as well as organic detritus which may serve as food for *P. fascialis*. Furthermore, due to the vruljas’ upward flow, a compensatory seawater flow generates on the bottom, thus enhancing feeding performance of *P. fascialis* colonies (Cocito et al. 2004).

Our research shows that *P. fascialis* must be permanently adapted to live in brackish water since vruljas are inactive for only a few days per year. Furthermore, the period of vrulja inactivity was never constant even for whole 24 hours period (Fig. 3). Although *P. fascialis* was recorded in water depths as shallow as 11 m in the Ligurian Sea (Cocito et al. 1998), our findings of colonies at 1 m depth in Kola cove is, to our knowledge, the shallowest record of this species. Cold vrulja water probably protects these colonies from the high surface temperatures during summer.

Physiologically the importance of temperature to brackish water animals can be explained by its effect on osmoregulation. The permeability of living membranes generally decreases with decreasing temperature (Winston 1977). This factor may explain why *P. fascialis* can survive in brackish water under the influence of vruljas outflow, e.g. low and constant temperature. While osmotic regulation is important, the selective regulation of specific ions or ionic regulation is essential, since protoplasmic integrity cannot be maintained in absence or excess of certain ions. For example, calcium added to low-salinity water that is ordinarily lethal may enable animals to survive (Vemberg 1983). In surveyed vruljas outflow the amount of calcium is high due to the karst limestone source (Romanov et al. 2003). Most of bicarbonate we measured originate from CaC0$_3$. The concentration of dissolved C0$_2$ and the amount of CaC0$_3$, which are important as a building material to *P. fascialis* colonies, were significantly higher inside vruljas’ outflows than in the seawater.

Beside *P. fascialis*, only nine other bryozoan species were found growing inside vrulja outflows. Most of them are widely distributed throughout the Mediterranean Sea and common in coastal waters (Hayward & McKinney 2002). Among bryozoans found in vrulja outflows, Winston (1977) reported *Aetea truncata* and other *Beania* and *Bugula* species to be found in brackish waters. Occhipinti Ambrogi (1981) reported *A. truncata* and *Bugula fulva* from the Adriatic brackish lagoons. All other bryozoan species found in vrulja outflows were not recorded from low and fluctuating salinity localities: *Beania magellanica*, *B. mirabilis*, *Diplosolen obelia* and *Patinella radiata*. *Schizomavella cornuta*, *Celleporina tubulosa* and *Schizobrachiella sanguinea* are for the first time recorded as brackish water species since they were found growing on the rocks inside the very centre of the vrulja outlets. The record of two cyclostomes (*D. obelia* and *P. radiata*) tolerant to fluctuating, lower salinity is unusual since cyclostomes are among least tolerant group to the diluted salinity (Winston 1977).

McKinney & Jackson (1989) studied the relation between bryozoan growth form and salinity. They found the ratio of uniserial to multiserial species to be extremely high in brackish water, while the ratio of encrusting to erect species was lower in brackish water than elsewhere. In vrulja outflows we found two uniserial (*Aetea truncata* and *Beania mirabilis*) and four multiserial species (*Beania magellanica*, *Diplosolen obelia* and *Patinella radiata* with biserial *Bugula fulva* included), while four species were mul­tilaminar (*Schizomavella cornuta*, *Celleporina tubulosa* and *Schizobrachiella sanguinea* with bilaminar *Pentapora fascialis* included). Not only salinity but strong currents influence bryozoan growth form within the vrulja outflows, which is probably the reason why encrusting and flexible erect species prevailed.

Several factors may be analysed as determinant for *P. fascialis* growth inside the vrulja’s outflow, such as nutrient and bicarbonate enrichment, strong and steady water current and salinity. Experiments are needed to better understand the prevailing influence of single environmental factors and to explain interactions among them in relation to the observed growth pattern.

5 CONCLUSIONS

The large colonies of the bryozoan *Pentapora fascialis* were found at four localities along Velebit Channel coast in the north Adriatic Sea, growing only within the reach of the outflow from vruljas (submarine freshwater springs). Two surveyed vruljas were active throughout the year except for 132, 9 hours during February and March 2003. The period of inactivity was never constant for the whole 24 hours period which means that *P. fascialis* must be permanently adapted to grow in the conditions of fluctuating, on average lower salinity. The temperature of the vruljas’ outflow was low and steady, and the outflow provides a strong and steady current throughout the year. The amount of total C0$_2$, dissolved C0$_2$ and bicarbonate is markedly higher in the outflow than in the seawater. The amount of nitrate within the outflow was 10 to 50 times higher then in the seawater. The authors conclude that both high concentration of C0$_2$ and bicarbonate, which are building material for *P. fascialis* and high concentration of nutrients, which stimulate a higher phytoplankton concentration in the area together with strong and steady currents, are the reasons why *P. fascialis* grows only inside vruljas outflow in the surveyed area.
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Ovicell development in the early calloporid Wilbertopora Cheetham, 1954 (Bryozoa: Cheilostomata) from the mid-Cretaceous of the USA

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ABSTRACT: The calloporid Wilbertopora Cheetham, 1954 is the oldest known cheilostome with brood chambers (ovicells). The pattern of initial ovicell formation, involving a single ooecial rudiment, is more reminiscent of ovicell development in some Recent cribrimorphs and other more advanced cheilostomes than it is of Recent calloporids that have a double rudiment. The distribution of early ovicell developmental types among cheilostomes is discussed. During later ovicell growth in Wilbertopora two lateral lobes fuse to form the hemispherical hyperstomial ovicell. This fusion process demonstrates how such ovicells could have originated from a more primitive bispinose precursor.

1 INTRODUCTION

Most cheilostome bryozoans possess prominent brood chambers called hyperstomial ovicells. Each ovicell comprises a hemispherical double-walled fold (ooecium), surrounding the brooding cavity and originating from either the maternal (egg-producing) or its distal daughter zooid. The internal wall is called the entooecium, the external wall the ectooecium, and there is an ooecial lumen between them that is connected with the perigastric coelom of the ovicell-producing zooid through one or more communication pores. The ovicell opening is closed either by the operculum of the zooidal aperture, or by an evagination of the maternal cystid wall called an ooecial (inner) vesicle or ooecial plug (see Ostrovsky 1998, 2002, Ostrovsky & Schäfer 2003 for further details and discussion).

Early stages of ovicell development have been studied in a number of Recent species. The first description of hyperstomial ovicell formation was made by Nitsche (1869) in Bicellariella ciliata (Linnaeus, 1758) (as Bicellaria). Studying non-bleached wet colonies, Nitsche found that each ovicell started its development as two small outgrowths - the future ooecium (‘helmbrömige Blase’) and the inner vesicle (‘rundliche Blase’ or ‘Deckelblase’) on the distal margin of the maternal zooid. His pictures (Nitsche 1869, figs 10-13) were schematically redrawn by Vigelius (1884, p. 50, unnumbered text-fig.), who compared the developmental patterns in sections of prominent ovicells (in Bicellariella) and immersed ovicells (in Terminoflustra membranaceotruncata (Smitt, 1868) (as Flustra membranaceo-truncata)).

Using sections of decalcified specimens of Bugula simplex Hincks, 1886 (identified as B. sabatierei Calvet), Calvet (1900) described early ovicellogenesis as the formation of two hollow vesicles, one of which, being formed from the maternal zooid, was a rudiment of the ooecial vesicle (‘vésicule ovicellienne inférieure’), whereas the second, originating from the daughter zooid, was a rudiment of the ooecium (‘vésicule ovicellienne supérieure’) (1900, p. 132, pi. 2, fig. 14, pi. 3, fig. 5). Calvet suggested that this ovicell type, in which its two parts (ooecium and inner vesicle) belong to different zooids, is the most common among cheilostomes. He thought that Bicellariella ciliata, as studied by Nitsche, was not an exception to this rule, despite the absence of a distal zooid in this species (see Ostrovsky, in press, for details and discussion).

Studying dried specimens, Levinsen (1893, 1894, 1909) figured in detail (but scarcely mentioned in the text) the earliest stages of the formation of the calcified parts of ovicells. According to him, ovicells in different taxa start with the development of either two small distal calcareous plates’ or ‘a continuous plate’, arising from the frontal edge of the distal [transverse zooidal] wall (1909, pp. 60-61). In other
words, he discovered two different patterns of the initial calcification of the future ovicell floor: (1) bilobate, with a double ooeccial rudiment; and (2) non-lobate, with a single ooeccial rudiment. Levinsen found a double ooeccial rudiment in, among other species, the calloporids Callopora dumerilii (Audouin, 1826), C. lineata (Linnaeus, 1767) and Tegel la unicornis (Fleming, 1828), and the cibriomorph Cribrilina punctata (Hassall, 1841). A single rudiment was described, for instance, in the bugulid Dendrobetaia murrayana (Bean in Johnston, 1847).

In contrast with Levinsen (1909), the earliest stage of ovicell development was described by Sifcn (1945, p. 9) in C. dumerilii as 'a flat and narrow prominence from the front part of distant wall [of the mother zoid] ... composed of two separate knobs'. Further research initially did not support this observation. In all cases where the double ooeccial rudiment was described its formation was characterized by a stage of two flat calcified plates, not knobs. However, since subsequent authors worked with skeletal walls only (Harmelin 1973, Nielsen 1985, Gordon 1993), the relationships between calcified and membranous parts of the developing ovicell remained unclear until study of unbleached air and critical-point dried specimens demonstrated that Levinsen was correct (Ostrovy & Schäfer 2003, Ostrovsky et al. 2003).

In the cases discussed above the initial stage of entooecium formation is simply a calcification of the proximal part of the frontal wall of the distal daughter zoid. Thus, the early ooeccial rudiment consists of only one calcified wall, the future ovicell floor. The second wall (ectooecium) appears when the entire ooeccial fold starts to grow up (see Ostrovsky & Schäfer 2003, Ostrovsky et al. 2003). In some cheilostomes even the early ovicell consists of two small disks which are the developing entooecium and ectooecium. For instance, in reteporids Levinsen found that the incipient ooeccium starts to grow 'from a narrow stalk-like proximal part and consists ... of two calcareous layers' [disks] (1909, p. 290). He also illustrated (but, again, did not describe) a similar process in the bugulid Dendrobetaia murrayana (1909, pi. 4, fig. 2a-e). A similar account was given by Waters (1913) who described the development of ovicells in Tryphyllozoon munitum (Hincks, 1878) (as Retepora monilifera var. umbonata MacGillivray), findings later supported by Harmer (1934) in a few more reteporid species (see also Okada 1920 and Buchner 1924). In all of these cases the initial calcification of the ooeccial floor (entooecium) was described as a 'horizontal disk ... with a circular edge' (Harmer 1934, p. 523). Thus, as with some of the cheilostomes described above, the rudiment of the future ooeccial floor has a roundish outline and is single. The incipient ectooecium was described as a 'crescentic horizontal plate' below the ooeccial disk (p. 523). Similar descriptions were later given by Soule (1973) for some Smittiniidae, Cook (1977) for Tremogasterina (Arachnopseidae), and Cook and Chimonides (1981) for some Petraliellidae. Nielsen (1981) described early stages of ovicell development as growth of a single roundish plate above the proximal cryptocyst of the daughter zoid in both Pacificincola insculpta (Hincks, 1882) (as 'Hippodiplosia') and Fennestraula miramara Soule, Soule & Chaney, 1995 (described as F. malusii (Audouin)).

Because ooeccial rudiments are extremely fragile they are poorly preserved in most fossils. To our knowledge no descriptions have been published of the early development of ovicells in extinct cheilostomes, except for a brief note in the paper of Checliam (1975). Therefore, any record of ooeccial development is of interest, especially for early cheilostomes. Well preserved colonies of some mid-Cretaceous calloporids allow us here to present a description of ovicell formation in material belonging to the Wilbertopora mutabilis species complex from the USA. Described as Wilbertopora mutabilis by Cheetham (1954, 1975), these bryozoans clearly represent a group of several species whose taxonomy is currently being revised (Cheetham et al. in review). The aims of the current paper are to (1) describe the early stages of ovicell development in Wilbertopora, and (2) discuss the possible value of this new data in cheilostome taxonomy and phylogeny.

2 MATERIAL AND METHODS

Among several hundreds of Albian and Cenomanian Wilbertopora specimens in the collections of the Natural History Museum, London (NHM), developing ovicells are present in many, among which the most informative specimens are the following, all from the Washita Group: D58502, Cenomanian, Grayson Formation; 150-250 yds (metres) to the east of the spillway of the Lake Waco Dam, McLennan County, Texas, USA; collected by M. Listokin. BZ1352, Grayson Formation; south-east face of Lake Waco Dam, McLennan County, Texas, USA; collected by M. Listokin. D57378, Grayson Formation (Del Rio Shale); behind Lake Waco Dam, McLennan County, Texas, USA; collected by C. Hoadley. BZ1124, Albion, Weno Formation; streamflows 4 miles north of Bokchito, Bryan County, Oklahoma; collected by M. Listokin.

Adult ovicell morphology in these specimens matches published descriptions (Cheetham 1975, Taylor & McKinn 2002) and that observed in a tootype of Wilbertopora mutabilis Cheetham, 1954: NHM D47068, Albion, Washita Group, Fort Worth Limestone, 1.25 miles north-west of Krum, Denton County, Texas.
All the colonies encrust bivalve shells, and were studied in an uncoated state using an environmental SEM (IS1 ABT-55).

3 RESULTS

Development of ovicells takes place close to the growing edge in Wilbertopora colonies. Ovicells always occur in groups, with the least developed ones situated furthest distally (Fig. 1A). Ovicellogenesis starts in the developing autozooid, avicularium or, incidentally, kenozooid, a long time before the completion of its skeleton.

The first sign of ovicell formation is a calcification of the proximal most part of the frontal wall of the distal zooid. Calcification starts from the transverse zooidal wall and expands distally, taking the form of a single flat plate with a rounded edge (Fig. 1B-C). The shape of this calcified area shows that it was distally surrounded by a crescent-shaped ooecial fold. This membranous outfold is not preserved in fossils, but recorded in Recent calloporids (Ostrovsky & Schäfer 2003, Ostrovsky et al. 2003).

Calcification continues to expand centrifugally (Fig. 1D-E), bordered by two deep lateral slits (see also Cheetham 1975, p. 553). The gymnocyst becomes more and more concave, forming the future ovicell floor, in contrast to the flat or slightly convex gymnocyst usually found in zooids not bearing an ovicell. In some cases an additional calcified wall was observed underlying both the lateral zooidal walls and the ooecial rudiment (Fig. 1D-E).

The completed proximal gymnocyst of the distal zooid constitutes the floor of the future ovicell. It has a tripartite construction in some specimens from the Weño Formation (Figs 1F-G, 2A). The most proximal strip of the ovicell floor seems to be formed by the distal gymnocyst of the maternal zooid. The middle section is apparently the proximal gymnocyst of the distal zooid above the basal pore chamber, and the distalmost strip an abrupt upward inflection of the proximal gymnocyst ending in the mural rim. Similar subdivisions were sometimes observed in material from the Grayson Formation (Fig. 2B), but the three parts were not as well expressed.

Because of the continued calcification, the lateral slits become reduced in length and separated from one another by a tongue of calcification along the midline of the zooid. For this reason, the initial ooecial fold should be transformed into two hollow symmetrical lateral lobes, precursory parts of the ooecium (Fig. 2A). Each lobe communicates with the proximal part of the zoecial chamber of the distal zooid through the large oval opening (Fig. 2C). Ringing the circumference of these openings, the lobes grow and form the ovicell roof (ooecium).

It is evident that the base of each lobe overgrows the gymnocyst in a proximal direction towards the maternal zooid. At the same time the frontal edge of the lobe grows upwards in an arc towards the midline of the zooid. We should stress that the size of the oval communication opening is much shorter than the total basal length of the lobe. This can be seen in a damaged ovicell by comparing the unbroken left and broken right lobes (Fig. 1G). The lower edge of each lobe is often clearly seen above the proximal gymnocyst from both inside (Fig. 1G, F) and outside the ovicell (Fig. 2D). The openings into the lobes are situated closer to the rim of the cryptocyst than they are to the transverse wall forming the proximal edge of the distal zooid (Figs 2C, 1G). However, in many broken ovicells it is easy to mistake fractured lobes for communication openings (Figs. 2B, IF) and consequently to overestimate the size of these openings.

Few examples have been found preserving an intermediate growth stage (Fig. 1H). Fusion of the lobes completes the hemispherical hood-like ovicell, with a medial suture clearly visible in many examples (Fig. 2E). Sometimes a slight crest is developed along the line of fusion. The ooecial coelomic lumen is possibly partitioned into two parts by an internal medial septum where the lobes fuse. This is suggested by the occurrence of ovicells that are broken along the medial suture (Fig. 2F).

4 DISCUSSION

Early stages of ovicell development in Wilbertopora differ from those described in related Recent calloporids where the ooecial fold, destined to form the floor of the ovicell, takes the shape of two flat, rounded plates. These plates originate independently of one another and sometimes have different sizes (Ostrovsky & Schäfer 2003, Ostrovsky et al. 2003). The second striking difference is that the ooecium in Wilbertopora is formed by the fusion of two lateral lobes that initially grow as independent structures. In some modern calloporids a bilobate pattern can be seen during the final stage of ovicell formation (Ostrovsky et al. 2003), but the ooecium itself always begins growth as a single semicircular fold. In contrast, in the absence of membranous parts, one can suggest that two soft outfolds - precursors of the lateral lobes - could have originated at the very beginning of ovicell development in Wilbertopora. The ooecial coelomic cavity in Recent calloporids communicates with the perigastric coelom of the distal zooid through an arch-like slit that is reduced during the course of calcification to a pore or pores. In contrast, in Wilbertopora coelomic cavities of the ooecial lobes evidently communicated with the zooid through two large oval openings reminiscent of structures present in the Recent cribrimorph
Figure 1. Scanning electron micrographs of ovicells in mid-Cretaceous Wilbertopora sp. from southwestern USA. A, distal edge of colony with complete and developing ovicells, BZ1352. B-C, earliest stages of ovicell formation showing single oocelial rudiment bordered by ooccial fold, D58502. D, further growth of the future ovicell floor, D57378. E, formation of the concave ovicell floor showing calcified layer underlying both the lateral zooidal walls and the ovicell floor, BZI352. F, broken ovicell with their lateral lobes partially destroyed (cf. communication openings depicted in Fig. 2C), BZ1124 (colony a). G, developing ovicell with right lateral lobe detached showing the short base of this lobe and the lower edge of the left lobe overgrowing the proximal gymnocyst, BZ1124 (colony c). H, intermediate stage of ovicell development showing hemispherical fold formed from fused lateral lobes and broken left lateral lobe, D57378. Scale bars: A = 250 pm; B-H = 25 pm.
Figure 2. Scanning electron micrographs of oovicells in mid-Cretaceous Wilbertopora sp. from southwestern USA. A. closed lateral lobes of an oovicell aborted at an early stage in its formation, BZ1124 (colony c). B. elongate lateral lobes of broken oovicell, D57378. C. broken oovicell showing the two communication openings, BZ1124 (colony c). D. slightly oblique view of a fully-formed oovicell, BZ1124 (colony c). E. one incomplete oovicell and three complete oovicells with median sutures, D57378. F. oblique view of the growing age with one oovicell (centre) broken along the median suture, D57378. Scale bars: A, C, D = 25 μm; B = 50 μm; E = 100 μm; F = 250 μm.

Puellina (see Ostrovsky 2002). Notably, Puellina also possesses a single ooecial rudiment (see, for instance Ristedt 1985, Bishop & Househam 1987). Thus, structural and developmental aspects of the brood chambers in the calloporid Wilbertopora show greater similarity to some cribrimorphs than to Recent calloporids. However, another Recent cribrimorph, Cribrilina punctata, has a double ooecial rudiment like that of Recent calloporids (Levinsen 1909). The phylogenetic significance of these observations awaits evaluation in the context of a cladistic analysis based on a more comprehensive range of characters.

Intermediate stages of oovicell development in Wilbertopora and Recent calloporids are similar. Many Recent calloporids and cribrimorphs resemble Wilbertopora in having a median suture where the two lobes of the oovicell fuse (reviewed in Ostrovsky 2002). Unfortunately, the internal structure of the oovicell is unknown in Wilbertopora - obtaining well oriented thin sections of oovicells with cavities not obscured by sediment or cement would be technically very demanding. An internal septum occurs in the distal part of the oovicell of the Recent cribrimorph Cribrilina annulata (Fabricius, 1780) (see Ostrovsky 1998), but it is not
known whether a similar structure is present in Wilbertopora either partially or totally dividing the coelom into two parts. Findings of oovicells that have been broken along the medial suture (Fig. 2F) support but do not prove the existence of a septum which may be very thin.

Frontal wall calcification during the development of distal autozooids supporting oovicells and those without oovicells are very similar. In both instances the proximal gymnocyist calcifies in a predominantly distal direction. However, whereas autozooids not bearing oovicells usually have a distally concave leading edge of gymnocyist, the equivalent structure in autozooids bearing oovicells has a rounded edge which is distally convex. Nevertheless, the single ooezial rudiment of Wilbertopora is similar to the initial gymnocyistal calcification in non-ovicellate zooids in that the leading edge of calcification is not bipartite. Spinose oovicells in several Upper Cretaceous calloporids (Ostrovsky & Taylor, 2004) show an unmodified proximal gymnocyist forming the ooezial floor of these primitive brood chambers. This floor grew as a single unit with no sign of partitioning, suggesting that a single ooezial rudiment is most probably the primitive state for this character. The proximal gymnocyist is normally flat or convex, whereas the ooezial floor in Wilbertopora and many more advanced cheilostomes is concave. This concavity may provide more space for the embryo and could represent the first stage in the progressive immersion of the brooding cavity, a trend which culminates in the endooecial oovicells seen in some cheilostomes.

It is difficult to understand why the double calcification of the ooezial rudiment originated in calloporids. If it is somehow connected with the evolution of bipartite structure of the oovicell itself why does Wilbertopora with its strongly bipartite oovicells have a single ooezial rudiment? Ostrovsky (1998, p. 314) suggested that 'paired primordia...may be considered as derivative of ooeicum formation from fused costae of the left and the right sides of the distal zooid frontal shield' in cheilostomes. Another interpretation is that in very primitive oovicells (like those found in Distelopora, Gilbertopora and Wilbertopora), there are essentially three skeletal components - proximal gymnocyist, ectooecium and entooecium. The oovicell floor is formed by the proximal gymnocyist with little or no contribution from the entooecium which produces only the dome-like inside of the roof of the oovicell. The bipartite structure of the ooezial rudiment (initial calcification of the oovicell floor) in more advanced cheilostomes (e.g. Recent calloporids) is because the proximal gymnocyist becomes reduced to nothing and the oovicell floor is then formed by entooecium which, as in Wilbertopora, has its origin from two flattened spines (see also below) and retains a vestige of this compound structure in the bipartite ooezial rudiment. In still more advanced cheilostomes, including ascophorans, all traces of the bipartite structure are lost. This evolutionary model hypothesizes a progressive 'shrinking' of the proximal gymnocyist until the oovicell is formed entirely by ectooecium and entooecium, giving it a double-walled structure throughout. To be tested both models require more data and analysis.

Early stages of oovicell development have not been used as characters in the taxonomy or phylogeny of the Cheilostomata, and their importance has yet to be assessed. The distribution of double and single ooezial rudiments (initial calcification of the oovicell floor) shows an interesting pattern among Recent cheilostomes, even though data is incomplete. An analysis of published descriptions and illustrations shows that double rudiments occur in Calloporidae (Callopora, Tegella, Crassitiijuginatea), Candidae (Smpocellaria, Tricellaria), Cribrilinidae (Cribrina) and Romancheinidae (Pseudolepralia) (Levinsen 1893, 1894, 1909, Harmelin 1973, Nielsen 1985, Gordon 1993, Ostrovsky & Schäfer 2003, Ostrovsky et. al. 2003). Single ooezial rudiments have been described in Bugulidae (Bugula, Dendrobeania), Cribrilinidae (Cribrina, Puellina), Hippothoidae (Cel leporat) and all other studied cheilostomes with umbonulomorph and lepralioid frontal shields (Levinsen 1909, Waters 1913, Harmer 1934, Ristedt 1985, Bishop & Househam 1987, Nielsen 1981, 1985, Hughes 1987, Ostrovsky 1998, see also illustrations in Cook 1977, Cook & Chimonides 1981, Cook & Hayward 1983, Gordon 1984, 1989, Chimonides & Cook 1993, Hayward 1995).

Thus, the bilobate ooezial rudiment is characteristic of a few groups with mainly simple frontal shields including some calloporids (the oldest family of cheilostomes with oovicells), whereas the non-lobate rudiment is known mainly among gymnocyistideans, umbonulomorphs and lepralioid cheilostomes which are undoubtedly more derived groups to judge from their morphologies and stratigraphical distributions. The finding of a single ooezial rudiment in Wilbertopora - the oldest, although not the most primitive, calloporid, suggests that this character may have undergone a more complex evolution from single to bipartite and back to single.

Ostrovsky and Taylor (2004) suggested that the bilobate oovicells of Wilbertopora could be derived from the bispinosc oovicells of Gilbertopora, a recently discovered genus of Cenomanian age. The suggestion was made that the unusual bispinosc oovicells of Gilbertopora, comprising two overarching claw-like spines, could have been further transformed by the enlargement and lateral fusion of the spines to form a hemispherical oovicell. Findings of all parallel stages of oovicell development in Wilbertopora, especially the pattern of formation of the lateral lobes which grow proximally from relatively small bases and short communication
openings, adds weight to this suggestion. This pattern may also be used as an argument in favour of the hypothesis that the transition from multicostate to bilobate ovicells was via reduction in spine number, with the retention and enlargement of only the two most distal spines (see Ostrovsky & Taylor, 2004), while disfavouring the alternative hypothesis of spine fusion.

It is difficult to interpret the presence of a second calcified layer apparently underlying both the lateral zooidal walls and the oocelial floor (Fig. 1E) in some young ovicells. Ostrovsky et al.’s (2003) study of ovicell wall ultrastructure and early ovicell development in Recent calloporids suggested the possibility of evolving complex multilayered skeletal walls by the fusion of initially separate gymnocystal and cryptocrystal components. The double-walled structure in these Wilbertopora ovicells may represent a precursor to this fusion. Alternatively, in the ovicell shown in (Fig. 1D), the lower wall may be the frontal wall of the large distal pore chamber and the upper wall the proximal gymnocyct of the distal zooid, the narrow gap between these walls being the most proximal part of the zooecial chamber of the distal zooid. More research needs to be undertaken before the identity of these enigmatc walls can be established.

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Taxonomy and distribution of Bugula (Bryozoa: Cheilostomata: Anasca) in Rio de Janeiro State, Brazil

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ABSTRACT: Seven species of the cheilostome bryozoan genus Bugula Oken, 1815 have been recorded to date from Brazil. However, this genus is almost unknown in Rio de Janeiro State where only one species has hitherto been recorded, Bugula neritina (Linnaeus, 1758). In this study we investigate the taxonomy and distribution of Bugula in three areas of Rio de Janeiro State: Arraial do Cabo, Guanabara Bay and Sepetiba Bay. Five species of Bugula were identified, including the previously recorded Bugula neritina and four new to the state: B. dentata (Lamouroux, 1816), B. uniserialis Illnicks, 1884, B. canalhoi Marcus, 1949, and B. stolonifera Ryland. 1960. Bugula dentata is also a new record for Brazil. Four of the five species are cosmopolitan or have disjunct distributions. These are considered to be cryptogenic for Rio de Janeiro State. The fifth species, B. carvalhoi, is endemic to southeastern Brazil.

1 INTRODUCTION

The bryozoan fauna of Brazil has been little studied. Following Ernst Marcus, who was responsible for numerous papers on Brazilian bryozoans (e.g. Marcus 1937, 1938, 1941, 1949, 1955), very few taxonomic studies have been published (Braga 1967, 1968, Buge 1979). Ecological studies have been more frequent, sometimes recording a small number of bryozoan species (e.g. Omena & Souza 1999).

The anascan cheilostome Bugula Oken, 1815 is a cosmopolitan genus characterised by having unilaminar, erect and branching colonies which are attached to the substratum by rhizoids. The zooids are elongate and arranged alternately in two or more series that face in the same direction. A frontal membrane occupies nearly all of the frontal surface of the autozooids, and lateral and basal walls are both lightly calcified. Marginal spines may be present and pedunculate avicularia usually occur. Ovicells are hyperstomial, typically globular but occasionally reduced (see Ryland 1960, Maturo 1966, Soule et al. 1995).

More than fifty species of Bugula have been recorded from around the world, including seven in Brazil: B. californica Robertson, 1905 (Marcus 1937), B. canalhoi Marcus, 1949 (Marcus 1949), B. ditrupae Busk, 1858 (Marcus 1937), B. flabellata (Thompson in Gray, 1848) (Marcus 1938, Correa 1948), Bugula neritina (Linnaeus, 1758) (Marcus 1937, Maturo 1966. Omena & Souza 1999), B. turrita (Desor, 1848) (Marcus 1937, 1955) and B. uniserialis Illnicks. 1884 (Marcus 1937). However, only Bugula neritina (Linnaeus, 1758) has hitherto been recorded from Rio de Janeiro State (Marcus 1937. Omena & Souza 1999). This species is often reported during ecological studies, occurring in large quantities and on different substrates, especially in Guanabara Bay (Marcus 1937. Omena & Souza 1999). Braga (1967, 1968) identified 18 species of bryozoans in sediments in the region of Cabo Frio but none of these belonged...
to lingula. To date no bryozans have been reported from Sepetiba Bay. Our aim in the present study is to identify the species of Bugula present at three coastal localities in Rio de Janeiro State, and to describe their morphology, ecology and distribution.

2 MATERIAL AND METHODS

Three areas were sampled in Rio de Janeiro State, southeastern Brazil: Arraial do Cabo, Guanabara Bay, and Sepetiba Harbour in Sepetiba Bay (Figure 1). Arraial do Cabo (23°(X)'S, 43°00'W) is located 170km east of Rio de Janeiro city. The area studied is situated in the Extractive Reserve of Arraial do Cabo, managed by IBAMA. This area is characterized by the upwelling of cold water rich in nutrients, especially from November to April (Valentin 1984, Gonzalez-Rodriguez et al. 1992). Guanabara Bay (22°40' to 22°55'S, 43°20' to 43°05'W) is located in the metropolitan region of Rio de Janeiro city, and has an area of approximately 377 km². Water temperature ranges from 20 to 30°C, and salinity is 27.33‰. Guanabara Bay is impacted by large quantities of organic and inorganic detritus due to human action (industrial effluents, domestic drains, pollutants of petroleum origin and other compounds), and it is regarded as a heavily polluted area (Silva et al. 1980, Kjerfve et al. 1997). Sepetiba Harbour (22°56'S, 43°50'W) is located on the north coast of Sepetiba Bay, in the south of Rio de Janeiro State. It is polluted by heavy metals (Lima-Junior et al. 2002) and receives an average of 300 large ships per year transporting ore, oil, containers and steel. This harbour was selected by the Globallast Program for study and monitoring of the fauna in order to identify endemic species and the possible introduction of exotics.

Samples were collected by SCUBA or skin diving at depths of 0.15 m, from various substrates, and were fixed in 70% ethanol. The specimens from Sepetiba Harbour were collected on both natural and artificial substrates by the team of the Globallast Program; specimens from Guanabara Bay were collected on artificial substrates (ships’ hulls and plates) by J.E.A. Gonçalves, C.E.L. Ferreira and one of us (G.M.). In Arraial do Cabo, collections were made by two of us (L.V.R. and G.M.). In Arraial do Cabo, collections were made by two of us (L.V.R. and G.M.) from rocky and artificial substrates. Camera lucida drawings were made using a stereomicroscope, and digital images were obtained of uncoated, dried specimens using a low vacuum scanning electron microscope (LEO 1455VP) at the Natural History Museum. London. Specimens have been deposited in the Bryozoan Collection of the Museu Nacional (MNRJ). Univrsidade Federal do Rio de Janeiro.

Acronyms: IBAMA, Instituto Brasileiro do Meio Ambiente e Recursos Renováveis; IEAPM, Instituto de Estudos do Mar Almirante Paulo Moreira, Arraial do Cabo; MNRJ, Bryozoan Collection of the Museu Nacional, Universidade Federal do Rio de Janeiro; NHM, the Natural History Museum. London.

3 SYSTEMATIC'S

Order Chilostomata Busk. 1852
Suborder Anasca Levinsen, 1909
Family Bugulidae Gray, 1848
Genus Bugula Oken, 1815

Type species: Bugula neritina (Linnaeus, 1758).

Revised diagnosis: Colony erect, branching, attached by rhizoids arising from frontal, lateral and basal surfaces of autozooids. Ancestrula upright. Autozooids arranged in two or more series, alternating along branch; boat-shaped, the proximal end forming a fork around proceeding zooid. usually truncate distally and somewhat attenuate proximally; septula in one or two rows, uniporous or multiporous; basal and lateral walls lightly calcified; frontal membrane occupying most of frontal surface; operculum lacking, the orifice closed by a sphencter; one to several spines present, often confined to distal angles; oviocell typically globular, hyperstomial, ectooecium membranous, opening closed by inner vesicle. Avicularia present in most species, pedunculate, shaped like a bird’s head.

Bugula neritina (Linnaeus, 1758) Figure 2
Figure 2. *Bugiila neriiina* (Linnaeus, 1758). A B. MNRJ015; A. branch frontal surface; B, fertile branch with five ovicells in a row. C-D, MNRJ007, scanning electron micrographs; C, bifurcating branch; D. three ovicells showing layered structure of ooecium. Scale bars: A-C = 200 μm; D = 100 p.m.

*Sertularia neritina* Linnaeus, 1758: 815.
*Acamarchis neriiina*, d’Orbigny, 1826: 59.

Revised diagnosis; Colony arborescent, branching, biserial. Orange to purple alive, orange or brown in alcohol (occasionally whitish); zooids large, longer than wide, frontal membrane occupying nearly all frontal surface, ovicells globose, asymmetrical, attached to inner distal corner of zooid, oriented obliquely to branch axis, the opening concealed; avicularia and spines absent.

Description. Colony arborescent, branched, resembling a seaweed, 1-4 cm high by 1-4 cm wide. Colour orange to purple alive (sometimes almost whitish), brown in alcohol.

Zooids arranged biserially, large, rectangular, longer than wide (Table 1). Frontal membrane occupying nearly all frontal surface (Fig. 2A-C). Intecodcs comprise 8-10 zooids. Spines absent. Tentacles numbering 18-21. Ovicells slightly wider than long, attached to inner distal corner of maternal zooid. Successive ovicells aligned in a row between the zooids (Fig. 2B-D).

Avicularia absent.

Ecology: This species colonises natural rocky substrates but also attaches to diverse artificial substrates such as nylon ropes, concrete piers and pilings, boat hulls (made of steel, fibreglass and wood), artificial plates and buoys (steel and wood). Epizoic animals commonly found over _B. neritina_ include foraminifera, sponges, serpulid polychaetes and other bryozoans (Scruparia ambugua (d'Orbigny, 1841), Watersipora suhovoidea (d'Orbigny, 1852), Actea sp., Bugida stolonifera Ryland. 1960). Depth: 0-7 m.


Remarks: Bugida neritina is morphologically most similar to _B. minima_ Waters, 1909 from the Red Sea but can be easily distinguished in lacking avicularia and having larger zooids. It is usually considered to be a cosmopolitan species, with a wide distribution around the world, mainly in tropical but also in subtropical and warm temperate waters (Canu & Bassler 1925, Maturo 1966, Soule et al. 1995). A common

Table 1. _Bitgula_ species measurements in microns (average, SD. minimum and maximum). Zooid length from base to top; zooid width from side to side; opesia length from base to end; avicularium length from beak to head end; avicularium height from peduncle-head articulation to top.

<table>
<thead>
<tr>
<th>Species</th>
<th>Zooid length</th>
<th>Zooid width</th>
<th>Opesia length</th>
<th>Avicularium length</th>
<th>Avicularium height</th>
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<tr>
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<td>750</td>
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<td>-</td>
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<tr>
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<td>679-1154</td>
<td>184-310</td>
<td>611-1018</td>
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<tr>
<td><em>B. stolonifera</em></td>
<td>630</td>
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<td>465</td>
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<td>55</td>
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<td>436-834</td>
<td>97-194</td>
<td>339-582</td>
<td>116-264</td>
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<td>78-145</td>
</tr>
<tr>
<td><em>B. uniserialis</em></td>
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<td>116-145</td>
<td>301-407</td>
<td>116-145</td>
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<td>466-630</td>
<td>175-213</td>
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<td>97-116</td>
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<tr>
<td><em>B. dentata</em></td>
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<td>410</td>
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<td>349-611</td>
<td>145-213</td>
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<td>78-110</td>
</tr>
</tbody>
</table>
fouling organism, *B. neritina* is prone to transportation by shipping (Marcus 1937, Winston 1982, Alvarez et al. 1986, Gordon & Mawatari 1992, Soule et al. 1995). In our study *B. neritina* was very common fouling harbour installations, ships' hulls, piers, nylon ropes and other artificial substrates.

Considered to be an introduced species in many areas, such as Hawaii and Victoria, Australia (Currie et al. 1998, Zabin 1999), the original, natural distribution of *B. neritina* is unknown and the species is best classified in Rio de Janeiro State as a cryptogenic species (*sensu* Carlton 1996). The existence of cryptic species within *Bugula neritina* has been demonstrated by molecular analysis, showing that it is a species complex rather than a single species (Davidson and Haygood 1999).

*Bugula stolonifera* Ryland, 1960 Figure 3


Figure 3. *Bugula stolonifera* Ryland. 1960. MNRJOOS. A, drawing of colony origin showing upright ancestrula attached to a wedge-shaped substratum. B, drawing of bifurcation with pedunculate aviculatum and ovicells containing dark embryos. C, scanning electron micrograph of bifurcating branch. D, detail showing oovicells, pedunculate avicularia and spines (two outer and one inner). Scale bars: A = 150 pm; B = 120 pm; C 200 pm; I) = 100 pm.

Rio de Janeiro State. Arraial do Cabo: MNJR-008, Fomo Harbour, 13/11/2002, Ramalho & Muncy Collection, depth 0.5 m: MNJR-017, Fomo Beach, 14/11/2002, Ramalho & Muncy Collection, depth 5 m.

Guanabara Bay: MNJR-032. Guanabara Bay, 01/2/2002, Ferreira Collection, depth 1 m; MNJR-036, hull of the hydrographic naval ship Sirius, 25/8/2003, Muricy Collection, depth 0.5 m; Sepetiba Harbour: MNJR-041, Alumina Terminal, artificial substrate, 09/11/2001, Globallast Collection, depth 7 m.


**Revised diagnosis:** Colony arborescent, small: ancestrula with two pairs of lateral spines and one proximal median spine; autozooids with two outer spines and one inner spine; avicularium located at bifurcation smaller than other avicularia.

**Description:** Colony arborescent, branching, forming small fan- or funnel-shaped tufts up to 15 mm high X 30 mm wide. Colour in Brazilian material white, both alive and in alcohol.

Autozooids bicipially arranged, longer than wide (Table 1). Frontal membrane occupying about three-quarters of the surface. True spines present, usually two outer and one inner (2:1); zoid at bifurcation with one outer and one inner spine (1:1) (Fig. 3B-D). Ovicells wider than long, subglobose, attached to the distal region of autozooid (Fig. 3B-D). Ancestrula with two pairs of lateral spines and one proximal median spine (Fig. 3A).

Avicularium pedunculate, large, birdhead type, with beak strongly curved, attached to the external margin of zoid in median-distal region (Fig. 3C-D). Avicularium located on zoid at bifurcation smaller than the other avicularia or absent (Fig. 3B).

Kcnozooids often present from base to beyond second bifurcation.

**Ecology:** Colonies arc attached to stems of hydroids or other bryozoans (B. neritina, Scrupocellaria diadenu Busk, 1852 and Watersipora subovoidea d'Orbigny, 1852), and artificial substrates (ship hulls, plates and piers). Depth 0-7 m.


**Remarks:** Bugida stolonifera Ryland 1960 has been confused with both R. californica Robertson, 1905 and B. avicularia (Linnaeus, 1758). Bugula californica differs from B. stolonifera in its strongly spiral growth, the presence of 2-3 outer spines, and in not having a smaller avicularium associated with the zooids at bifurcations. Bugula stolonifera and B. avicularia have the same number of spines (2:1), but the size of the avicularia differs (0.18-0.24 mm and 0.25-0.30 mm respectively), and the beak is shorter in the first species. Marcus (1937) mentioned the occurrence of B. californica Robertson, 1905 in Brazil (Santos, São Paulo State). However, examination of specimens identified as B. californica and donated by Marcus to the NHM show that they belong to Bugula stolonifera because of the presence of small avicularia at bifurcations and the characteristics of the ancestrula.

Bugula stolonifera has a cosmopolitan distribution, occurring mainly in subtropical and temperate waters. It is found principally in polluted areas characterised by low velocity currents such as harbours and ports (Hayward & Ryland 1998, Soule et al. 1995), and is considered to be a fouling organism capable of being transported on ship hulls. In Rio de Janeiro State B. stolonifera is generally found in association with or in the same environments as B. neritina. It was probably introduced into Rio de Janeiro State by shipping but, as its native distribution is unknown, it should be considered a cryptogenic species.

**Bugula uniseriatis** Hincks, 1884 Figure 4


**Material examined:** Type: NHM 1899.5.1.413, Western Australia, Hincks Collection.

Rio de Janeiro State. Arraial do Cabo: MNJR-018, Farol Beach, Cabo Frio Island, on Sargassum furcatum. 19/1/2000, Ramalho Collection, depth 4 m; MNJR-019, Farol Beach, Cabo Frio Island, on Sargassum furcatum, 13/2/2003, Ramalho Collection, depth 4 m; MNJR-020, Pedra Vermelha, Cabo Frio Island, on Sargassum furcatum, 27/2/2003, Ramalho & Melo Collection, depth 10 m.
Figure 4. *fitigiis uniserialis* Hincks. 1884. A B, VÍNRJ01 9; A, drawing of frontal surface showing autozooids with lateral walls folded at distal comers and pedunculate avicularia; B, drawing of dorsal surface. (D, MNRJ018; C, scanning electron micrograph of branch; I), scanning electron micrograph of aviculanum, with strongly curved beak, attached to basal tube. Scale bars: AB 150 µm; C = 100 µm; I) = 20 µm.

Comparative material: NHM 1948.2.16.22, Santos (SI*), Brazil. Marcus Collection.

*Revised diagnosis*. Colony arborescent, small, biserial, transluscent white; true spines lacking; avicularium attached to proximal part of zooid basal tube. *Description*: Colony arborescent, branching dichotomously, 6 mm high x 8 mm wide, with alternating biserially arranged zooids, appearing uniserial at first sight. Colour very pale yellow to white, both alive and in alcohol.

Autozooids rectangular, longer than wide (Table 1). Basal tube arising from proximal zooid in distal region, extending for almost entire length of adjacent zooid. Frontal membrane occupying about half of frontal surface (Fig. 4A-C, Table 1). At distal corners.
lateral wall protrudes or is folded, sometimes forming a spine-like structure (Fig. 4A-C). Autozooids at bifurcations bud two daughterzooids (Fig. 4A). Table 1 Ovicells not seen in material examined.

Avieularia pedunculate, birdhead type, one per autozooid. attached to a short peduncle on proximal part of basal tube (position can be misleading because avieularia seem at first to be attached to the distal part of the proximal zooid (Fig. 4A-B)). All avieularia of similar size, with a short, strongly curved beak (Fig. 4A-D).

Kenozooids present as radicle fibres arising from dorsal sides, opposite proximal edge of frontal membrane (Fig. 4B).

Ecology: Colonies were found exclusively attached to Sargassum furcatum and articulated calcareous algae (e.g. Jania sp.) at depths of up to 10 m. The algae themselves were fixed onto natural rocky substrates.

Distribution: Rio de Janeiro State: Arraial do Cabo (present study). Brazil: Santos, São Paulo State (Marcus 1937). World: eastern Pacific (Galapagos, California), eastern Indian Ocean (Western Australia), western and south Atlantic (Florida and Brazil) (Hincks 1884, Hastings 1930, Marcus 1937, Winston 1982).

Remarks: This species is well characterized by its minute size, the avieularia positioned in the proximal region of the zooid basal tube, and the pseudouni serial arrangement of the zooids. Hincks (1884) mentioned that the zooids have a uniserial arrangement but Hastings (1930) noted that this is due to the considerable attenuation of the basal portions of the zooids (see Figure 4B). Hincks (1884) also described the avieularium as positioned at the top the autozooid, in the holotype and in Brazilian specimens it is positioned on the proximal part of the basal tube, as was also noted by Hastings (1930). Ovicells were not seen in the specimens studied here, but Marcus (1937) mentioned them as hyperstomial, Hat, and attached to the inner angle of the distal margin of the autozooids. In our samples from Rio de Janeiro State, B. uniserialis always occurred on algae (phacophytes and calcareous). Its preference for this type of substrate was previously noted in Western Australia. Brazil (São Paulo State) and the USA (Florida) (Hincks 1884, Marcus 1937, Winston 1982). The species has not been recorded on artificial substrates, reducing the probability of introduction by shipping. The disjunct distribution of the species may be due to its rarity or perhaps its small size leading to it being overlooked. There are no clues to the natural distribution of B. uniserialis, and it is therefore considered cryptogenic.

Bugula carvalhoi Marcus, 1949 Figure 5

Bugula carvalhoi Marcus, 1949: 17.


Revised diagnosis: Colony arborescent, small, biserial, transparent white in colour; autozooids with short and thick, spine-like tubercles at each distal corner; ovicells wide, flattened; avieularia attached to lateral wall of autozooid about mid-length.

Description: Colony arborescent, opening as a fan. 20 mm high X 15 mm wide, branching, with biserial zooids. Colour transparent white.

Autozooids almost rectangular, much longer than wide (Table 1), the proximal region narrow. Two spine-like tubercles present distally, inner and outer, short, thick, unjointed, sometimes very pronounced. Inner tubercle generally shorter than outer tubercle, often bending distally over frontal surface. Frontal membrane occupying almost entire frontal surface. Basal tube arising dorsally in distal region of proximal zooid (Fig. 5A). Bifurcation Type 4 of Manner (1923, 1926) (Fig. 5B). Ovicells with cap-like hood, attached to distal margin of zooid without peduncle, distally flattened, wider than long am not very large (Fig. 5A, C-D, Table 1). Ancœstrula not observed in our material.

Avieularia large, pedunculate, with a small curved beak; relatively constant in size within colony (Table 1); attached to lateral wall of distal half of autozooid, always on outer side (Fig. 5A, C-D).

Ecology: This species was found attached directly to rocks at 10m depth.


Remarks: This species is similar to B. turrita (Dacos 1848) and B. rylandi Maturo, 1966 in having two spine-like tubercles distally (1:1). However, it differs from these species in several characters: B. turrita has a folded lateral margin of the frontal membrane between the outer tubercle and the position of the avieularium; the avieularium is shorter than the width of an autozooid, and bifurcations are of Type 3 of Harmer (1923, 1926). Furthermore, B. rylandi has longer ovicells than B. carvalhoi, the frontal membrane is smaller, and the avieularia are more distally located. Marcus (1949) noted that B. carvalhoi can Iк triserial but this was not observed in our material, perhaps because our colonies were small and sparse.

 Provisionally a Brazilian endemic, B. carvalhoi is restricted to the Paulista Biogeographic Province (sensu Palacio 1982). It was previously recorded only from the coast of São Paulo State (Marcus 1949) and
its occurrence at Arraial do Cabo extends its distribution along the Brazilian coast to Rio de Janeiro State. As *B. carvalhoi* is very similar to *H. turrita* and the latter has a wider geographical distribution, previous records of *B. turrita* should be verified as some may be *B. carvalhoi*.

**Bugula Jen ta ta** (Lamouroux, 1816) Figure 6

*Acamarchis Jentata* Lamouroux, 1816: 135.
Figure 6. *lingula denutta* (Lamouroux. 1816). VÍNRJ021. A, frontal surface of branch. B, dorsal surface, with zooids lettered, illustrating Type 4 bifurcation. C, two ancestrulae attached to a substratum (bottom). D, ovicell with embryo (c). E, scanning electron micrograph of zooids in two adjacent branches. Scale bars: A-l) = 150 μm; E = 100 gm.

**Material examined:** Type: NHM 99.7.1.6604, Australasia, Busk Collection ex Lamouroux Collection. Rio de Janeiro State. Arraial do Cabo: MNRJ-021, Praia do Forno. 14/11/2002, Ramalho & Muricy Collection, depth 8 m; MNRJ-022, Pedra Vermelha, Ilha de Cabo Frio. 27/2/2003, Ramalho & Melo Collection, depth 6 m; MNRJ-023, Pedra Vermelha, Ilha de Cabo Frio, 24/5/2002, Ramalho Collection, depth 8 m; MNRJ-024, Wreck Teixeirinha. 16/1/2000, Ferreira Collection, depth 15 m.

**Comparative material:** NHM 1888.4.16.27, Pernambuco, Brazil, H.N. Ridley Collection; NHM 1977.1.8.1, Portsea Jetty, Victoria, Australia, C. Russ Collection; NHM 1923.7.26.4, Agulhas Light, South Africa, O’Donoghue Collection.

**Revised diagnosis:** Colony spiralled, biserial, green or green-blue in colour; autozooids with true spines, two or three outer and one inner (2-3:1); ovicell slightly wider than long, reaching insertion point of avicularium...
of distal zooid, closing membrane chitinized; avicularia attached to proximal part of autozooid, level or slightly below base of frontal membrane; ancestrula with 2-3 outer and 2 inner spines distally, and one outer and one inner spine near proximal edge of opesia.

**Description:** Colony arborescent, spiralled, comprising large tufts up to 40 mm high X 55 mm wide, with biserially arranged zooids. Colour green or green-blue, becoming pale green to pale blue in alcohol, rarely turning completely white.

Autozooids arranged alternately, longer than wide, more or less rectangular (Fig. 6A, Table 1), arising from distal part of proximal zooid (Fig. 6B). Frontal membrane occupying less than half of frontal surface. Spines large, located at distal corners. 2-3 outer and one inner spine (2-3:1); when three outer spines occur, one is located distally, opposite the inner spine, and the other two arc located more proximally, arising almost together, the most proximal being directed laterally over the frontal membrane and the distal one erect (Fig. 6A, E). Ovicells somewhat longer than wide, almost elliptical, attached to distal region of zooid (Fig. 61); large, reaching insertion point of avicularium of distal zooid; closing membrane chitinized. Ancestrula (Fig. 6C) similar to an autozooid but distal end of opesia more rounded; distal spines having same disposition, a pair of additional spines located on proximo-lateral edge of the opesia, directed distally. Lophophore with very slender and long tentacles.

Avicularia large, pedunculate, one per autozooid, attached to outer margin, below or level with proximal edge of opesia. Size not varying along branch (Table 1). Beak long, tip curved. Avicularia frequently absent, leaving attachment scar of peduncle (Fig. 6A).

Kenozooids occurring in large numbers as radicle fibres at colony base, hiding ancestrula and early zooids.

**Ecology:** This species attaches directly to rocks, concrete piers and wreck. Sponges, bivalves, foraminifera, hydroids, other bryozoans and serpulids may overgrow colonies. Depth: 0-15 m.

**Distribution:** Rio de Janeiro State: Arraial do Cabo and ? Pernambuco (present study). World: Atlantic (Madeira, Cape Verde, South Africa and Brazil), Mediterranean (Cadiz Bay), western Pacific (Celebes Sea), Indo-West Pacific (New Zealand, Australia, New Guinea and Japan) (Lamouroux 1816, Calvet 1931, Mackie et al. 2002).

**Remarks:** The position of the avicularium suggests that *Bugula dentata* is related to *B. pacifica* Robertson, 1900, both species having the avicularium close to the base of the opesia. However, in *ti pacifica* there are two outer spines and one inner spine, the ovicell is remarkably small, shallow and flat, and colonies are often purple but can be slightly yellow, white or greenish.

In the type material and other NHM samples of this species it was not possible to observe the ancestrula but other characteristics are the same as Brazilian material, although our material is neither as robust as that from Victoria (Australia) nor as delicate as that from South Africa.

A slide containing a dry colony from Pernambuco (northeastern Brazil) was found in the NHM collection. This is green-blue in colour, with 2-4 outer and 1 inner spines (often broken). The possible ancestrula has three outer and two inner spines, plus one lower spine. Some doubt remains about the true identity of this specimen.

*Bugula dentata* has a wide but disjunct distribution in temperate to tropical regions, occurring mainly in the Indo-West Pacific and in the central and south Atlantic. Our new record is the first for Brazil. The possibility of introduction of this species by ships is relatively high, since it commonly encrusts ship hulls, but there is no evidence that its natural distribution was restricted to the Indo-Pacific. It is thus best classified as a cryptogenic species.

4 DISCUSSION AND CONCLUSION

We report four new records for species of *Bugula* along the coast of Rio de Janeiro State: *B. carvalhoi*. *B. dentata*, *B. stolonifera* and *B. uniserialis*. *Bugula dentata* is also a new record for Brazil. This species is particularly abundant in the harbour and on rocks in Arraial do Cabo, suggesting that it is well suited to the conditions pertaining here.

This study has shown that *Bugula* is much more diverse in Rio de Janeiro State than previously thought, with at least five species instead of the one previously recorded by Marcus (1937). This number is particularly high when compared with the seven species of *Bugula* now known for the entire Brazilian coast (Marcus 1937,1938,1949, 1955. Correa 1948, Mature 1966, Omena & Souza 1999).

Many bryozoans, including *Bugula*, encrust artificial substrates such as ship hulls, and therefore have the potential for introduction as exotic species, particularly species which are well adapted to polluted areas like ports and harbours (Ryland & Hayward 1977, Gordon & Mawatari 1992, Soule et al. 1995, Keough & Ross 1999). This ability, coupled with the cosmopolitan or disjunct distribution of four of the five species of *Bugula* studied here (*B. carvalhoi* is an endemic of southeastern Brazil provides the exception), suggests that they may have been anthropogenically introduced into Rio de Janeiro State. Their status as exotic species is, however, uncertain because
their natural distributions are unknown: therefore, we classify them as cryptogenic species. Taxonomic problems caused by sibling species and cryptic speciation may be masking the true distributions of these species. In future they will need to be studied using molecular techniques such as DNA sequencing, RAPD-PCR, or allozyme electrophoresis (Hillis & Moritz 1990) to discriminate cryptic species.

During the course of this research, we found a previously overlooked collection of Brazilian bryozoans which had been collected and identified by E. Marcus and donated to NHM in 1948. This collection has already allowed us to compare material of *B. californica* identified by Marcus with the holotype of *B. stolonifera*, leading to the conclusion that *B. californica* does not occur in Brazil. The collection donated by Marcus will permit a more precise identification of Brazilian bryozoans and will help to evaluate their true diversity.

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Bryozoans and stratigraphy, Upper Richmondian (Cincinnatian, Ordovician)

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ABSTRACT: Bryozoan diversity in the upper part of the Richmondian Stage was much reduced and consisted of one to only a few species in the genera Rhombotrypa, Parvohallopora, Constellaria, Bythopora, Escharopora, Heterotrypa, Homotrypa, Peronopora, Batostoma, Gortaniopora, Tarphophragma, Amplexopora, Monticulipora, Creipora and Graptodictya. Except for the large species of Rhombotrypa, Parvohallopora, and Heterotrypa, they are generally fragmentary specimens in fine-grained calcarenitic debris facies that form thin, sheet-like, shallow subtidal sediments. The Drakes Formation, in central and northcentral Kentucky, and the correlative Whitewater Formation in southeastern Indiana form the upper part of the Richmondian Stage of the Cincinnatian Series (Upper Ordovician). Within this succession the number of bryozoan-bearing beds are relatively few. In central Kentucky, the Drakes Formation rests with regional unconformity on a number of different members within the middle Cincinnatian Bull Fork and Ashlock formations and has at least 60 m of topographic relief across the Cincinnati Arch (Central Kentucky Middle Richmondian hiatus). The upper part of the Whitewater thickens into the Sebree Trough and represents the youngest Richmondian strata present in outcrop.

1 INTRODUCTION

A stratigraphic framework is necessary to an understanding of the stratigraphic distributions of upper Richmondian bryozoans. For more than 150 years, the paleontologic and stratigraphic relations in the upper part of the Upper Ordovician Cincinnatian Series have continued to raise a number of questions as the various stratigraphic approaches to the study of its rocks and fossils have changed and been modified. In part, this situation results from subtle, but rapid, facies changes, limited continuous outcrops, and the prevailing stratigraphic philosophy of the geologists at the time. For example, until the 1960s or the 1970s, the occurrences of distinctive fossils were considered to mark identifiable (time) horizons (Nickles 1903, Cumings 1908, 1922, Cumings & Galloway 1913, Caster et al. 1955). Beginning in the late 1960s and continuing through the 1990s, major and minor lithologic facies changes began to be emphasized and most fossils became interpreted as representative of biofacies in the various stratigraphic sections (Hay et al. 1981, Karklins 1984, Tobin 1986). This combined lithologic-biofacies approach, supplemented to some extent with fossil occurrences, was carried out over a larger area, as in the U.S. Geological Survey mapping program in Kentucky in the late 1960s, 1970s, and 1980s, and was successful in introducing new ideas into the stratigraphic interpretations of the region (Weir et al. 1984). This involved defining mappable lithologic units, considering major lithologic changes as facies changes, using arbitrary lateral cut-offs of members and formations, and even having the same named members in different formations (Weir et al. 1984). Although this approach was common in many of the studies throughout the region in the 1970s and 1980s, this seems particularly true of the U.S. Geological Survey’s stratigraphic and mapping interpretations in central Kentucky, where the middle to upper Cincinnatian formations and members are mapped as a series of lithologic lateral facies and arbitrary stratigraphic cut-offs. Because Weir et al. (1984) did not consider their stratigraphic units to be separated by unconformities, but rather as lithologic recurrences, the same member names were retained for similar lithologic units even if they appeared in different formations and in different stratigraphic positions. Their stratigraphy (Weir et al. 1984) was correlated so that a named lithologic member may be a member in two or more formations (and each occurrence may be a
different age). This has resulted in a difficult and, at times, a confusing nomenclature.

Thus, there remained the idea that the Cincinnatian successions were continuous and their lithologic successions lacked any major breaks in deposition and, hence, lacked major stratigraphic unconformities and lacked events recorded in the stratigraphy that might be useful in correlation. More recently, there have been attempts to apply the Vail et al. (1977) concepts of sequence stratigraphy to the Late Ordovician. Ross & Ross (1995) applied the concepts to the Ordovician System in general and Holland (1993), Holland & Patzkowsky (1996, 1997), Pope & Read (1997) and Ross & Ross (2002) to the Cincinnatian Series in particular. These studies identify at least six major depositional sequences in the rocks that form the Cincinnatian Series, although each study differs in some important stratigraphic details. For example, what appears, to some workers, as minor depositional sequence boundaries near the middle of the Cincinnatian Series in one area, are or have become, to other workers, major sequence boundaries in other parts of the area. This suggests that as the details of the depositional packages are better known, the number of identifiable major sequences will probably increase.

The stratigraphic nomenclature of the Cincinnatian Series seems unduly complex, fraught with contradictions, has not consistently been applied in the field from worker to worker or by the same workers from outcrop to outcrop. In general, it is not an exercise for the faint of heart. For a discussion of the development of Cincinnatian stratigraphic nomenclature, and a good introduction to the various stratigraphic approaches that have been used in the past to investigate both biostratigraphy and lithostratigraphy, the reader is referred to the excellent summary by Davis & Cuffey (1998). In a previous paper (Ross & Ross 2002) used the concepts of sequence stratigraphy to trace depositional packages through the succession and examined the details of the latest Richmondian depositional sequence. We draw on data from that paper.

2 GEOLOGICAL SETTING

This study examines bryozoans of the uppermost Cincinnatian, upper Richmondian Stage strata, which are the youngest Ordovician strata in the area. The western exposures of these strata are along the western margin of the Cincinnati Arch from near Richmond, Indiana, in the north, and extend southward beyond Frederickstown, Kentucky, in the south, about 220 km (Figs 1, 2, 3). This outcrop belt is relatively narrow, about 20 km wide, is a shallow shelf-margin facies and passes to the west into the Sebree Trough. To the east, these rocks are bounded by beds that are lower in the Richmondian Stage or even down in the Maysvillian Stage, and, to the west, by a major regional unconformity that is overlain by the Silurian Brassfield Limestone. At both the northern and southern ends of the Cincinnati Arch, this outcrop belt of upper Richmondian beds swings eastward across the arch and connects to outcrops of the Preachersville Member (upper member of the Drakes Formation) on the eastern flank of the Cincinnati Arch. The lower members of the Drakes Formation are not present (except for the possibility that the Otter Creek beds at the base of the Preachersville Member are a thin Bardstown Member equivalent) and were either not deposited or removed by erosion so that deposition is not as complete as on the western side of the arch.

The upper Richmondian beds and sedimentary features we are calling the Whitewater-Drakes depositional sequence. Admittedly a term of convenience, it makes use of two stratigraphic names that are recognized in this upper part of the stratigraphic section and which define fairly well a large third-order depositional sequence in the uppermost Richmondian Stage. Parts
Figure 2. Stratigraphic nomenclature and relationships for the upper part of the Richmondian Stage and various usages. See Davis and Cuffey (1998) for further details of the southeastern Indiana formations. Note the change in the middle of the chart from a north to south to an east to west orientation.

of the Whitewater-Drakes depositional sequence have been variously called in Indiana (Fig. 2) but include the Whitewater Formation in its broader usages. The upper member or tongue of the Whitewater has been called the Elkhorn beds (or Formation) near Richmond, Indiana, and Hitz beds in western central Kentucky. Near the middle of the Whitewater is the Saluda Member (or sometimes Formation) and the beds below form the lower member or tongue. These lower beds have been variously included in the upper part of the Tanner’s Creek Formation, or the upper part of the Dillsboro Formation, or the upper part of the Brookville Formation, or the ‘Liberty Formation’. Ross & Ross (2002, fig. 1, section 7) erroneously placed the lower portion of the lower member in the ‘Liberty’ instead of as the basal beds of the Whitewater Formation.

In west-central Kentucky, equivalent strata are the Drakes Formation (Weir et al. 1965) with its several members, the Rowland, Bardstown, and Saluda. In east-central Kentucky (on the eastern side of the Cincinnati Arch), the Rowland Member is restricted to the southern part of central Kentucky. The overlying Preachersville Member is much more extensive (Weir et al. 1984) and it is traced northward into Ohio as far north as Dayton, Ohio, where it becomes a silty and clayey facies of the upper member of the Whitewater Formation. Thus, the middle and upper Whitewater and the Preachersville complete an encirclement of the uplifted center of the Cincinnati Arch.

In addition to our own measured and described stratigraphic sections (Ross & Ross, 2002, and unpublished), which were collected for bryozoans, we have referred to, and remeasured and redescribed, most of the stratigraphic sections published by Hattin et al. (1961), Fox (1962), Utgaard & Perry (1964), Hatfield (1968), Hay et al. (1981), Weir et al. (1984), Davis & Cuffey (1998) and a long, long list of others, which, when combined, provide a great deal of additional information. The papers noted above cover much of southeastern Indiana, southwestern Ohio, and northern west-central Kentucky and permit good stratigraphic ties to the studies by Weir et al. (1984) in south-central and west-central Kentucky. We remeasured and reinterpreted many of Weir et al.’s (1984) published stratigraphic sections in Kentucky because we found the published sections to be too generalized and did not record the data we needed. In particular, these sections recorded only the general lithologies and did not describe the details of bedding features or unconformities.

The exposures of the Whitewater-Drakes depositional sequence (Ross & Ross 2002, fig. 1, section 52) show classic features of shallow water depositional facies in the south near Fredericktown, Ky, that gradually pass northward through a thick, shallow-water, shelfal, silty and silt-size dolostone facies of the Saluda Member, and then into a slightly deeper facies of the Whitewater Formation toward the north end of
Figure 3. Summary sections of the Whitewater-Drakes depositional sequence along a north-south line from north of Versailles, Indiana, to south of Fredrickstown, Kentucky. They show the facies changes of the unit from shallow off-shore in the north to shallow near-shore environments in the south. Wavy lines in the Whitewater Formation are minor (metre scale) unconformities that can be traced into the Saluda Member and the Bardstown and upper part of the Rowland members to the south. Sections are oriented on the 30 cm black siltstone and shale bed in the Saluda Member. The base of Brassfield Limestone is considered an irregular, but relatively horizontal surface. Considerable more lithologic detail for individual stratigraphic sections is provided by Hatfield (1968), Hattin (1961), Fox (1962), Weir et al. (1984), Utgaard & Perry (1964) and Ross & Ross (2002).

The exposed depositional facies are highly oblique to the depositional dip. In Kentucky, the Cincinnati Arch is to the east of the line of sections and the Sebree Trough is toward the west, but, in southeastern Indiana, the north end of the line of section crosses into the Sebree Trough (Kolata et al. 2001) (Fig. 1). Fox (1962) and Hatfield (1968) in their studies of the Saluda Dolostone Member found a 30 cm thick, black, pyritic siltstone and shale within the Saluda which they were able to trace northward and southward for a total of 220 km in the sections shown in Figure 3 before it changed facies and no longer was recognizable. We interpret this black, pyritic siltstone and shale bed to be a ‘maximum flooding surface’ of a third-order depositional sequence and the facies below it as a ‘transgressive systems tract’ and the facies above it as a ‘highstand systems tract’ in the sense of Vail et al. (1977). This forms our Whitewater-Drakes Depositional Sequence.

3 BRYOZOANS IN THE WHITEWATER-DRAKES DEPOSITIONAL SEQUENCE

The upper Richmondian bryozoan faunas and their distributions are shown in Table 1 and representative bryozoans are illustrated in Figures 4, 5, 6. Large, intact Parvohallopora are common in the beds beneath the Mid-Richmondian unconformity (Fig. 4). In the Whitewater-Drakes beds, several bryozoan genera are

consistent present and include common Rhombotrypa, Parvohallopora, Constellaria, Heterotrypa, Bythopora, Homotrypa and cryptostomes (Figs 5, 6).

3.1 Frederickstown section

The Rowland Member in the lower part of the Drakes Formation in central Kentucky rests unconformably on a middle Richmondian erosion surface (the Central Kentucky hiatus) and does not extend northward beyond central Kentucky (Weir et al. 1984). Fossils are scarce in most of the Rowland which is dominated by siltstone and very silty calcarenite. At Frederickstown, we interpret the Rowland to be mainly an estuarine deposit and to the north, near Bedford, it grades into marginal marine deposits. Within the Rowland, especially seen in the Frederickstown section where the member is 13.3 m thick, two well-developed fourth-order depositional cycles or paracycles are separated from the underlying deposits of the Reba Member of the Ashlock Formation by an erosional unconformity 0.8 m above the base of the Rowland Member as defined by Weir et al. (1984) and another unconformity 8.0 m higher in the member. The top of this second cycle extends upwards to the base of a calcarenitic packstone/grainstone at 8.9 m which Weir et al. (1984) actually place about 4 m up in their Bardstown Member. Each of the two Rowland cycles has a uniformly-grained, silty calcarenite that has gently sloping cross-beds and lies above an erosional surface having several centimetres of relief. They form typical fourth-order sequences.

At Frederickstown, the Bardstown Member also includes parts of two fourth-order sequences. The lower depositional cycle starts with a ripple-bedded calcarenitic packstone/grainstone, 2.7 m thick, (which rests on top of the second Rowland cycle below). This cycle is 6.7 m. The second cycle starts with a ruble of overturned coral heads that is 1.3 m thick, which Weir et al. (1984) placed in the upper Bardstown, and extends higher into the Saluda Member, 4.2 m thick. This is capped by a 1.6 m siltstone which forms the top of the Drakes Formation and which is a weathered interval beneath the Brassfield Dolostone.

Many beds of the Bardstown Member are abundantly fossiliferous (Figs 5A, B, C). Samples from the lower cycle contain a succession of Heterotrypa, Homotrypa, abundant Parvohallopora, Homotrypella, Rhombotrypa, and Bythopora? The 1.3 m beds with the overturned corals have Rhombotrypa, Escharopora, Bythopora, and Graftodictya in the lower part and Parvohallopora, Graftodictya, Bythopora and fragments of trepostomes and cryptostomes in the upper part. Higher in this cycle, but in the part called Saluda, the dark siltstone/shale marker bed has Escharopora, Graftodictya, and Parvohallopora (Figs 5D, c). The highest bryozoan-bearing collection from burrowed, sandy, dolomitic siltstone in the upper part of the Saluda has Parvohallopora and trepostome fragments.

3.2 Clifty Creek section

In this section and the nearby Madison section (which is now a better exposed section) show the Saluda Member well. Using the black to dark pyritic siltstone and shale bed as a marker, these unconformity-bounded depositional units can be traced northward where they thicken and change facies into dolomitic siltstone and dolostone and thus include the Bardstown cycle in the lower part of the Saluda (Fox 1962,
Figure 4. A, B, C. Transverse, oblique and longitudinal sections of *Parvohallopora* in a dolomitic limestone, probably the Liberty Formation, just below the middle Richmondian unconformity, Caesar Creek spillway at Caesar Lake State Park, Ohio.
Figure 5. A, B. *Parvohalupora* and other fragments of trepostomes in a slightly recrystallized, very silty, fine calcarenite in the lower four-order depositional unit of the Bardstown Member, Drakes Formation. C. *Rhombotrypa* with an overgrowth of *Panothallopora*? and burrowed by a sponge or gastropod, upper fourth-order depositional unit of Bardstown Member. D. Recrystallized calcareous siltstone and calcarenite with fragments of trepostome and other fossil fragments and vugs filled with sparry calcite, Saluda Member, Drakes Formation, Frederickstown section, Kentucky (see Ross & Ross, 2002, figure 1, Section 52).
Figure 6. A, B, D. Bythopora, cryptostomes, trepostomes, echinoderm columnals, and other fossil fragments in a reddish, dolomitic, recrystallized mudstone from the top of a red-bed succession (Queenston delta elastics) in the base of the Preachersville Member of the Drakes Formation, Ohio Brush Creek sections, north of West Union, Ohio (see Ross & Ross, 2002, figure 2, Section 10). C. Trepostome and cryptostome fragments in a dolomitic recrystallized, siltstone and shale with recrystallized ostracodes and brachiopods, Saluda Member, Frederickstown section, Kentucky.
Hatfield 1968, Davis & Cuffey 1998). At least three or four different positions have been suggested for the base of the Whitewater as shown by Ross & Ross (2002, fig. 1, section 7) in the nearby section along U.S. highway 421 at Madison, Indiana. Hattin et al. (1961) placed the boundary at the base of the prominent dolomitization of beds, Ross & Ross (2002) would now place the boundary about 6 m higher at the base of a prominent fourth-order package of sediments, Cuffey (1998) placed the boundary 8 to 9 m higher at the beds immediately below the lower Tetradium bed, and Hatfield (1968) considered a position 10 m higher still with the first occurrence of massive bedded laminated siltstones. Higher, beds in the Saluda appear beneath the Brassfield unconformity and, in addition, some thin beds of the upper tongue of the Whitewater may be locally present at the top just below the Brassfield transgression.

Samples from the ‘Liberty Formation’, or upper portion of the Brookville Formation, at the Clifty Creek Power Plant section near Madison, Indiana, contain small Parvohallopora, Homotrypa, Peronopora, Bythopora, and Rhombotrypa. A sample 1.5 m below the top of the ‘Liberty Formation’ has Parvohallopora, Bythopora, Escharopora, Graptodictya, Crepipora and numerous small fragments of cryptostomes which occur in a coarse late-phase sparry calcite cement. Above, two samples in the lower 2 m of the lower tongue of the Whitewater Formation have Bythopora, small Parvohallopora, Rhombotrypa, Graptodictya, numerous trepostome fragments and Tarphophragma?, Heterotrypa, Crepipora?, and many compound and solitary corals in higher beds. About 3 m higher, in the lower part of the Saluda Member, the bryozoan fauna includes Parvohallopora, Monticulipora?, Graptodictya?, Rhombotrypa, Bythopora, Stictopora, Escharopora, and abundant trepostome and cryptostome fragments, along with the coral Tetradium. And 1.5 m higher, just below the black siltstone/shale marker bed, algae and trepostome fragments are common, but the fauna is very limited in variety possibly reflecting salinity changes (Butler and Cuffey, 1996) or cooler water temperatures as the end of the Ordovician glacial period neared. Higher, in the upper part of the Saluda, bryozoans are sparse and usually lacking. The highest sample, identified as basal Brassfield, is probably from the topmost bed of the very thin upper tongue of the Whitewater Formation exposed at this locality. It contains Parvohallopora?, cryptostomes, trepostome fragments, a tabulate coral (?), a stromatoporoid, and a few crinoid columnals.

3.3 Versailles section

The Versailles, Indiana, section includes the lower tongue of the Whitewater Formation, which been called the upper part of the Tanner’s Creek Formation, the ‘Liberty Formation’, a much reduced Saluda Dolomite Member, and part of the upper tongue of the Whitewater (Hattin et al. 1961, Ross & Ross, unpublished). Here, and to the north at least as far as Hamburg and to the south as far as Clifty Falls, the lower and upper tongues of the Whitewater have well-developed metre-scale transgressive-regressive depositional cycles with exposure surfaces and transgressive sedimentary features at the base of each one. In the vicinity of Versailles, Fox (1962) and Hatfield (1968) were able to trace the transgressive cycles laterally from the Whitewater Limestone facies southward into the Saluda Dolostone facies. They showed that the lower part of the Saluda (below the black silstone/shale marker bed) at Clifty Falls was equivalent to the lower tongue of the Whitewater and that the upper part of the Saluda passed laterally into the lower part of the upper tongue of the Whitewater. The Versailles section represents a section near the northern limit of the Saluda Dolostone outcrop.

At Versailles, from the lower tongue of the Whitewater, the lowest bryozoan sample includes abundant Parvohallopora and Bythopora. The overlying two samples have Bythopora and numerous small trepostomes. Three samples from the Saluda are dolomitic mudstones and contain a limited fauna of Bythopora and numerous fragments of trepostomes. In the overlying upper tongue of the Whitewater, faunal diversity increased and Bythopora, Dekayid, Dekayia and numerous trepostomes occur low in the member, followed higher in the section by Parvohallopora and Bythopora in a fine calcarenite grainstone with large crystals of sparry calcite cement and an unidentified trepostome in a mudstone. Near the top of the exposure, Bythopora occurs along with fragments of small trepostomes in a mudstone, and trepostome fragments with gastropods, brachiopods and a variety of shell hash occur in a grainstone/packstone with sparry calcite cement. A mudstone near the top of the exposure contains Parvohallopora, Bythopora?, and trepostomes.

3.4 Localities north and east of Versailles

Utgaard & Perry (1964) studied bryozoans in a series of Whitewater outcrops from Versailles, toward the north to Richmond, Indiana, and then eastward to the Wright Brother’s Memorial, northeast of Dayton, Ohio. As they had no marker beds that they felt they could use as a stratigraphic horizon within this interval of the Richmondian, they located their collections stratigraphically based on the distance below the Brassfield-Richmond contact. They reported bryozoan faunas including Monticulipora, Homotrypa, Homotrypella, Mesotrypa, Peronopora, Heterotrypa, Cyphotrypa, Stigmatella, ‘Batostomella’ Constellaria, Nicholsonella, Amplexopora, Rhombotrypa, Hallopora (=Parvohallopora), and Batostoma. Many of these
are from only one or a few samples, and some are possibly actually from below the mid-Richmonian unconformity.

On the east side of the Cincinnati Arch, one set of bryozoan samples (Figs 6A, B, D) are from the base of the Preachersville Member at the Ohio Brush Creek section, north of West Union, Ohio. These are in a thin, reddish, silty or muddy limestone immediately above ‘Queenstown redbeds’. The bryozoans are in a coquina and include Bythopora, Rhombotrypa, Ampelxopora, Graptodictyda, and a small Parvohallopora.

4 CONCLUSIONS

The Whitewater-Drakes depositional sequence forms the upper part of the Richmondian Stage of the Cincinnati Series and is an extensive sedimentary package around the Cincinnati Arch. The general regional structural interpretations of Ettensohn (1991, 1999) and Pope & Read (1995), place the origins of the Sebree Trough during the Mohawkian Stage (Ordovician) with the uplift of the Lexington Platform. We see the Whitewater-Drakes depositional sequence as bounded at its base by the regional unconformity associated with a mid-Richmonian uplift and erosion in the central Kentucky area and renewed downwarping of the Sebree Trough as one of several late Ordovician tectonic reactivation phases during structural adjustment to the Taconic orogeny. The basal boundary is, therefore, if defined strictly, a tectonic sequence boundary. This was followed by a gradual rise in sea level and an influx of sands, silts, and clays from sources to the east which intertongued with shallow water marine deposition in the west. The Whitewater-Drakes deposition is terminated by the unconformity at the end of the Ordovician and beginning of the Silurian which had a hiatus of 7 MA or more. The distribution of lithofacies in the Whitewater-Drakes depositional sequence fits well into such an interpretation.

Bryozoan faunas in the Whitewater-Drakes sediments are consistent in having the same association of genera present. Genera include Monticulipora, Homotrypa, Homotrypella, Mosetotrypa, Pneronopora, Hetemtrypa, Cyphotrypa, Stigmatella, ‘Batostomella’, Constellaria, Nicholsonella, Ampelxopora, Rhombotrypa, Parvohallopora, and Batostomatida. Most genera that are present range up from older units but in the Whitewater-Drakes the diversity of species in these genera is remarkably lower and the number of fossiliferous beds are much more limited. However, those genera and species that do occur form a consistent association of surviving Richmondian genera. Taking lithologic facies distributions and bryozoan occurrences into consideration, on the eastern side of the Cincinnati Arch in the siltstones and silty beds of the Preachersville Member, bryozoans are rare and often poorly preserved. On the western side, in the Bardstown and Saluda members, bryozoans occur in marine tongues, commonly relatively thin, of marine limestones, and commonly as resedimented fragments in shallow, near-shore facies. In the Whitaer facies, they appear more commonly but again in limestones and silty limestones at the margins of the Sebree Trough.

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Bryozoan facies in deep-sea Pleistocene environments of southern Italy

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ABSTRACT: The analysis of Pleistocene bryozoan species present in deep-water sediments and rocky substrata presently cropping out in southern Italy lead to the recognition of seven different assemblages. The hard bottom assemblage is oligospecific, comprising a few encrusters whereas soft bottom assemblages are altogether more diversified except for the usually monospecific foraminiferan oozes. In all other soft bottoms, a-diversity and specimen abundance seem together with species and zoarial growth form distributions seem roughly positively related to bathymetry and to bottom grain-size.

1 INTRODUCTION

In the present day Mediterranean the bathyal zone develops from 150-250 m, corresponding to the transition from the circalittoral zone down to the deepest bottoms. Whereas Pérès & Picard (1964) and Pérès (1982) highlight a general depth homogeneity, according to Carpine (1970) an epibathyal zone, down to about 500 m, followed by a mesobathyal zone, ranging down to about 2000 m can be recognised. Further attempted models, such as that by Emig (1997), appear complex.

Although knowledge on these largely inaccessible environments is still largely inadequate, two different biocoenoses have been described: the White Corals Biocoenosis (CB) and the Bathyal Mud Biocoenosis (VP). The former is characterised by scleractinians, mainly Lophelia pertusa Linnaeus, 1758 and Madrepora oculata Linnaeus, 1758 locally associated with Desmophyllum cristagalli Milne-Edwards & Haime, 1848, which form deep bioconstructions on hard bottoms up to depth of 1200 m. The latter biocoenosis develops on soft bottoms and, according to Pérès and Picard (1964) and Pérès (1982), shows six facies in relation to topographic and edaphic conditions i.e. firmness or fluidity of bottom muds and presence of a certain amount of sandy or gravelly fractions, in turn, largely linked with hydrodynamism. The facies identification is made using macrofaunas, i.e. the cnidarians Funiculina quadrangularis (Pallas 1766) and Isidella elongata (Esper 1788) (and above all the swimming decapods and Parapeneaus longirostris (H. Lucas 1846), respectively, following Carpine 1970) the sponge Phoronema gravi Saville Kent, 1886 the echinoid Brissopsis lyrifera Forbes, 1841 and the brachiopod Gryphus vitreus (Bom 1778). The above cited authors do not use bryozoans, seemingly for their small sizes and relative unimportance in the assemblage.

Assemblages referable to the above recorded biocoenoses have been reported from the Plio-Pleistocene of southern Italy. According to Di Geronimo (1987) the dominance of the different scleractinian species allows local variations to be detected within the CB Biocoenosis whereas the VP Biocoenosis shows variations in relation to palaeociffs proximity, involving local enrichment in organogenic sands. Observed differences relate to mollusces, barnacles, brachiopods and cnidarians. Again, also Di Geronimo (1987) makes no mention of bryozoans.

Changes in composition and structure of Pleistocene deep-water assemblages have been stressed recently (Barrier et al. 1996, Di Geronimo et al. 1997) above all for bathyal muds suggesting that ‘several soft bottom facies do exist, conditioned by a close interaction of bathymetric, edaphic and hydrodynamic factors’ (Di Geronimo et al. 1997). A distributional scheme of nuculoid bivalve associations has been attempted, mainly in relation to depth (La Pema 2003).

As regards bryozoans, it has been already stressed that both Pliocene and Pleistocene faunas are compositionally different (Moissette & Spjeldnaes 1995, Rosso 1990, 2002a, 2002b, 2003, Di Geronimo et al. 1996, Rosso & Di Geronimo 1998) from those living in the Mediterranean at the present (d'Hondt 1977, Harmelin 1979) or even during the Holocene (Di Geronimo et al. 2001), and more similar to the Recent Atlantic ones. Notwithstanding almost nothing is known about composition and structure of deep-water assemblages as efforts mainly relate to taxonomy in both NE Atlantic (cf. Hayward 1979, 1994) and the Mediterranean where studies have been mainly
focussing on evaluating relations with the Atlantic faunas (Harmelin & d'Hondt 1992, 1993 for instance).

The present paper attempts to analyse the composition and structure of Pleistocene bryozoan assemblages in relation to edaphic conditions (sediment size largely related to bottom hydrodynamic conditions, sediment supply and \textit{in situ} biogenic production) and inferred bathymetry.

Data comes from southern Italy where deep-sea assemblages are rather common in deposits of Pleistocene age. The strong Plio-Quaternary tectonic activity, involving extensive vertical displacements, allowed usually small, post-orogenic basins to develop. They were normally affected by sintectonic activity and often developed rapidly, in time and space, until they reached bathyal depths. Consequently infilling deep-water sediments also deposited in proximally located palaeoenvironments often swept by strong bottom currents. Presently, outcroppings expose shallowing and/or deepening successions, often including deep-water fossiliferous siliciclastic or mixed sediments, sometimes side by side with fossilised deep scarp-faults, once bounding paleobasins, and/or deep rocky reliefs. Skeletal remains are usually preserved \textit{in situ} or in subprimary position on and near rocky substrata, as they were suddenly covered by muddy or silty sedimentation. These fossil assemblages, although somewhat biased by diagenesis (preventing the fossilization of several organisms), usually reflect original palaeocommunities, thus representing a suitable source of information about deep-water facies, their distributional pattern and their lateral replacement.

2 MATERIALS

All samples come from southernmost Italy, mostly from the Messina Strait zone and neighbouring areas (Fig. 1); a few come from south-eastern Sicily. The former zone is part of the Kabilo-Calabrian Arc, a sector of the Apennine Chain. According to Barrier (1986, 1987) during Plio-Quaternary time, it was dissected by sintectonic faults in several blocks acting as ‘tectono-sedimentary entities’ evolving independently. Sediments comprise basal white marls (Trubi), Lower Pliocene in age, followed by ‘lower bioclastic calcarenites and sands’ testifying different palaeoenvironments; clays and marls containing deep-water assemblages; ‘upper bioclastic sands’ and ‘clinostratified gravels and conglomerates’, interpreted as fore-sets of a delta-Gilbert system. Basin individuation and evolution together with facies spatial and succession distribution within blocks are diachronous. It follows that deep-water sediments deposited from Lower to Middle Pleistocene.

Bryozoans were studied, mainly from bulk-samples (quantitative samples) consisting in a sediment volume of about 6 dm$^3$; in the few instances of smaller samples data were normalised to 6 dm$^3$ to enable comparisons. Sediments were routinely treated i.e. washed, sieved by 250 pm mesh net and picked for all bryozoan colonies and fragments; the 250-500 pm fraction examined for articulate, slender species. Attention was paid to identify displaced (abraded and old-looking) and ecologically incompatible species and specimens in order to select assemblages corresponding to \textit{in situ} palaeocommunities. Specimens were scored and relative abundances calculated to evaluate the community structure.

Also qualitative samples, not comparable in size or in mesh sizes with the previous ones, as they were usually not specifically collected for bryozoan studies, were used. Finally, careful field observations were performed on wide surfaces of uncollectable, rocky bottoms. In these latter instances species lists were obtained and abundances of species only roughly estimated.

Samples come from different localities and palaeoenvironmental situations.

Some were collected near fault-scarps. This is the case of the Fumari outcrop (north eastern Sicily). There a fault plane is well exposed, colonised by spaced corals, serpulids and bivalves (Fig. 2), and largely affected by early diagenesis also cementing discontinuous coral rubble deposits within pockets along the scarp (Di Geronimo et al. in press). Silts, Lower Pleistocene in age deposited laterally, at an inferred depth of 400-500 m. Two quantitative samples (F in

Figure 1. Location of the studied bryozoan bearing Pleistocene deep-water outcrops from southern Italy: L: Lazzàro; A: Archi; C: Vallone Catrica; F: Fumari; Me: Messina neighbouring; SB: Serra S. Biagio, near Fiumefreddo; CF: Contrada Falconara; P: Palione river.
Fig. 1), one from a rubble pocket (Fig. 7) and one from the silts, a dozen metres from the scarp-foot, were analysed. Observations were made along the palaeoescarpment.

The situation is similar in the Lazzàro quarry, on the eastern side of the Messina Straits (Barrier 1987, Barrier et al. 1996). There the ‘Lazzàro marls’, about 13 m thick, deposited on and near the scarp foot, caused by a main NE-SW fault system, at a depth of more than 500 m, during the Lower Pleistocene (Violanti 1988) or partly during the Middle Pleistocene, as suggested by Aifa et al. (1987). The grey bathyal marly unit lay on a basal hard ground and show a sub-horizontal stratification marked by the presence, at 3-4 m from the base, of some silty layers, 20-30 cm spaced (Fig. 8). These layers are rich in the bathyal bivalve *Delectopezeten vitreus* (Gmelin 1791) (Fig. 9). Boulders (some cubic decimetres to some cubic metres in size) are also present, mainly in their basal part, originated from different depths along the fault scarp (Barrier et al. 1996) and fallen down within the bathyal marls depositional basin. Their surfaces are often heavily encrusted by sessile bathyal fauna (Figs 3-6) mainly serpulids, such as *Neovermilia fal-cigera* (Roule, 1898), corals such as *Lophelia pertusa*, *Madrepora oculata*, *Caryophyllia coronata* Seguenza, 1864 and *Keratozisis melitensis* (Goldfus 1826) and the bivalve *Spondylus gussoni* (O.G.Costa 1829). Boulders are draped by coarse biogenic sediments and surrounded by bioclastic rims (Figs 4-6), whose width is related to their sizes. These organogenic sediments contain complete or fragmented skeletons of species, which lived on the boulders. Sixteen quantitative samples (L in Fig. 1) were selected to document all these situations.

Rocky palaeoescarpments seemingly do not crop out presently in the Messina neighbourhood but their presence is documented by thick coral-rubble bodies (Di Geronimo & Vertino 2003, Vertino 2003) which can be interpreted as rubble apron (*sensu* Freiwald et al. 1997) once bordering foot scarps and by isolated, large blocks, collapsed within deep, pelitic to silty-sandy, sediments and encrusted by deep-sea faunas. Depositional settings vary from shelf-slope transition to shallow upper-slope. Several qualitative samples (M in Fig. 1), mainly from Monte Spalatara, Scoppo, Calorenni, Salice, Camaro, S. Filippo, have been screened. Depositional age seems to be Calabrian for all but Calorenni sediments, deposited during the Sicilian (Violanti 2003 pers. comm.).

In the Archi quarry a 9m thick, Lower to Middle Pleistocene (MNN19e and MNN19f Zones) pelitic succession is exposed (Di Geronimo et al. 1997). It is composed of two superimposed bed sets, the lowermost one involved in a gentle flexure seemingly caused by near-bottom currents acting as eddies making the bottom wavy, and the, unconformably laving, uppermost one, constituted by basal silty-to-sandy layers evolving into true muds. Changes in hydrodynamic conditions are documented along the section affecting sediment size and depositional rate together with composition and structure of bottom palaeocommunities, which presumably lived between 500 and 1,000 m. In the quarry 12 samples (A in Fig. 1) were collected, two from coarse sediment layers.

Additional samples come from the Vallone Catrica area. There, erosional surfaces are largely encrusted by deep-sea scleractinians and coral-rich sands locally fill depressions. A Lower Pleistocene succession approximately 20 m thick follows, consisting of basal displaced biogenic gravels evolving into deep-water marls testifying a progressive deepening, from the shelf-break to the upper-slope (Barrier 1987). Five samples come from the basal part of the marly sequence (C in Fig. 1).

Along the Serra S. Biagio Hill (Fiumefreddo) Sicilian marls, approximately 10 m thick, crop out within a quarry (Lanzafame et al. 1997). Near the base some, pectinid-bearing, sandy layers are interbedded. Several (qualitative and quantitative) samples (SB in Fig. 1) were collected, mainly in the marls.

A few other samples come from southern-eastern Sicily, along the northern side of the Hyblean Plateau. There, during Lower Pleistocene, marly-to-clayey sediments deposited along the upper slope of basins formed by the normal faulting, which affected the margins of the Hyblean foreland (Pedley et al. 2001). The studied samples come from a 12 m thick pelitic succession sampled along the Paliano river (Di Geronimo et al. 2003), where only one silty layer delivered bryozoan assemblages (P in Fig. 1), and from a 20 m thick marly succession showing sparse macrofaunas in Contrada Falconara (Grammichele; CF in Fig. 1).

3 RESULTS

3.1 Bryozoan assemblages

As already known (Harmelin 1992, Moisette & Spjeldnaes 1995, Rosso & Di Geronimo 1998) Pleistocene bryozoan faunas consist of Recent Mediterranean species, either with wide bathymetrical distributions, either restricted to bathyal environments. They also comprised a lot of species, which seem to be presently lacking from this basin, although still living in the near Atlantic, from the shelf-break to the upper bathyal zone and/or in deeper bottoms. *Crépis longipes*, *Buskea billardi*, and *Exidmonea flexuosa* belong to this stock and add to the list given by Rosso & Di Geronimo (1998). Finally a pool of palaeoendemic species is present, a few recently described (Rosso 1998, 1999, Rosso & Di Geronimo 1998) and others probably to be discovered in further material and/or
Figures 2-9. (2) Detail of the Furnari fault plane showing an encrusting base of the isidid *Keratoisis*. Scale bar: 5 cm. (3) The surface of a block from the Lazzàro quarry, heavily colonised by serpulid polychaetes. Scale bar: 10 cm. Figure (4) A metre cube block within the marls of the Lazzàro quarry. Scale bar: 50 cm. (5) A detail of the upper surface of a block from the Lazzàro quarry colonised by serpulids. Surficial depressions were filled by pectinid-bearing mud. Scale bar: 5 cm. (6) Upper surface of a block covered by rabble largely constituted by individual scleractinians. Scale bar: 10 cm. (7) Rubble largely constituted by coral fragments from a rubble-poket along the Furnari fault. Scale bar: 10 cm. (8) Pectinid-rich layers from the Lazzàro quarry. Scale bar: 1 m. (9) Close-up of a layer showing planar disposition of *Delectopecten vitreus* (Gmelin) valves. Scale bar: 5 cm.
re-evaluating species described or recorded mainly by Seguenza (1880) and Nevianif 1895,1898,1900,1904).

It is preliminarily worth noting, as bryozoans are completely absent only from sediments entirely or largely constituted by clays. Coarser sediments, even if they are muds with only slight silty or fine sandy fractions, contain bryozoans (Table 1), although invariably subordinate to other benthic taxonomic groups, such as molluscs and corals and secondarily, serpuloid polychaetes and brachiopods, as it is the case for Recent communities. Nevertheless, Pleistocene bryozoan assemblages seem to be rich and diversified if compared with Holocene and present day Mediterranean homologous ones (Rosso & Di Geronimo 1998, for a review, Di Geronimo et al. 2001), although the absence of quantitative data makes comparisons hard.

The specimen number varies greatly among samples (Table 1) and, if only one or a few specimens were found in some samples, other ones contain more than two thousand bryozoan colonies and/or fragments. These values seem to be comparable with data from the Lowermost Pleistocene epi-bathyal bryozoan assemblages from Rhodes (as evaluated from Moissette & Spjeldnaes 1995). The specimen number per sample, although some shifting, seems positively related to the species number, and better, with sediment grain size and, above all, with the presence of coarse, sandy and gravelly fractions, as expected.

As a whole 120 species have been detected with a sharp dominance of ‘ascophoran’ cheilostomes with about 60 species, the remaining number equally distributed between cyclostomes and anascans. This value outnumbers that recorded by Rosso & Di Geronimo (1998) of about 50 species, enlightening that future investigation will surely lead to further increases. This increment is mainly due to ‘ascophoran’ cheilostome species, rising from 42 to 50% (cf. Rosso & Di Geronimo 1998), thus involving a lowering of cyclostomes from 31 to 25%, a value close to that recorded by Harmelin (1988) for present day deep-water bottoms.

As a result of the common presence and also dominance of ‘ascophoran’ cheilostomes, rising from 42 to 50% (cf. Rosso & Di Geronimo 1998), thus involving a lowering of cyclostomes from 31 to 25%, a value close to that evaluated by Harmelin (1988) for present day deep-water bottoms. The species diversity per sample (Table 1) ranges from 1 to 41, most samples accounting for more than a dozen species. As for specimen number, comparisons with literature data on both Recent and fossil assemblages are inaccurate as none or little information is usually available about samples. Nevertheless these values are higher than those deduced from Moissette & Spjeldnaes (1995) for 250-400m deep bryozoan assemblages from Rhodes, never exceeding 11 species. These data seems comparable to that from the oceans where, according to Schopf (1969) 82% of samples from 200-600 m deep number more than 10 species, whereas less than 4% shows peaks of more than 50 species. Moreover, Pleistocene deep-water bryozoan diversity is comparable-to-very high in relation to that recorded from the Recent Atlantic, the Alboran sea (from about 200 to 600 m: Harmelin & d’Hondt 1992) and the north-western Mediterranean (from 180 to 350m: Zabala et al. 1993), where species number per sample usually ranges from a few to a dozen, with a few exception (from 19 to 22, and 31 in a single instance). Nevertheless, it could be stressed as bryozoan diversity suddenly lowers in shallower environments, at the shelf-break, where only 19 species have been listed, from 12 to 14 per sample, in south-eastern Sicily. This feature appears in contrast with the highest values (over 50 species) recorded by Harmelin & d’Hondt (1992), for 145-170m deep samples in the Alboran Sea.

In spite of the total species richness, most species are sporadic, sometimes present in single samples and accounting for low percentages (Table 3). They are extremely rare species, some of which deserve taxonomic investigation.

The bulk of the assemblages is given by only 13 species (6 of which cyclostomes) whose relative abundances range from about 40 to 90% in single samples, and mainly from 60 to 70%. Other 17 species are relatively common and abundant so that 12 cyclostomes and 18 cheilostomes constitute from 60 to 90% in each sample, usually from 70 to 80%. Sometimes a single species may account for extremely high percentages in a single or a few samples, seemingly as its distribution is related to peculiar favourable conditions occurring in certain sites, thus needing further investigations.

3.2 Bryozoan facies
At first sight, samples appear superficially similar owing to the common presence and also dominance of some species, mainly Tessaradoma boreale, Exidmonea triforii, Tervia irregularis, Hornera frondiculata, Anguisia verrucosa, Setosellina roulei and, to a less extent, Reteporella sparteli, Tervia barrieri, Tubulipora sp. 1, Heliodoma angusta, Setosella vulnerata and Gemellipora eburnea. Notwithstanding, taking into account the diverse palaeoenvironmental contexts, several facies can be distinguished, which appear to be mainly related to bottom features (Tables 1-3).

3.2.1 Hard bottom facies
Only some observations were made on palaeo-rocky bottoms (fault scarps and blocks) and sampling was performed only by picking. Bryozoans are very rare and barely detectable.

Assemblages are oligospecific, characterised by only a few encrusting species. Until now only five taxa have been found on rocky substrata, namely Copidozoum exiguum, Smittina crystallina, Stereachmella buski, Crépis longipes and Sertulipora guttata. Only partly preserved colonies and, sometimes, isolated zooids are available in the studied material for all of
Table 1. Species and specimen abundance and taxonomic structure of the Pleistocene deep-water bryozoan assemblages from southern Italy.

<table>
<thead>
<tr>
<th>Depth range (m)</th>
<th>400-500 up to 1,000</th>
<th>150-300</th>
</tr>
</thead>
<tbody>
<tr>
<td>Facies</td>
<td>Hard bottoms</td>
<td>Rubble</td>
</tr>
<tr>
<td>Quantitative sample number</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Qualitative sample number</td>
<td>some</td>
<td>some</td>
</tr>
<tr>
<td>Total diversity</td>
<td>5</td>
<td>75</td>
</tr>
<tr>
<td>Diversity ranges</td>
<td>0-3</td>
<td>12-41 (30-41)</td>
</tr>
<tr>
<td>Cyclostomes</td>
<td>23</td>
<td>21</td>
</tr>
<tr>
<td>Cheilostomes</td>
<td>5</td>
<td>52</td>
</tr>
<tr>
<td>Ctenostomes</td>
<td>Specimen number</td>
<td>not evaluated</td>
</tr>
<tr>
<td>Specimen number (max range)</td>
<td>not evaluated</td>
<td>&gt;2340</td>
</tr>
</tbody>
</table>

Table 2. Growth form structure of the Pleistocene deep-water bryozoan assemblages from southern Italy.

<table>
<thead>
<tr>
<th>Depth range (m)</th>
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<tr>
<td>Facies</td>
<td>Hard bottoms</td>
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</tr>
<tr>
<td>Quantitative sample number</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Qualitative sample number</td>
<td>some</td>
<td>some</td>
</tr>
<tr>
<td>Colonial growth form</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erect rigid</td>
<td>54-80(73-80)</td>
<td>41-70 (50-57)</td>
</tr>
<tr>
<td>Erect flexible</td>
<td>10-31</td>
<td>7-31 (7-17)</td>
</tr>
<tr>
<td>Encrusting</td>
<td>*</td>
<td>1-6</td>
</tr>
<tr>
<td>Setoselliniform</td>
<td>1-17</td>
<td>16-50(18-27)</td>
</tr>
<tr>
<td>Cellarinelliform</td>
<td>0-1</td>
<td>0-1</td>
</tr>
</tbody>
</table>

them, but $S.$ buski, forming wide sheets, yet not exceeding 1-2 cm². It is known that all these species form small-sized colonies, the former two species showing spot-like colonies whereas the latter two adopt a fugitive strategy developing running uniserial colonies. Owing to their sporadic presence and attained sizes, these species are extremely subordinate within the assemblage as a whole.

C. longipes and $S.$ guttata presently live in the Atlantic, being restricted to the Gibraltar Straits, whereas all other species also thrive in the Mediterranean sea. Nevertheless they seem to be very rare in this basin and have been recorded invariably from hard substrata constituted by rocky fragments or by skeletons of the scleractinians Lophelia and Madrepora (Harmelin 1979, Harmelin & d'Hondt 1992, Rosso 2003).

3.2.2 Rubble facies
Sediment is gravely sand or sandy gravel, usually rich in corals, corals and brachiopod or corals and serpulids, sometimes comprising centimetre-to-decimetre bio­clasts. This facies is present along palaeo­cliffs and at their base and also on blocks and in rims around them, usually from a few to some cm thick and a dm to a metre wide, rarely more.

This facies is the most rich and diversified. As a whole 75 species, largely cheilostomes (52: 69%), have been detected. The number of species per sample is usually higher than 30, with a maximum value of 41, and a single low value (12). Also the specimen number is high ranging from about 600 to 3000, with the lower values in correspondence of smaller blocks with the only exception (212) of the very large­sized rubbles along the Fumari fault scarp.
Table 3. Systematic list of the most frequent and abundant taxa constituting the Pleistocene deep-water bryozoan assemblages from southern Italy. For each species the frequency (number of findings on the total number of samples) and the ranges of relative percentages (in brackets) for each recognised facies, is given. Stars indicate presence when only qualitative samples were available. No value is given for subordinate species with wide bathymetric distributions. Bold marks species restricted to bathyal environments and underlined species distributed from the shelf-break to bathyal environments, in both Recent (Atlantic and/or Mediterranean) and fossil assemblages. § = Palaeo-Mediterranean endemic; ° = Absent from present day Mediterranean but living in the Atlantic.

<table>
<thead>
<tr>
<th>Depth range (m)</th>
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<th>150-300</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Hard bottoms</td>
<td>Rubble</td>
</tr>
<tr>
<td>Quantitative sample number</td>
<td>some</td>
<td>5</td>
</tr>
<tr>
<td>Qualitative sample number</td>
<td>some</td>
<td>some</td>
</tr>
</tbody>
</table>

Species

- **§ Crisia lenella longinodata** Rosso: 1(2)
- **Crisia conferta** Busk: 6(1-5), 2(4-9)
- **Crisia spp.**
- **Anguisia verrucosa** Jullien: 2(1-9), 6(1-30; 27-30), 5(1-12), 1(2)
- **?Anguisia sp.**
- **Annecotypma major** (Johnston)
- **Annecotypma tubulosa** (Busk)
- **Entalophoroecia deflexa** Couch: 2(<1), 4(<7), 2(2-9)
- **Entalophoroecia gracilis** Harmelin: 3(1-9), KD
- **Diplosolen obelium** (Johnston)
- **Frondipora verrucosa** (Lamouroux) §
- **Tervia barrieri** Rosso: 3(2-13), 3(6-20), 1(5), 1(9)
- **Tervia irregularis** Meneghini: 5(1-18), 6(2-12), 7(4-27), 2(1-5), 2(11-14)
- **Exidmonea coerulea** Harmelin KD 1(1)
- **Exidomonea cf. flexuosa** (Pourtales): 2(2), 2(1-9)
- **Exidomonea triforis** (Heller) 4(3-14), 5(1-10), 5(6-18), 2(3-8), 2(9-42)
- **Cardioecia watersi** (O’Donoghue & de Watteville) 4(1-4), 1(6), 4(2-14)
- **Platonea stoechas** Harmelin §
- **Tubulipora notomale** (Busk) 4(1-3), 3(1-3), 3(1-4), KD 1(3)
- **Tubulipora sp.** 1 (<D)
- **Homera lichenoides** (Linnaeus) 5(1-12), 8(5-45), 7(1—4), 3(2-9)
- **Homera frondiculata** Lamouroux 4 (<10), 5(2-10), 2(1-5), 2(11), 2(1-3)
- **Hornera lichenoides** (Linnaeus) 4(1-3), 3(1-3), 3(1-4), KD 1(3)
- **Aetae spp.**
- **Copidozoum exiguum** (Barroso) 4(1-3), 1(6), 4(2-14)
- **Amphibiestrum lyraatum** (Calvet) 5(1-12), 8(5-45), 7(1—4), 3(2-9)
- **Chaperiopsis annulus** (Manzioni) 3(1-3), 3(1-4), KD 1(3)
- **Onychocellla marioni** (Jullien) 5(1-12), 8(5-45), 7(1—4), 3(2-9)
- **Setosella capriensis** (Waters) 4(1-3), 3(1-3), 3(1-4), KD 1(3)
- **Setosella roulei** Calvet 5(1-12), 8(5-45), 7(1—4), 3(2-9)
- **Heliodoma angusta** Rosso 3(<1), 7(3-20), 2(1-4), 3(3-9)
- **Stereochmella buski** Lagaiij KD 1 Ki
- **Setosella vulnerata** (Busk) 5(<4), 4(1-15; 11-15), 5(1-9), 1(3)
- **Cellaria fistulosa** (Linnaeus) 4(1-3), 4(1-4), 1(<D), 2(2)
- **Cellaria salicornioides** Audouin 4(1), 4(1-10), 3(2-9), 2(1-10)
- **Cellaria sinuosa** (Hassall) 5(<21), 4(1-5), 4(<9), 2(<1)
- **Euginoma vermiformis** Jullien 5(1-2), 1(1), 3(1-3), 1(1)
- **Caberea boryi** (Audouin) 3(1-5), KD 4(1-5)
- **Caberella ligata** Jullien 3(1-5), KD 4(1-5)
- **Scrupocellaria incurvata** Waters KD
- **Scrupocellaria jullieni** Calvet
- **Scrupocellaria spp.**
- **'Bugulella ' elegans** Hayward 1(1), 3(1-3)
- **'Crepis longipes** Jullien 1(<D)
- **Hippothoa flagellum** Manzioni 2(<1)
- **Gemellipora eburnea** Smitt 3(3-9), 2(1), 8(12-46), 1(7)
- **Bryocryptella koehleri** Jullien & Calvet 2(1-5)
- **Smitllina cervicornis** (Pallas) (continued)
<table>
<thead>
<tr>
<th>Facies</th>
<th>Depth range (m)</th>
<th>400-500 up to 1.000</th>
<th>150-300</th>
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</thead>
<tbody>
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<td></td>
<td></td>
<td>Rubble</td>
<td>Sandy mud</td>
</tr>
<tr>
<td>Quantitative sample number</td>
<td></td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>Qualitative sample number</td>
<td>some</td>
<td>1 (&lt; 1)</td>
<td>2</td>
</tr>
</tbody>
</table>

**Smittina crystallina** (Norman)  
**Tessaradoma boreale** (Busk)  
**Adeonella calveti** Canu & Bassler  
**Adeonellopsis distoma** (Busk)  
**Diporula verrucosa** (Peach)  
**Microporella ciliata** (Pallas)  
**Chorizopora brongniarti** (Audouin)

**Characodoma mamillatum** (Seguenza)  
Deep form  
2 (< 1)  
2 (< 1)  
1 (21)  
2(1-11)  

§ **Characodoma reclinatum** Rosso  
§ **Characodoma rostratum** Rosso  
**Palmicellaria elegans** Alder  
**Palmiskenea skenei** (Ellis & Solander)  

**Sertulipora guttata** Harmelin & d’Hondt  
**Jaculina tessellata** Hayward  
**Buffbnellaria divergens** (Smitt)  
**Schizoretepora solanderia** (Risso)  
**Reteporella couchii** (Hincks)  
**Reteporella couchii biavicularia** Waters  
**Reteporella elegans** Harmelin  
**Reteporella sparteli** (Calvet)  
**Omalosecosa ramulosa** (Linnaeus)  
**Buskea dichotoma** (Hincks)  
**1 Buskea billardi** (Calvet)  
**Celleporina globutosa** d’Orbigny  
**Celleporina hassalli** (Johnston)

Erect rigid species sharply prevail representing from half, usually more than 70%, to about 80%. They are represented by some of the commonest species, mainly T. boreale, T. irregularis, T. barrieri, E. triforis, H. frondiculata, Palmicellaria elegans and R. sparteli. Erect flexible, usually rhizoid bearing, species (among which Caberea ligata, Cellaria spp. and Scrupocellaria spp.) follow ranging from 10 to 30%. Also setoselliniforms are well represented, mainly with S. vulnerata and S. roulei, although greatly varying from 1 to 17%. Encrusting species, although numerous and always present, appear very subordinate (1-6%) in spite of the availability of large substrata, which seem suitable for settlement of bryozoans in present day deep-water environments (see Harmelin & d’Hondt 1992, Zabala et al. 1993). The only species deserving a mention are S. bushi, C. longipes and Hippothoa flagellum, the former two also present in the hard bottom facies.

3.2.3 Sandy-silt facies
Sediment is silt with varying percentages of sand to which small amounts of gravel locally add. This facies is found in relatively distally located palaeo-environments, seemingly swept by bottom currents.

Both species and specimen richness are lower in comparison with the previous facies. Out of the 57 recognised species, 21 are cycllostomes, thus accounting for the 37%. Species diversity per sample shows a wide range, with most values from 6 to 21, with only two exceptions (37 and 40). Specimen number parallel this trend, with values usually ranging from 14 to more than one hundred, raising to 450 and 650 in the two more diversified samples. Noteworthy, high values were found in samples with slightly higher sandy fractions. Thus it seems that two subgroups could be distinguished but differences among them minimise when species composition and growth forms are analysed.

Erect rigid species still prevail, although they strongly lower in respect to the previous facies, ranging from about 40 to 70%, usually 50-57%. The commonest and more abundant species are almost the same as in the rubble facies, i.e. T. boreale, T. irregularis, T. barrieri, Exidmonea spp. H. frondiculata, to
which Anguisia verrucosa, Entalophoroecia spp. and Hornera lichenoides add. The decrease of erect species is balanced by a sharp increase of setoselliniforms, which range from about 16 to 27%, with peaks of about 50%. They are mainly represented by Setosellina roulei and Heliodoma angusta and subordinate by Setosella vulnerata. Erect flexible species remain substantially unchanged. Finally encrusting forms, absent in several samples, reach no more than 2%.

It could be stressed that A. verrucosa is more abundant in finer sediments, where it often reaches 27-30%, whereas an opposite trend is shown by S. vulnerata and H. lichenoides, which seem to prefer coarse gravel fractions.

3.2.4 Pectinid-rich mud facies
Sediment is mud with varying percentages of clays, always containing a coarse sandy fraction plus a little amount of gravel, largely represented by valves or fragments of the thin-shelled, deep-water bivalve Delectopecten vitreus. The life of such pectinids, and their possible slight displacement and mechanical accumulation, was enabled by bottom currents strong enough for prevent mud deposition at least periodically. Layers containing this facies are decimetre-thick and interbedded within finer sediments.

Assemblages consist of 54 species as a whole, but only 14 cyclostomes (26%) have been detected. Nevertheless, the number of species per sample is low and highly variable, usually from 9 to 15 with peaks of 26 and 27 in two instances. Also specimen number varies greatly, usually from 100 to 500, nevertheless some samples show lower values down to 20-40 and others reach 800-1100 specimens. These latter high values correspond to the most species-rich samples. Once again, it could be stressed that these samples are those in which the coarse fraction and pectinid shells were particularly abundant, as expected. On the contrary low specimen numbers were found in samples with very low amounts of pectinid fragments.

Looking at the composition, the distinctive feature of this facies is the high percentage of encrusting species accounting for 15-46% of the assemblage as a whole. Also Gemellipora eburnea (abundant in all samples: 12-46%) is included in this group as its colonies (consisting of erect articulate branches arising from a wide encrusting uniserial running base) need relatively large substrates, offered in this environments by the thin shelled Delectopecten vitreus valves. Pectinids are known to constitute the substratum for this species also in the Recent (Busk 1884). Also Cellarinelliforms, i.e. erect rigid rooted species, seem well adapted to this facies, although they are present, with highly variable percentages (3-21%), in only one half of the samples. Euginoma vermiciformis is the most common, though not the most abundant, species whereas Characodoma reclinatum is present in a single sample reaching 21%. Erect rigid species decrease more and more lowering to 26-40%, sometimes reaching about 50%. Also setoselliniforms sharply decrease in respect to the sandy facies, although present in almost all samples accounting for 1 to 9% (17% in a single instance). They are mainly represented by S. roulei and S. vulnerata, the latter being more abundant in coarser samples. Finally, among erect flexible species, altogether accounting for 14—32%, Caberea ligata and ‘Bugulella’ elegans are frequent and abundant.

3.2.5 Sandy-mud facies
Sediment is somewhat similar to that of the previous facies, yet containing only little quantities of sands, seemingly deposited during periods of low hydrodynamic flows increasing mud deposition.

A sharp diversity lowering in comparison to previous facies, is obvious. As a whole, only 35 species have been detected, 12 of which (33%) cyclostomes; the number of species per sample varying from 9 to 28. The specimen number ranges from 11 to about one hundred, with a single exception (a little more than 300).

From a compositional point of view, the main difference with the previous facies is the nearly complete absence of encrusting forms present in a single instance, with a good percentage. Erect rigid species remain substantially unchanged ranging from 35 to 56%. T. boreale, H. frondiculata, T. irregularis, Exidmonea cf. ßexuosa. E. triforis are the more frequent and abundant species. Also setoselliniforms (4 to 18%), always present and mainly represented by S. roulei and H. angusta, show the same trend together with the erect flexible forms (17-33%), although deep species, as Crisia conferta and Scrupocellaria incurvata, account for low percentages.

3.2.6 Foraminiferal ooze facies
Bryozoan assemblages are often lacking in pure globigerinid oozes; when present they seem particularly scant or tend to be oligo-to-monspecific. The rooted species ‘Bugulella’ elegans seems to be the characteristic species. This facies is often characterised by the presence of exiguous-to-large quantities of inputs from shelf, mainly shallow, environments. Crisia spp. and Scrupocellaria spp. intemodes are usually involved as they can be easily floated off and settled where current energy decreases, as observed in present day bathyal ooze oozes off north-eastern Sicily (Di Geronimo et al. 2001 and personal data). In Tertiary comparable palaeoenvironments Batopora rosula (Reuss) exploited the same ecological niche (Moissette 1996).

3.2.7 Sandy silt facies in the circalittoral-bathyal transition
Sediment is silt containing low percentages of organogenic sand and gravel, which deposited at and/or near the shelf-break, at inferred depths of no more than 300 m.
Total diversity is extremely low in comparison with all other facies: only 20 species have been found, of which cyclostomes, which thus account for over than 52%. In spite of this, the species number for sample is relatively high ranging from 12 to 14. Also the specimen number is considerable ranging from about 350 to 800.

The growth form structure is extremely simple as only erect rigid species are present, either fixed by a calcareous base, either by means of rhizoids. The former group, accounting for about 90%, is mainly given by T. irregularis, E. triforis, T. boreale and Entalophoroecia species, followed by H. lichenoides, Tubulipora notomale and R. sparteli. Cellarinnelliforms belong to Characodoma mamillatum and C. rostratum. Adeonellopsis distoma adds to these species in one of the quantitative samples and it is frequent and common also in several of the qualitative samples together with Bryocryptella koehleri, Palmiskenea skenei and P. elegans and sometimes with Amphibiestrum lyratum and Buffonellaria divergens.

4 DISCUSSION AND CONCLUSIONS

Seven different deep-water bryozoan assemblages have been distinguished analysing the distribution of 120 species from 26 quantitative samples and about an equal number of qualitative samples joined to field observations from Pleistocene southern Italy localities. Among them a single hard bottom facies is present plus six soft bottom facies, each characterised by different grain sizes ranging from sandy-gravelly rubbles to foraminiferan oozes. Assemblages mainly consist of species having a wide bathymetrical distribution to which pure bathyal, usually subordinate, species add, as expected. Pérès & Picard (1964), and Carpine (1970) have stressed comparable structures for the upper horizon of Mediterranean bathyal zone as a whole.

Assemblages can be recognised basing on a-diversity and taxonomic structure, joined to specimen richness and presence/absence, frequency and relative abundance of the species and the zoarial growth forms.

Some relatively euriecious taxa are widespread and common to assemblages belonging to different facies. This feature is not fully unexpected as several ecological, mainly climatic, factors are relatively constant and homogeneous in bathyal environments.

A few taxa, on the contrary, are restricted to a single facies, often to a single sample, where high percentages are sometimes reached. C. reclinatum, C. rostratum and, to a less extent S. julieni and B. koehleri, are examples. These are poorly known species or palaeo-endemic taxa known from single localities, probably extremely rare and/or linked to peculiar microenvironmental conditions.

In the depth range (150-1,000 m) inferred for studied assemblages, the distribution of species appears related to bathymetry. Only some species (A. lyndatum, A. distoma, C. mamillatum, B. divergens, O. ramulosa and B. dichotoma), whose upper limit raises to circalittoral bottoms, seem to prefer the shelf-break and the very shallow epibathyal. On the contrary, a numerous group of taxa (C. tenella longinodata, A. verrucosa, T. barrieri, E. flexuosa, Tubulipora sp. 1, C. exiguum, S. roule, H. angusta, S. buskii, E. vermiciformis, C. ligata, S. jullieni, B. elegans, C. longipes, G. eburnea, S. crystallina, C. reclinatum, S. guttata and/ or tessellata) seems to be restricted at major depths, seemingly below 400 m.

Taking into account only deep facies, the comparison of faunal composition among and within assemblages gives some insights about ecological factors, which controlled bryozoan species distribution. It is obvious that the main factor is the substrate and the bottom nature. A few encrusting taxa, are restricted to hard bottoms or to relatively large sedimentary, usually biogenic, grains, thus being common to the hard bottom and to the rubble facies. Several species are common to all soft bottoms, except for foraminiferan oozes, only colonised by B. elegans, also spreading to coarser bottoms, probably in strictly pelitic microhabitats. Other species are restricted to two or three facies, or are more frequent and abundant in these facies (Table 1). Among setoselliniform species, for instance, which are particularly well adapted to colonise soft bottom also encrusting sand grains on pelitic, even clayey, bottoms, increasing their base and floating on the substratum using setiform avicularian mandibles, preferences can be argued. S. vulnerata, also widespread in shelf environments, seems better adapted to coarse bottoms or at least, bottoms containing a certain percentage of large (gravel) grains. S. roule and, above all, H. angusta, the latter often found on Orbulinula universa d’Orbigny tests, show a marked preference for fine grained bottoms where they are more frequent and abundant. These latter species tend to become dominant when gravelly and/or sandy fractions decrease or disappear. Finally G. eburnea seems to prefer pectinid rich bottoms.

All the recorded taxa are small-sized. Most species, usually accounting for highest percentages, possess erect, both rigid and flexible, slender colonies involving exiguous encrusting bases or the presence of rhizooids or show growth adaptations to directly colonise soft bottoms. Likely, most erect rigid species lived as epibionts on deep-water large gorgonaceans and other soft-bodied cnidarians, sponges or other benthic invertebrates. Although not common, these organisms directly colonising the bottom, constitute veritable islands at bathyal depths, as observed in the Recent Atlantic (Tyler & Zibrowius 1992, Freiwald et al. 2002).
Similarly blocks collapsed from palaeociffs, seemingly acted as present day drop stones enabling colonization by species needing a hard substratum, which, in turn, constituted the physical and/or ecological support for other organisms. When dead, skeletons contributed to change the grain size of the surrounding bottoms, thus enhancing further, otherwise impossible, colonization. Thus the presence of boulders caused an environmental feedback triggering high diversity spots.

The apparent, among and within facies, composition similarity can be ascribed to exiguous lateral development of biotopes sometimes leading to potential displacement and mixing of sedimentary, including bioclastic, grains, caused by local biostratinomic and taphonomic processes, although the general strong rate of pelitic deposition usually enabled in situ burial.

The hard bottom facies appears fully referable to the White Corals (CB) biocoenosis, whereas most of the soft-bottom recognised facies (sandy silt, sandy mud, pectinid-rich mud and foraminiferan oozes), linked to different kinds of soft bottoms, represent facies of the bathyal mud (VP) biocoenosis. The rubble facies and the silty mud facies from shallow waters could be interpreted as transitional respectively between the CB and the VP biocoenoses and between the circalittoral and bathyal zones. Among soft bottom facies, only the pectinid-rich one seems to have a modern relative in the 'Amphilepis norvegica-Pecten vitreus' community described by Petersen (1918) from the muddy bottoms of some Norwegian fjords, characterised by the bivalve Delectopecten vitreus, although nothing is known about bryozoans. At present, no further correlation is possible between the Pleistocene recognised bryozoan deep-water facies and those suggested for the Recent Mediterranean and further studies, also taking into account other benthic organisms, are needed.

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Variation in zooid size in two west European species of *Alcyonidium* (Ctenostomatida)

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ABSTRACT: Two smooth species of *Alcyonidium* encrust macro-algae on western European shores: *A. gelatinosum* and *A. polyoum*. In >140 collections made within the limits 42-62°N and 11°W-15°E, one or both were obtained from 28 of 48 coast-including geographic cells, 2° latitude x 2° longitude, for which sea surface temperature (SST) data were available from satellite imagery. The SSTs show east-west as well as north-south trends. *A. gelatinosum* is the more abundant, and is distributed from north Brittany to Shetland and Denmark; *A. polyoum* is more southerly (Spain to Scotland). Lengths, L, and widths, W, of 20 zooids from five colonies in each collection were measured; the differences in both L and calculated area, A, between colonies were frequently significant (ANOVA, \( P < 0.05 \)) and between locations very great (\( P < 0.001 \)). L and W were often not correlated; A had a higher coefficient of variation (\( V^* \)) than either L or W. In both species there was a significant negative correlation between zooid length and colony age, presumably reflecting the pattern of zooid ageing and/or colony growth found in *Alcyonidium*. This important and previously unreported phenomenon probably explains the lack of negative correlation of L and A with any manifestation of SST, the lack of positive correlation between \( V^* \) for L and A with SST annual range, and the lack of any zooid size difference between the two species.

1 INTRODUCTION

Many species of *Alcyonidium* Lamouroux, 1813 (Ctenostomatida) are superficially very similar in both colonial and zooidal morphology. For example, the European *A. duplex* Prouho, 1892, *A. gelatinosum* (Linnaeus, 1761), *A. hirsutum* (Fleming, 1828), *A. mýtili* Dalyell, 1847, *A. polyoum* (Hassall, 1841) and *A. variegatum* Prouho, 1892, all form a firmly gelatinous, whitish-grey to pale brown encrusting layer over various living or inert substrata. The absence of calcification, as characterizes cheilostomates, deprives taxonomists of the use of skeletal features such as ooecia, morphometry of the orifice, and the form and arrangement of heterozooids (avicularia, vibracula and spines). Therefore, reliance must be placed on characters of the polypide, such as tentacle number and morphology of the gut, and of reproductive biology, which may be apparent only at particular times of the year (for example, the presence of an inter-tentacular organ and numerous small oocytes in *A. mýtili* (Cadman & Ryland 1996)). The utility of zooid morphometries has not been investigated in *Alcyonidium* but in widely distributed species, if we extrapolate from other bryozoans and non-modular poikilothersms, is likely to be complicated by the effect of environmental temperature on size (Atkinson 1994).

In this paper we investigate zooid size across the geographic range of two especially similar species, *A. gelatinosum* and *A. polyoum*.

These two species, together with *A. mýtili*, are so alike that they have been confused and misidentified since they were described. The demonstration that *A. mýtili* is oviparous (Cadman & Ryland 1996), while *A. gelatinosum* and *A. polyoum* are larviparous, provided the first step towards clarification but did not entirely resolve the nomenclature. We have shown recently (Ryland & Porter 2003, 2004) that *A. polyoum* is a valid species and cannot be subsumed into *A. gelatinosum*. *A. gelatinosum* has been known variously and incorrectly as *A. mýtili* and *A. polyoum*, in consequence of which it was mistakenly redescribed as *A. reticulum*, but most of the separating characters, including differences in reproductive seasonality, are now well established (Ryland 2002, Ryland & Porter 2000, 2003, 2004). It can be difficult, however, reliably to identify non-breeding colonies, and it was hoped that zooid morphometry would provide an additional character, despite changes in shape and form that may occur during astogeny and ontogeny.

Though Bergmann’s size rule (see Atkinson 1994), that geographically variable species tend to be larger.
in the colder parts of their range, was originally formulated with respect to homoiotherms, it has long also been known that cold-water poikilotherm conspecifics or relatives may also be larger than those from warmer waters (e.g. Murray & Hjort 1912, Kinne 1970). Whether this should apply to the zooids in modular invertebrates was not considered in Atkinson’s (1994) review, although Kinne (1956) had studied the effect of temperature on the growth of the hydroid Cordoniphora caspia, Menon (1972) had done the same for two bryozoan species (Conopeum reticulum and Electro pilosa), and some effect might be argued from metabolic considerations (Sebens 1979, Ryland & Warner 1986). Latitudinal effects on bryozoan zooid size had also been reported, e.g. in comparing four European species of Haplopora (Ryland 1963a) and specifically, within H. sciaphilum (Silén & Harmelin 1976). More recently, there have been several observational and/or experimental studies on the temperature-zooid size relationship in cheilostomate bryozoans (Okamura & Bishop 1988, Hunter & Hughes 1994, O’Dea & Okamura 1999, 2000, O’Dea & Jackson 2002).

Alcyonidium gelatinosum is widespread in northwestern Europe (Ryland & Porter 2003, 2004), reaching western Norway, extending across Denmark into the southwestern Baltic, though apparently not reaching southwestern Iceland. It occurs all around Ireland (Ryland & Porter 2004) and southwards at least to northern Brittany. A. polyoum has a range from northeastern Scotland to Spain (d’Hondt et al. 1993). The two species between them thus cover a substantial geographic area, likely to experience a wide range of environmental conditions. Our procedures would first establish whether there were significant differences in zooid size between samples. We shall show that there were. Our objective was then to determine the likely cause(s) of the observed variation, e.g. fundamental size differences between species and/or correlation with one or more manifestations of sea surface temperature. In the event, we present an unanticipated result which possibly masks either or both of the above, and which has important consequences for any future study of ctenostomate zooid size.

2 MATERIALS AND METHODS

Collections of intertidal Alcyonidium have been made throughout Britain and Ireland, and elsewhere in western Europe. They range latitudinally from the rias of Galicia (~42°N) to the Shetland Isles (~60.5°N), and longitudinally from western Ireland (~10°W) to southeastern Denmark (~12°E). Material was collected from as many clumps of Fucus and other macroalgae as time and tide permitted, while trying also to ensure a range of colony sizes. It was not, indeed could not be, selective in terms of the colonies actually present on the Fucus thalli - generally in great abundance - and should therefore be representative and free from any systematic bias. Identification is easier on live material and was based on reproductive characters (presence or absence of embryos and/or newly settled colonies) in conjunction with time of the year, together with (in winter) presence or absence of white zooid walls. We have used only samples in which identity was free from doubt. Whenever possible the Alcyonidium-bearing alga was fixed in 4% seawater formaldehyde for 48 h or until return to Swansea, and then rinsed and transferred to 70% ethanol for storage.

Five colonies from each sample were selected and the lengths (L) and widths (W) of 20 zooids measured using a Wild Makroskop and video image analysis (Image-Pro). An index of zooid surface area (A) was estimated as $A = L \times W$, and the data analysed by standard statistical procedures. These included the correlation between L and W, the coefficient of variation (as $V^* = \frac{s}{\bar{x}}$, Sokal & Rohlf 1995) for L, W and A, and ANOVA of L and A among the five measurement sets (colonies) in each sample. Sea surface temperature (SST) data (mean annual, mean monthly maximum and minimum, and range of means) were derived from satellite imagery (Land-Ocean Interactions in the Coastal Zone (LOICZ) Project of the International Geosphere-Biosphere Programme (IGBP)) downloaded into

![Figure 1. Map covering the known distribution of Alcyonidium gelatinosum (■) and A. polyoum (□) and the location of sites sampled during the present study. Sea surface temperature data have been obtained and averaged for each 2° X 2° rectangle and this grid provides the framework for Figs 2-4.](image-url)
Excel from the environmental section of the Hexacoral Database at the University of Kansas (www.kgs.ukans.edu/hexacoral). The area under study, 42 to 62°N and 10°W to 14°E was divided into rectangles (on Mercator’s projection) of 2° latitude by 2° longitude, judged to be appropriate to the scale of the study and physical data (Fig. 1). The SST values employed are the averaged data (variable in number) for each rectangle, and cover 1985-2003. Graphic plots for each species were prepared (using the pooled mean for each sample) of L and A vs Mean Annual SST, Mean Monthly Maximum SST and Mean Monthly Minimum SST, the correlation coefficients calculated (and their probabilities for \( n - 2 \) degrees of freedom, which are not given by Excel, obtained from tables (Rohlf & Sokal 1995)).

3 RESULTS

3.1 European distributions of the two species

Over 140 collections containing *Alcyoniumidium gelatinosum* and/or *A. polyolum* have been made between 1992 and 2003. They range from Shetland in the north to Galicia in the south, Connemara, Ireland, in the west and the extreme southeast of Denmark in the east (Fig. 1). Presence or absence has been recorded on the 2° grid (Fig. 2). A few unambiguous literature records have been added to these but in the extensive region of overlap (where both species occur on the same fucoids though rarely together at exactly the same locality) it is generally impossible to decide which species authors obtained. *A. gelatinosum* (Fig. 2A) is generally the commoner species around Britain and Ireland, and extends further north and further east. It is plentiful in Hardangerfjorden, southwest Norway (Brattegard 1966), and recorded from outer jelterfjorden (Bergen) by Nordgaard (1906) although Ryland (1963b) did not find it in the inner Bergen fjords. The authors failed to find it on two shores in southwest Iceland, but it was present at every suitable site visited in eastern Denmark and it reaches the southwest Baltic (Ryland & Porter 2003). To the south of Britain, it is still abundant on fucoids in the Isles of Scilly and Jersey in the Channel Islands. It occurs subtidally in northern Brittany (Prenant & Bobin 1956, as *A. mytili*) but we have no records from any further south in France.

*A. polyolum*, which our investigations show to be a much less common species, is essentially southern (Fig. 2B), reaching northern Spain (d’Hondt et al. 1993) and the rias of Galicia (also the southern limit of *Fucus serrans*, its commonest algal support). On the western side of the British Isles it extends northwards into the Clyde sea area but we have no positive identification from the western isles. The northern limit is in Dornoch Firth (57°50.6’N, 4°08.3’W), in northeast Scotland. The two species rarely occur together on algae, though when *A. polyolum* is dominant on low-shore *Fucus* (as at Church Island in the Menai Strait), *A. gelatinosum* may be present on boulders. Surprisingly, given its southern distribution, *A. polyolum* was not observed on Guernsey or in the Isles of Scilly.

3.2 Variation in zooid size: the sample data

It was first necessary to determine the pattern and extent of variations in zooid size. Samples were selected geographically to cover as many 2° cells as possible (Fig. 1, Table 1). Zooid length, width and surface area were measured or calculated. Key features of the resulting statistics are summarized in Table 1. One-way ANOVA was performed on each set of five sub-samples for both length and area (columns 3 and 4 respectively): almost all sets (the exceptions asterisked)
Table 1. Statistics of *Alcyonium* zooid measurements. First two columns show reference number (Fig. 1), locality, 2° X 2° grid reference (latitude °N, longitude °E; Figs 1, 2) and date of collection. Third and fourth columns show probability (\(P\)) based on one-way ANOVA, that the means of the five subsamples do not differ - those conforming to the null hypothesis marked *. Fifth column shows the correlation coefficient (\(r\)) for the relationship between width (W) and length (L), significant correlations indicated * (\(r > 0.195\)) or ** (\(P < 0.05\)). Final three columns compare the corrected coefficients of variation (\(V^*\)) for zooid length, width and area (A) respectively, showing the high variance of measurements of area.

<table>
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<th>No.</th>
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showed significant within set differences, often at \(P < (or \approx) 0.01\) (i.e., variation is small within a colony but considerable between colonies collected at the same time and place). It would be statistically preferable, but impracticable, to keep all the sub-samples separate; further observations, therefore, are based on the merged data, \(n = 100\) per sample.

Between sample data were then compared by two-way nested ANOVA (Model II, Sokal & Rohlf 1995), showing differences between the 22 samples many orders of magnitude greater than that within samples (\(P = 1.54 \times 10^{-164}\)). Thus, not only does zooid size vary significantly between colonies at a site (Table 1) but so - even more - do colonies between sites.

In more than half of the samples length and width were not correlated (Table 1, column 5). The variances of the three measurements, length, width and area, expressed as the corrected coefficient of variation, \(V^*\) (Sokal & Rohlf 1995), to make the variance independent of the magnitude of the mean, are given in Table 1 (columns 6-9). While \(V^*\) values are very similar for length and width, they are much higher (by —50%) for area. This is probably a consequence of the lack of any consistent relationship between length and width; that there is such high variance associated with the measurement of area makes it less suitable than length as a univariate index of zooid size.

3.3 Geographical and seasonal variation in sea surface temperature

Satellite data for sea surface temperature (SST) are averages for the 18 y period 1985-2003. Four attributes of SST, averaged over each of the 2° X 2° cells, are shown in Fig. 3. The data are complex. The north-west of the area (influenced by the thermally stable Atlantic Ocean and the Gulf Stream) has water that is cool in summer but never cold in winter. The north-east of the area, with a continental climate, has water which is very warm in summer but cold (around zero)
in winter, so there is a large range. Thirdly, in the southwest, the water is permanently warm, with a rather small seasonal range. The annual range is thus low in the west at all latitudes and rises as continental influence increases to the east, being greatest in Danish waters (Fig. 3D) at the eastern border of the study area. *A. gelatinosum* is common where the annual mean (Fig. 3A) and the winter mean (Fig. 3C) are relatively low, *A. polypoium* where the annual mean and the winter mean are relatively high. Neither distribution shows similarity with summer mean (Fig. 3B) or range (3D).

When SST variables were plotted on the 2° geographical grid (Fig. 3), differences were revealed that appeared to correlate with the two species’ distributions. When zooid length and area are plotted on the same grid, however (Fig. 4), despite substantial differences between localities, no obvious patterns can be discerned. The relationships between zooid size and attributes of SST in the relevant 2° grid cells, together with correlation coefficients, are shown in Fig. 5. There are no significant correlations for any of the relationships in *A. gelatinosum* and only two for *A. polypoium*. In the latter there are significant positive correlations between length and both mean annual SST (\( P = 0.025 \), Fig. 5A) and maximum mean monthly SST (\( P = 0.037 \), Fig. 5E), but not for area. This rather unexpected result - which will later be qualified - shows that, in *A. polypoium*, zooid length significantly increases with SST, whether that is expressed as the summer maximum or the annual mean.

### Interspecific comparisons

The original objective of this work had been to compare zooid size for the two species over their complete geographical ranges. However, using the relationship between width and length (Fig. 6A), there are no differences between the two species (\( P = 0.338 \)).

#### Influence of colony age on zooid size

The final possible relationship investigated, that between zooid length and the approximate age (in days) of the colony when it was collected, provided the clearest correlations. In *A. gelatinosum*, which breeds in winter, a settlement date of 1 January was assumed, and in *A. polypoium*, which breeds during the summer
Figure 4. Zooid size in two species of *Alcyonidium* based on one locality within each 2° X 2° rectangle. (A) *A. gelatinosum*, zooid length; (B) *A. gelatinosum*, zooid surface area; (C) *A. polyoum*, zooid length; (D) *A. polyoum*, zooid surface area. Circle diameter is proportional to the measurement (mm or mm²), shown numerically at bottom right of each chart.

or autumn, according to locality, an arbitrary settlement date of 1 September was allocated. The graph (Fig. 6B) shows a strong negative correlation between zooid length and age in both *A. gelatinosum* \(r = -0.656, P = 0.021\) and *A. polyoum* \(r = -0.6740, P = 0.033\) (actual collection dates in Table 1). In *A. polyoum* the decline is not at first apparent but becomes pronounced as colonies grow older (Fig. 6B).

4 DISCUSSION

The differences in geographical distribution between the two species of *Alcyonidium* are unambiguous. *A. gelatinosum* is the more northern, in line with its winter breeding season; *A. polyoum* is more southern and breeds during summer and/or autumn when the water is warmest (de Putron & Ryland 1998, Ryland 2002). It is striking that the two species never seem to share dominance on the intertidal fucoids; even when they co-occur on what is nominally the same shore (as at Black Rocks, Dale, Milford Haven), they are spatially separated. The species absent from one particular shore may be the dominant on a shore nearby (as in Arran, Milford Haven and Jersey); or *A. polyoum* may dominate on the fucoids but *A. gelatinosum* be abundant on stones and boulders. While the different timing of larval release appears to facilitate cohabitation on the same algal substrata (Ryland 2002), our observations suggest that it normally does not.

The results demonstrate two different sources of variation in the population at any locality (Table 1). The first is intra-colony variation. Since zooids produced by budding are genetically identical, they should - once beyond the zone of astogenetic change - be of similar size (Boardman & Cheetham 1973, Cadman & Ryland 1996). However, the geometry of colony growth necessitates that zooids vary in the ratio of width to length (Thorpe & Ryland 1987). In the *Alcyonidium* studied here, however, in contrast to the cheilostomates discussed by Thorpe & Ryland (1987), this leads to a marked lack of correlation between width and length. Perhaps as a consequence of this, the variance of estimates of surface area within samples was very high; area therefore was judged less suitable than length as a measure that could be analysed by univariate statistics such as ANOVA. The second source of variation, however, affects length and arises because each separate colony has developed from a genetically unique larva.
Figure 5. Relationships between zooid size (length, surface area) and sea surface temperature (SST) in two species of *Alcyonidium*. (A) length vs mean annual SST; (B) area vs mean annual SST; (C) length vs minimum monthly mean SST; (D) area vs minimum monthly mean SST; (E) length vs maximum monthly mean SST; (F), area vs maximum monthly mean SST. Charts A and E indicate significant positive correlations between *A. polyoum* zooid length and mean annual and minimum monthly mean SST respectively; no other correlations for length and none for area were significant.

(Williams 1975, Ryland 1981); between (as opposed to within) colony variation in zooid length may therefore be very high. The lesson for comparative studies based on zooid morphometry is clear: within colony measurements may be few (unless there is evidence for specific age-related changes, see below), but there must be several between colony measurements. We used 20 measurements in each of five colonies: perhaps 10 from 10 would have been better.

Some cheilostomates exhibit a size-temperature relationship that simulates Bergmann’s rule, viz. zooid size increases with decreasing ambient temperature. Thus, in *Haplopoma*, both congeners (Ryland 1963a) and samples within *H. sciaphilum* (Silén & Harmelin 1976), display larger zooids at higher latitudes. The present study, aided by the ready availability of accurate sea surface temperature data averaged over the last 18 years, was performed to ascertain whether zooid size in two ctenostome congeners - *Alcyonidium gelatinosum* and *A. polyoum* - varied in the same way. Zooids in 22 samples, covering both species, were measured, the results analysed, and any relationship with ambient temperature investigated.

Despite large differences in zooid size between sites, there were no demonstrable correlations with annual mean, summer maximum or winter minimum SSTs in *A. gelatinosum* but a positive (and probably spurious, see below) correlation between zooid length...
and both annual mean and summer maximum SST in *A. polyomum*. The explanation probably lies in what is potentially the most significant conclusion from this study, that as *Alcyonidium* colonies grow (from settlement in late winter (*A. gelatinosum*) or summer-autumn (*A. polyomum*)) - in some situations at least - they thicken (i.e. the zooids become taller and narrower), so that the size of the maturing zooids is probably better expressed by their volume than by their surface dimensions. Certainly, in incrusting species of *Alcyonidium*, zooids forming at the margin are flat and recumbent, with the orifice distal; those in the central, thicker, older part of the colony tend to be more upright with the orifice central (though this has not yet been fully investigated). Assessing zooid size from uni- or bi-dimensional measurements may be inadequate in this genus. That two species of *Alcyonidium* do not conform to the so-called temperature-size rule (Atkinson 1994), which has repeatedly been shown to apply to cheilostomates (Ryland 1963a, Menon 1972, Silén & Harmelin 1976, Okamura & Bishop 1988, Hunter & Hughes 1994, O’Dea & Okamura 1999, 2000, O’Dea & Jackson 2002), may possibly be an artifact induced by our having used a surface manifestation of zooid size which decreases substantially as the colony grows. Valid comparisons would have to be based only on colonies of the same age and stage of development.

Similarly, while two-way nested ANOVA demonstrated huge differences between colonies (*P*<<0.001) there was effectively none between species (*P* = 0.338). This contradicts our earlier view (Ryland & Porter 2000, Fig. 2A) that, consistent with a slightly higher tentacle number (Porter et al. 2000), *A. polyomum* had larger zooids. In the light of the clear effect on zooid surface dimensions of time of the year, any valid test for differences in size would have to be based on comparative samples taken simultaneously from nearby sites (such as Dale and Angle in Milford Haven, or two nearby shores in Lamlash Bay, Isle of Arran) during both winter and summer seasons.

O’Dea & Okamura (2000), in a range of cheilostome bryozoans, found that the coefficient of variation for both length and frontal area - in zooids representative of the whole colony - was positively correlated with the annual range of sea surface temperature (MART) at their site of collection. This conforms to the finding that the higher the ambient temperature the smaller the zooids within the colony (Hunter & Hughes 1994), so the bigger the temperature range the greater the spread of zooid sizes. Ranges in our data tend to cluster within the limits 7 to 13°C, except for those from Danish localities which are very high (~20.5°C). In the two species of *Alcyonidium* studied we have found no such correlation; although our coefficients of variation (*V**) vary substantially (Table 1), they do not obviously do so in relation to SST range - the two Danish points do not separate from the rest and three of the correlations are actually negative, though none is significant. Once again, however, the possibly confounding effect on our results of variations in colony age must be borne in mind.

Despite the strides made during the last decade in understanding the biology of intertidal species of *Alcyonidium*, much more study is required. There must be, especially, a focus on ontogenetic and astogenetic changes to zooids; overall, a substantial amount remains to be understood.

REFERENCES


ABSTRACT: The diverse facies of the Eocene sediments of the St Vincent Basin, South Australia, contain a wide range of bryozoan faunas, ranging from high to low diversity and abundance assemblages, regarding both taxonomy and growth forms. The basin was probably often restricted from the open ocean by the Kangaroo Island basement high. The initial transgressive marine facies resulted in the greatest diversity and abundance of bryozoans throughout the basin. This is interpreted as a well oxygenated and moderate energy environment. Trends in the bryozoan assemblages include a decrease in ‘sand fauna’ species up-section (Melicerita, Siphonicytara and free-living species), and a reduction in species and growth form diversity. Late Eocene assemblages indicate deep water environments, which may be an artefact of the restricted environment.

1 INTRODUCTION

The fossil fauna of the St. Vincent Basin is both abundant and diverse. Most of the past research on the palaeoenvironments of the basin used fossils such as Foraminifera (e.g. Lindsay 1969, McGowran & Beecroft 1986), palynology/palaeobotany (Chapman 1935, Christophel & Greenwood 1987, Scriven 1993), ostracods (McKenzie 1979, 1987, McKenzie et al. 1991, Majoran 1993, 1995, 1996a, 1996b) and mol­luscs (Buonaiuto 1979). Dinoflagellates (Harris 1985), echinoids (McNamara 1987), trace fossils (Glaessner & Pledge 1985) and vertebrates (Jenkins 1974) have also been studied in some detail.

Bryozoans constitute a significant proportion of the abundance and diversity of the fossils, often to the extent of comprising the bulk of the sediment. Bryozoan research, however, has been restricted to taxonomic papers by Tenison Woods (1865), Waters (1885) and Stach (1936a). None of these papers discuss palaeoenvironmental issues, nor do they give adequate stratigraphic or locality information of species occurrences. This article gives an overview of the results from a recent study on the Eocene Bryozoa.

2 GEOLOGICAL SETTING

The global climate during the Middle to Late Eocene was still in a Greenhouse state, before the onset of wide-spread glaciations in the earliest Oligocène (McGowran et al. 1997). Although the St Vincent Basin was positioned at 55°S latitude (20° further south than today, Fig. 1), the climate was mesothermal (sub-tropical) with extensive rainforests (Scriven 1994). Sea levels were relatively high and flooded basins along the western and southern Australian margin, which had largely been initiated during the rifting of Australia and Antarctica in the Cretaceous. Both continents were still connected via Tasmania

Figure 1. Australia in the Eocene, with major Tertiary Basins outlined in grey; Late Eocene position of East Antarctica also shown. Inset B shows St Vincent Basin with sample areas indicated (H = Hartz Mine, K = Kingscote).
based on the assumption that the present is the key to the past. Although this assumption appears to generally hold up, such uniformitarianism can have exceptions (Bottjer & Jablonski 1988).

There is probably no direct way of inferring palaeobathymetry from fossils or sediments, as they only reflect factors such as water energy, nutrients, sedimentation rates, etc. These factors are often linked with bathymetry, but can vary widely for the same depth in different circumstances.

The term 'specimen' here refers to any fragment of a fossil (complete bryozoan colonies and ancestrular regions were almost never found, with the exception of nodular and some lunulitiform specimens). Counts were carried out using each fragment as one individual. The potential bias towards growth forms that fragment easily may be offset by the fact that such forms are also more easily diagenetically removed from the sediment. Percentages and other abundance indicators quoted here are derived using specimen counts; and represent the proportion of total specimens from a sample. Sample sizes were standardised to allow direct comparisons between them. Species diversity per growth form (Moyano 1979) is used in addition to specimens per growth form to offset possible bias towards easily fragmented forms.

Growth form terms used here are the simplified version as in Fig. 3. A more detailed analysis using the

4 BRYOZOAN ASSEMBLAGES - RESULTS AND DISCUSSIONS

The taxonomic assemblages at the family and genus level share similarities between most formations, despite significant lithological differences. Many of the species are also shared between facies, indicating that these taxa are opportunistic with wide ecological tolerances. The presence of so many opportunistic taxa may be the result of continuously changing environments.

4.1 Eastern basin margin

The stratigraphy of the eastern margin is very similar between the embayments, and is characterised by a progression from fluvial to deltaic to open marine to restricted marine to open marine again.

The oldest marine stratum is the late Middle Eocene fossiliferous Tortachilla Limestone (Fig. 2). The lower unit (LTL) contains abundant goethite pellets and is generally unconsolidated. The middle unit is similar with less goethite, and has three subdivisions (MTL(l), MTL(m), MTL(u)). The upper unit (UTL) becomes
Figure 3. Bryozoan growth form terms utilised in text (adapted from Bone & James 1993).

<table>
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<td>2. FOLIOSE</td>
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<td>8. ENCRUSTING</td>
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<td>11. FREE-LIVING</td>
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Erect rigid and flexible growth forms dominate (Fig. 4A), and are largely delicate branching (mostly cyclostomes), but are generally not of high diversity (Fig. 4B). Encrusters, in contrast, are diverse, but rarely constitute a significant proportion of specimens (peaking at 25% in MTL(m)). Free-living, nodular and articulated zooidal forms are initially common, but decrease up-section and are absent in the UTL (their diversity remains constant where they are present). Articulated branching forms are consistently common, and composed of similar amounts of cheilostomes and cyclostomes, apart from the MTL(u), where no articulated branching cyclostomes occur. Fungiform colonies are only present in the MTL(u). Celleporaria ‘gambierensis’ is relatively common in the UTL and is more encrusted by other bryozoans than in the lower members.

Other common fossils include pectinid bivalves, turritellid gastropods, irregular and regular echinoids, and terebratulid brachiopods, which together comprise 10-50% of the specimens.

4.1.2 Tortachilla Limestone - discussion

The Tortachilla Limestone overall contains a high abundance and high diversity (regarding both taxa and growth forms) bryozoan fauna, which shows little dominance of any group (regarding mainly taxa, but also growth forms). The up to 183 bryozoan species occurring in the MTL constitute a high diversity assemblage. This indicates a relatively normal marine bryozoan meadow assemblage, which is consistent with other interpretations.

The lower and middle unit facies are often interpreted as sea grass meadow environments (James & Bone 2000), but no direct evidence of sea grasses (e.g. bioimmured stems or leaves) was found during this study, except one specimen of Figularia rugosa (Maplestone), which appears to wrap around a relatively thin (<0.5 mm) flat substrate.

This probably indicates deposition under increasingly restricted conditions. The top may represent an exposure surface.

Deep water (>100m depth) indicators include the consistently low ratios of encrusters to erect forms (Fig. 5A; McKinney & Jackson 1989, Zägorsek 1996), as well as the modern deep-water genera Melicerita (Hageman et al. 1996) and Siphonicytara (Bock & Cook 2001) in the lower horizons of each basin margin. Such deep-water indicators are difficult to reconcile with the shallow depth of the basin, which today is

by a delicate Cellaria sp. in the UTL with 10%. This is interesting as no other Cellaridae are present, whereas there are at least four species of this family in each of the other units. The proportion of cyclostomes to cheilostomes increases from between 20% and 30% in the lower three units, to between 50% and 75% in the upper units.

The bryozoans dominate the macrofauna both by number of fossil specimens, by volume of sediment, and by taxonomic diversity throughout the Tortachilla Limestone, except the UTL, where they drop to less than 20%. Many species occur commonly throughout, but none clearly dominates the fauna numerically or volumetrically. The greatest percentage is achieved...
Figure 4. Stacked area plots of growth form abundances for A, B, Maslin Bay, C, D, Yorke Peninsula, E, F, Kangaroo Island. A, C, E, show specimens per growth form. B, D, F, show species per growth form (sample abbreviations as in text).
less than 40 m deep. Even with the higher relative sea level during the Eocene, it is unlikely to have reached depths greater than 100 m.

Colonies of *Celleporaria* generally appear free of any encrusters. This could not be observed for certain, however, as none of the large biohermal colonies was observed complete in these sediments, but rather only as smaller fragments.

4.1.3 Blanche Point Formation - results
The Blanche Point Formation overlies the Tortachilla Limestone on a possible exposure surface. It is a sponge spicule- and opaline silica-rich marl (James & Bone 2000). It is subdivided into four members (Fig. 2): the basal Tuketja Member (BPF(t)) is still relatively fossiliferous and contains glauconitic pellets and common bivalves, turritellid gastropods, brachiopods, and minor bryozoans. The subsequent Gull Rock (BPF(gr)), Perkana (BPF(p)) and Tuit Members (not accessible during this study), however, are dark in colour, due to unoxidised organic matter (McGowran & Beecroft 1986). The fauna is dominated by infaunal turritellid gastropods, sponge spicules, and occasional sponge body fossils. Bryozoa are present in variable but mostly low abundances and taxonomic diversity, and only become common and moderately diverse in a few beds. The most conspicuous Bryozoa are large colonies of multilaminar *Celleporaria*.

The low diversity bryozoan fauna (6 species) of the Tuketja Member is dominated by delicate branching forms (60%, mostly cyclostomes). The remainder is multilaminar massive *Celleporaria* sp. (28%) and fenestrate (12%) forms.

The Gull Rock Member is dominated (70%) by the multilaminar massive *Celleporaria 'gambierensis*', which forms characteristic hollow arborescent forms. The only other forms are fenestrate and foliose, which are common in fossiliferous horizons. No cyclostomes were observed.

4.1.4 Blanche Point Formation - discussion
The Blanche Point Formation is usually interpreted to represent a relative deepening of the basin compared with the Tortachilla Limestone, possibly through eustatic sea level rise (e.g. McGowran et al. 1992). This is based on the fine grained sediment, complete fossils (including sponges) and undisturbed layers. Darker organic carbon-rich sediments imply eutrophic environments with no marginal marine influence evident in the coastal outcrops (Cooper 1979), whereas coccoliths and planktonic diatoms imply clear surface waters (Harris 1985). Ostracoda have indicated deep-water facies of 75 to 100 m depth (McKenzie 1979) or even deeper (Majoran 1996), along with low oxygen levels, poor circulation and cool temperatures (~15°C). Low ratios of the Foraminifera *Cibicedes/ Uvigerina* in the unfossiliferous horizons of the Gull Rock and Perkana Members indicate oxygen deficiency (Fachrman 1979), contrasting with high ratios in the fossiliferous ones. Gastropods such as *Spirocolum* are also often interpreted as an indicator of sub-oxic conditions (this may not always apply, Allmon 1988).

The geography of the basin, however, may complicate a simple palaeoenvironmental interpretation. A rise in relative sea level should flood the Kangaroo Island basement high and thus increase the access of the basin to the open ocean, in turn bringing in higher energy waves and currents from the much longer fetch of the widening Southern Ocean, and increase the overall agitation of the basin waters, thus producing an environment more like that which prevailed during the deposition of the Tortachilla Limestone.

The Blanche Point facies may therefore be the result of a shallowing through relative sea level fall. The marine passages could have been shallow water to emergent, resulting in a restricted basin with a
stratified water column. The high surface runoff of the prevailing climate may have dramatically lowered the salinity to create estuarine conditions. Most marine animals, such as bryozoans, do not tolerate hyposaline conditions (McKinney & Jackson 1989), and local declines in bryozoan diversity near river outlets are a commonly recognised phenomenon (e.g. Rhône Delta, Lagaaïj & Gautier 1965). Contemporary Eocene sediments and fossils (mostly in situ body fossils of sponges) in the Bremer Basin (Fig. 1) are also estuarine (Gammon et al. 2000), and although the sediments give the impression of cool deep-water conditions, they are actually shallow, warm, eutrophic, low energy water deposits.

Occasional horizons within the Blanche Point Formation (mainly the Gull Rock Member) contain higher diversity fossil assemblages, including a significant component of bryozoans. These may have been the result of temporary deepening events, which resulted in more normal marine environments through open ocean access or even storm events mixing the water column. Such events may have been short-lived and only allowed pioneering species to establish themselves. Stressed conditions may have returned before the communities could reach later stages in the faunal succession (including encrusters and erect delicate branching forms). This corroborates the interpretation that the suitable conditions were only temporary and subject to fluctuations, possibly on Milankovich timescales.

Although growth rates of multilaminar massive colonies are usually considered to be slow (Moissette & Pouyet 1991, Taylor & Voigt 1999), modern Celleporaria species have been found to have some of the highest growth rates (Key et al. 1999). Their dominance in the fossiliferous horizons and the absence of cyclostomes, which overall have the lowest growth rates, supports the idea that these horizons represent short-lived events.

The genera and even some species occurring in the Gull Rock Member also occur in the Tortachilla Limestone. The Gull Rock Member contains less diverse and abundant assemblage, dominated by a few species, such as Celleporaria ‘gambierensis’, Nudicella cribiforma Schmidt & Bone and various species of Phidoloporidae. This may indicate that these particular taxa are generalists or r-strategists, which thrive in eutrophic and often unstable environments. They appear to cope with unstable environments by colonising other organisms such as sponges (digitate sponges are postulated for Celleporaria). Phidoloporidae are often interpreted to prefer environments where deposition is slow or absent (Lagaaïj & Gautier 1965).

The Tuketja Member shares similarities with both the underlying Tortachilla Limestone (abundant delicate branching forms) and the overlying Gull Rock Member (common fenestrate and multilaminar colonies). It appears to be a transitional facies between the latter two with respect to the bryozoan assemblage: no longer open marine, but not yet completely restricted.

A similar situation of alternating stressed and normal marine conditions has been proposed for the Lower Jurassic Posidonia Shale in the South-West German Basin (Röhö et al. 2001), which was restricted from the Tethyan Ocean by a series of islands and sills. Monsoonal rains in summer created a surficial low salinity layer and produced estuarine circulation, while high rates of evaporation in winter created anti-estuarine circulation. These season-driven circulation patterns allowed thorough mixing of the whole basin when sea level was high. The exchange with the open ocean was weaker and a permanent redox-boundary could establish itself near the sea floor throughout the whole year when sea level was low.

Surface run-off from the high rainfall in the surrounding hinterland may have increased the levels of tannins (Christophel & Greenwood 1987, Scriven 1994) in the surface waters, significantly lowering photic levels and creating artificial ‘deepening’ effect for light dependent organisms.

The origin of the opaline silica may have been from upwelling (McGowran et al. 1997), volcanic (Jones & Fitzgerald 1987), or terrestrial (Gammon et al. 2000). There is no evidence in any Eocene basins along the south eastern margin for similar silica levels.

4.2 Yorke Peninsula

The Mulloowurtie and Rogue Formations (Fig. 2) on the western margin (east coast of Yorke Peninsula, Fig. IB) are mostly siliciclastic and only contain occasional fossiliferous beds (Stuart 1970). These are generally dominated by bivalves. The greatest abundance and diversity of Bryozoa occurs in one outcrop directly overlying the Cambrian basement rocks, which formed a palaeohigh (arrowed in Fig. IB) near today’s Hartz Mine.

There was probably a greater terrestrial sediment and freshwater influx, which generally restricts bryozoan faunas.

4.2.1 Mulloowurtie Formation - results

The Mulloowurtie Formation consists mostly of silt- and sandstones, and only contains occasional fossiliferous beds (Stuart 1970). Pectinidae, brachiopods, regular and irregular echinoid, serpulids and bryozoans occur rarely.

In outcrop the most conspicuous bryozoan fossils are rare nodular (probably rooted Sphaeropora sp. and Alupocellal sp.) colonies, which make up half the bryozoan forms. Flat robust branching constitute a quarter, foliose a fifth and articulated branching the remainder. Cyclostomes are absent.
The only highly fossiliferous horizon within the Mulloowurtie Formation is located in a shallow depression on elevated Cambrian metamorphic basement rock. It consists largely of bryozoan fragments with coarse quartz sand. The taxonomic assemblage is similar to that of the Tortachilla Limestone, but differs in foliose colonies dominating one third, while delicate branching colonies comprise one quarter. Free-living, nodular forms and fungiform colonies also occur. Cyclostomes comprise 14%.

No evidence of any encrustation, such as oysters or basal colony attachments, was found on the metamorphic basement rock along the whole outcrop of this horizon. The fossils are relatively unfragmented compared to the Tortachilla Limestone.

4.2.2 Mulloowurtie Formation - discussion

The Mulloowurtie Formation is almost completely devoid of bryozoans and other fossils throughout most of the sections, apart from pervasive burrowing trace fossils. The largely homogenous silty to fine sand sediment was probably unconsolidated at the sea floor and therefore did not offer a suitable substrate for most sessile benthic organisms. It was probably also near-shore and slightly brackish, discouraging colonisation by much of the benthic fauna. Some rooted forms have been shown to be the only bryozoans to settle relatively close to river outlets (e.g. Butler & Cufey 1991). The presence of articulated crinoid stems and ostracods indicate that this was a low energy environment.

Interpreting the fossiliferous locality overlying the basement as ‘normal marine’ is placed in doubt by the absence of any encrusters (e.g. oysters and barnacles), as well as the low degree of fragmentation. The slight concavity of the basement rock containing the fossiliferous outcrop may have created a local environment sheltered from wave energy, while at the same time allowing quicker accumulation of sediment, thus not enabling direct colonisation of the bedrock.

4.2.3 Lower Rogue Formation - results

Most of the Rogue Formation consists of poorly fossiliferous silty sandstone, in laterally continuous, decimetre scale layers (LRF(s)) with occasional crossbedding. Pectinidae are abundant and relatively unfragmented, but none is encrusted. Bryozoans are rare and dominated by delicate branching (58%), and multilaminar forms (Celleporaria sp., 31%). The only other forms are flat robust branching and delicate branching. Cyclostomes remain low at 5%. Adeonellopsis is the only other significant species at over 3%.

There are fossiliferous horizons (LRF(l)), which largely contain bivalves. Bryozoans are present, but are usually poorly preserved. They are dominated by articulated branching forms (90%), which are all cheilostomes. The numerous Cellaria specimens are too altered to identify specifically, but may contain species that make up a significant percentage on their own. Most other forms (apart from fungiform, articulated zooidal and nodular) are present in low abundance. Cyclostomes comprise only 1%. Buffonellaria roberti is the only identifiable species to comprise a significant proportion (3%).

4.2.4 Lower Rogue Formation - discussion

The environment was probably near-shore and possibly occasionally brackish from the proximity to high surface run-off. The relatively consistent, decimetre scale beds with only rare cross-beding appear to indicate low physical and biological disturbance. The dominance of articulated branching forms creates a ‘sand fauna’ assemblage (Cook 1981). The rooted sand fauna genus Melicerita angustiloba, however, is notably absent, whereas it is present in sediments on both the eastern and southern margins.

No specimens of Catenicellidae or Crisia were found in any of the samples from Yorke Peninsula. Both taxa are common and even dominant in both the Maslin Beach and Kangaroo Island sections. Their absence could be post-mortem, as they are small and thus easily removed through winnowing or dissolution.

4.3 Kangaroo Island

On the southern margin (near Kingscote on Kangaroo Island, Fig. 1B) the Eocene to Early Miocene Kingscote Limestone is a cemented, massive limestone The predominant macrofossils are infaunal echinoids such as Monostichia and Fibularia, and Bryozoa are common but rarely become dominant. Only the lower member of the Kingscote Limestone (LKL) is discussed here as the middle and upper members are considered post-Eocene in age. It is here subdivided into five units, lowest LKL(U), lower LKL(12), middle LKL(m), upper LKL(u) and top LKL(t) units.

4.3.1 Lower Kingscote Limestone - results

Abundance of bryozoan specimens remains relatively high throughout the LKL (ranging from 294 to 848 specimens per sample), as does the species diversity (22 to 57 species per sample). The cyclostome:cheilostome ratio drops gradually from 1:1 in the lower units to over 1:9 in the upper ones.

The bryozoans of the LKL(ll) and LKL(12) are dominated by delicate branching and articulated branching forms (similar species to those in the Tortachilla Limestone, but with a higher proportion of cyclostomes). The latter form is in turn dominated by the cyclostome Crisia sp. (15-30%), which does not occur in the upper three units, the delicate branching cheilostome Ogivalia and flat robust branching Ogiva are slightly less dominant. All other forms except fungiform are present in small percentages. Free-living
forms occur in the lower units but vanish in the middle and upper ones. Fungiform colonies are only present in the LKL(m). Fenestrate forms are most common in the LKL(m). Adeonellopsis symmetrica (Waters) becomes more common up section until it comprises a third of the fauna in the LKL(u).

The rooted Melicerita is abundant in the lowermost sample (along with the also rooted Siphonicytara) but becomes increasingly less common in the overlying two horizons and is finally absent in the uppermost horizons.

A multilaminar maculate Lichenopora sp., which forms large spherical colonies, only occurs here, while Celleporaria ’gambierensis ’ is less common than in the other formations.

Serpulids are the most common macrofossil in the lower horizons, while echinoids (especially Fibularia and Monostychia) dominate in the upper horizons.

4.3.2 Kingscote Limestone - discussion

These horizons are the only ones in the Eocene St Vincent Basin where clearly dominant species occur. The area where the Kingscote Limestone is found is often considered to be one of the shallow inlets to the St Vincent Basin (Milnes et al. 1983). This may have therefore been one of the only places where almost normal marine prevailed. It is therefore interesting to find such taxonomic and growth-form dominance among the Bryozoa, whereas apparently more stressed environments on the other margins display lower degrees of dominance.

5 BASINWIDE PATTERNS

There is an overall intra-basinal difference in macrofaunal assemblages between the three margins. In general terms, the Eocene eastern margin is initially dominated by bryozoans and to a lesser extent molluscs and echinoids and later by sponges and to a lesser extent molluscs and bryozoans; western margin of the St Vincent Basin is dominated by infaunal organisms, in particular echinoids, and occasionally molluscs; the southern margin is dominated by shallow infaunal echinoids and to a lesser extent bryozoans. Although the relative abundance patterns of bryozoan growth forms also display variations within the sections and overall patterns appear different between the sections on the three basin margins, there are some common trends shared among them (Fig. 4), which will be discussed below. These could be indicative of larger scale temporal and/or spatial changes, which are less influenced by local effect.

5.1 Encrusters

Encrusting forms are consistently a small proportion of the overall growth form fauna (the greatest fraction is 25% in the Middle Tortachilla Limestone). Correspondingly, the ratios of encrusting vs. erect species are generally well below 0.5 (Fig. 5 the peak is again in the Middle Tortachilla Limestone at 0.4).

There may have been a greater original abundance of encrusters in the biocoenoses, which are not preserved in the thanatocoenoses due to various post-mortem effects (Gordon 2000). Even if the observed species diversity of encrusters is double, however, the encruster/erect ratios still remain low.

Such direct comparisons with modern faunas would indicate depths greater than 300 m where encruster/erect ratio = 1.0 (i.e. 50% of species are encrusters) for all the Eocene St Vincent Basin, and even deeper than 1000 m where encruster/erect ratio = 0.5 (i.e. 33% encrusters) in many horizons. It may therefore be unrealistic to compare these percentages directly with those of studies on Recent faunas (e.g. McKinney & Jackson 1989), and more informative to use the fluctuations of percentages as a means to estimate relative (not absolute) sea level changes (see also Zágorsek & Kázmér 2001). In this case both the Tortachilla Limestone and the Lower Kingscote Limestone are initially relatively deep and become shallow in the middle horizons, and deepen again towards the top. The Mulloowurtie Formation also has a relatively deep assemblage in the basal facies, but it then deepens even further in the general Mulloowurtie Formation and the Lower Rogue Formation. This appearance of rapid deepening in the later Eocene horizons could again be an effect of the restricted environment within the enclosed basin.

If the dominance of erect growth forms over encrusters is actually a primary feature, it could be the result of a lack of predators. Predators in shallow water usually preferentially prey on erect colonies, and their increased efficiency through the Phanerozoic has possibly ‘pushed’ erect colony forms into deeper water (Vermeij 1977). The environments of the St Vincent Basin may have been hostile to predatory organisms at times, and thus enabled erect bryozoans to flourish.

5.2 Sand fauna

The two rooted genera Siphonicytara and Melicerita, as well as the free-living and nodular colony forms all occur commonly in the lowermost sediments throughout the basin and become less common upsection, until they are absent in the Upper Eocene. This indicates a decrease in ‘sand fauna’ facies through the Eocene in the basin. Cyclostomes become increasingly dominated by delicate branching forms towards the Upper Eocene throughout the basin. Both trends may be indicative of initial high energy environments (‘transgressive shallow facies’) with subsequent quieter water (‘deepening’). This contradicts the interpretation
Neither the growth form nor taxonomic assemblages for the development of bryozoans, such as tilaminar/massive ('cerioporid' and 'celleporiform') assemblages using current ecological understanding. The apparent to give results that allow objective interpretation of diversity among the multilaminates here. (Hara 2001). It is unclear why there is no similar shore environment with abundant supply of nutrients shallow-water, moderate to high energy and near colonies suggests favourable environmental conditions for the development of bryozoans with availability of hard substratum (Brood 1972). Many growth forms (Hara 2001). The 'cerioporid' growth form is independent of water depth but dependent on availability of hard substratum (Brood 1972). Many different kinds of colonial forms of bryozoans with a clear preponderance of massive multilaminar forms occurring in the siliciclastic sediments. Rivers and the resulting high sedimentation rate dominated this margin and low salinity inhibited bryozoan colonisation. The shallow sediments on the southern margin are dominated by infaunal echinoids throughout, and bryozoans are occasionally sub-dominant. This was probably a shallow passage through a chain of ‘Kangaroo Islands’.

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REFERENCES


Infestation of a temperate reservoir by freshwater bryozoans: an integrated research programme

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ABSTRACT: Freshwater bryozoans grow on surfaces throughout Southern Reservoir water treatment station, Dunedin, southern New Zealand. Since 1996, this infestation has affected operation of the plant, caused damage to filters, and impeded delivery of drinking water. We report here on a multi-staged research investigation of this fouling by freshwater bryozoans. The microstrainer hall at Southern Reservoir hosts Paludicella articulata and Plumatella repens, while a more detailed survey of the Dunedin area discovered two additional species in reservoirs and slow rivers, but none in fast-running streams. Further studies investigated effects of control strategies on settlement, population structure, genetic affinities of the Dunedin Paludicella articulata, and effects of extreme conditions on the resting stages of Southern Reservoir’s bryozoans. This wide-ranging research programme has enabled the Dunedin Water Department to understand the scope of the infestation, to limit the potential for further colonisation, and to design strategies for controlling the problem.

1 INTRODUCTION

Water treatment officials in the southern New Zealand city of Dunedin have had to cope since 1996 with heavy and pernicious infestations of brown ‘weeds’. The freshwater bryozoans Paludicella articulata (Ehrenberg, 1831) and Plumatella repens (Linnaeus, 1758) grow on hard surfaces, in water intake pipes, on floats, and throughout the microstrainer hall at Southern Reservoir and the associated water treatment station in Dunedin. Their presence has intermittently affected normal operation of the plant, particularly when clumps are torn off the sides of pipes and walls, clogging microstrainers and filters, sometimes causing considerable damage. Bryozoans living in pipes may also reduce effective pipe bore diameter, increasing friction and thus slowing water velocities. The presence of fouling bryozoans increases workloads, reduces efficiency, and has impeded the delivery of drinking water to Dunedin residents.

The Dunedin City Council Water Department and scientific consultants from AMS Research (Dunedin) have devised a multi-staged research approach to the problem of fouling by freshwater bryozoans. Literature reviews on both Paludicella articulata and Plumatella repens were carried out, followed by a survey of the microstrainer hall at Southern Reservoir. A more detailed survey of all Dunedin’s water treatment facilities and intake streams was carried out in summer of 2002. Along with these surveys to ascertain the magnitude of potential fouling, there has been an active experimental programme, including monitoring over three years of the populations in the microstrainer hall at Southern Reservoir, investigation of control strategies and water treatment programmes on settlement of freshwater bryozoans, an international study of the genetic affinities of the Dunedin Paludicella articulata population, and a longer-term project investigating the effects of extreme conditions on the resting stages (hibernacula and statoblasts) of Southern Reservoir’s bryozoans.

This paper summarises the results of these studies. The overall aim of the project is to allow the Dunedin City Council Water Department to understand the scope of the infestation, to limit the potential for further colonisation by these and other species, and to design strategies for controlling the problem in future.

2 MATERIALS AND METHODS

Southern Reservoir is an open, concrete-lined reservoir with two streams leading into it (Figure 1), about 40,000 m² in area, located to the southwest of Dunedin (45°55’S, 170°28’E). Water is collected by submerged intake and piped to the nearby water treatment hall, where three large tanks with rotating microstrainers process the water before chemical...
Freshwater bryozoans are found on surfaces around the Reservoir, in and on the intake pipes, and throughout the microstrainer hail. Particularly in summer, they can cover all surfaces very densely, to a thickness of 10-20 cm.

2.1 Species present at Southern Reservoir and around Dunedin

Samples from Southern Reservoir, collected at the height of the summer infestation (March 2001), were identified using keys of Rogick (1959), Mundy (1980), Ricciardi & Reiswig (1994) and Wood et al. (1998). Both whole colonies and resting stages (both stoloblasts and hibernacula) were examined using dissecting microscope and SEM.

Twenty-two sites around Dunedin were surveyed, including 4 reservoirs, 2 wide slow-moving rivers, 1 borefield pump and 15 smaller streams, most of which are involved in water supply to Dunedin City.

2.3 Bryozoan growth, development, and density at Southern Reservoir

A three-year population monitoring programme at Southern Reservoir was carried out beginning in November 2000. A series of six white PVC settling plates (25 X 25 cm) in two stacks of three were installed in each of three chambers in the microstrainer.
Hall at Southern Reservoir. In each stack the plates were immersed to a depth of 20 cm, 50 cm and 80 cm of water. At each location, one stack was scraped clean after each observation and the other was left to grow and develop. Plates were photographed and described weekly-to-fortnightly from November to April, resulting in 22 visits and 703 photos. After that, six plates (two stacks) were left for a further two years and visited fortnightly-to-monthly.

In total, 69 visits were made to Southern Reservoir between November 2000 and June 2004. A total of 1300 photos were taken to document growth and development. In addition to observations of the settling plates, descriptions of growth on the micro-strainer chamber walls were also made. Over the same 3.5 years, water quality measurements (temperature, pH and turbidity) were taken almost daily by Dunedin City Council staff.

2.4 Controlling settlement of freshwater bryozoans

Control strategies to be used in drinking water are obviously limited. Here we investigated the effect of four different potable water treatments on settlement and survival of freshwater bryozoans: sonication, acidification, ultraviolet irradiation, and increasing water flow. A system was built which collected raw water from Southern Reservoir and split it into fifteen pipes, consisting of three replicates each of five treatments: control, ultrasound, lowered pH (below 6.0, if possible closer to 5.0), ultra-violet light irradiation, and high-velocity (13 l/min) treatment. In each treatment, the water was treated while in transit through the system to 15 settlement pipes, each 50 cm long, 15 cm in diameter, mounted horizontally in a randomised arrangement. The experiment ran for 70 days and was checked daily during that time (February to May 2002).

At the end of the experiment, each growth pipe was opened and drained into a sieve, the inside of the pipe photographed and described, and then scrubbed and drained into the sieve, so that all material inside was collected. The retrieved material was weighed (drained wet weight) and described.

Ultimately, the Dunedin City Council decided to investigate a chemical water treatment regime using both acid and caustic chemicals to clean filtration membranes and treat potential pathogens in the water. We decided to examine the effect of these chemical treatment methods on *Paludicella articulata* and *P. repens*. Living bryozoan colonies of both species were collected, rinsed, and divided into 30 ml subsamples. Subsamples were subjected to standard Clean-In-Place (CIP) water treatment solutions from Veola Water systems Australia. Caustic CIP (0.25% hydrogen peroxide, 0.14% EDTA sodium salt, 2% sodium hydroxide, 0.2% Memclean C, 97.41% distilled water), Acid CIP (0.1% sulphuric acid, 0.05% EDTA sodium salt, and 99.85% distilled water), or both together (a 50:50 mixture) were each used at room temperature (20°C) and at 35°C, with one control, for a total of seven treatments. Treated samples were examined and photographed under a binocular microscope for the state of polypides, walls, and statoblasts. Statoblasts were removed and the attempt was made to germinate them.

In a different study, over two years *P. repens* statoblasts were subjected to various degrees of drying, storage, heating, and soaking in Clean-In-Place (CIP) water treatment chemical components. Subsequent germination (when the valves split) and évagination (germinated statoblasts that produce a zooid) rates were compared with untreated statoblasts.

3 SPECIES PRESENT AT SOUTHERN RESERVOIR

3.1 Paludicella articulata

Colonies of *Paludicella articulata* look like tangled mats of greensh-brown threads, reaching a diameter of 6-8 cm, formed of dozens of club-shaped zooids (Figure 2A, C). In general, growth is seasonal, with colonies growing in spring and dying off in autumn (Wöss 1996). Asexual reproductive structures, hibernacula (Figure 3), persist during adverse conditions, usually cemented to the substrate, and are probably the main method of reproduction in *P. articulata*.

*P. articulata* has been recorded from much of the northern hemisphere in cold climates, including Quebec Canada (Ricciardi & Lewis 1991), Poland (Kaminski 1984) and northern Norway at latitudes greater than 70°N (0kland & 0kland 2000). In New Zealand, *P. articulata* has been recorded only at two sites, both in Dunedin and both in drinking water reservoirs. A century ago, *P. articulata* was recorded at Ross Creek Reservoir (Hamilton 1902). It was 93 years before it was again recorded in New Zealand, this time at Southern Reservoir (and not at Ross Creek) (Wood et al. 1998). As far as has been recorded in the literature, *Paludicella articulata* is found only at one site in the southern hemisphere: Southern Reservoir.

*P. articulata* has a long history of fouling water treatment stations and pipes. From Europe and the UK to Canada and the USA, *P. articulata* has interfered with filtration, reduced pipe diameters, reduced water quality, and encouraged a wide variety of other unwanted animals in water pipes, even disrupted UV light disinfection (Harmer 1913; Aprosi 1988; Wood & Marsh 1999). This persistent biofouler is tolerant of a range of environmental conditions (Bushnell 1966;
Figure 2. Colonies of (A) *Paludicella articulata* and (B) *Plumatella repens* growing on the wall of a microstrainer at Southern Reservoir, Dunedin, New Zealand (Scale bar = 10 cm). Details of zooids of (C) *Paludicella articulata* and (D) *Plumatella repens* (Scale bar = 1 mm).

Colonial growth is limited by low temperatures (<9°C), low pH (<5.9), disturbance, and drying (Okland & Okland 2000). Hibernacula, on the other hand, tolerate at least some degree of drying, starvation, cold, and disturbance.

### 3.2 Plumatella repens

Plumatellids are the world’s most widespread and abundant freshwater bryozoans, and *Plumatella repens* is widely reported, though identification has proved to be problematic (Wood 1996). *Plumatella repens* is reported to have two subspecies in New Zealand: *typica*, found only in the South Island and *rugosa*, found mostly in the North Island (Wood et al. 1998). *P. repens* is a relatively large bryozoan, with reddish-brown branches about 0.5 mm in diameter, and colonies that may reach 12 cm in height (Figure 2B, D). Under benign conditions, *P. repens* can grow rapidly, doubling in size every 4 to 7 days (Bushnell 1966), but it is a short-lived species and colonies rarely persist longer than 3 months. Reproduction is ordinarily by production of statoblasts (Figure 3), both floatoblasts (in the water column) and sessoblasts (attached to the substrate), which germinate when conditions are favourable. Dispersal of floatoblasts is particularly effective and explains why this species is so common and widespread.

*Plumatella repens* has been recorded from tropical to temperate latitudes in both hemispheres, including Hawaii (Baily-Brock & Hayward 1984), Europe (Kaminski 1984; Taticchi 1989; Wöss 1996), North America (Bushnell 1965; Ricciardi & Reiswig 1994), New Zealand (Wood et al. 1998), and elsewhere. Its
New Zealand distribution ranges from Auckland to Dunedin, from lakes to rivers and ponds to ditches. Floatoblasts (Figure 3) collected show that both subspecies of *P. repens* are found in the Dunedin area (Wood et al. 1998), including Southern Reservoir.

*Plumatellids* are extremely tolerant of various environmental conditions (Bushnell 1966), which makes them very effective biofoulers. Found in nuclear power plants (Aprosi 1988), aquaculture ponds (Baily-Brock & Hayward 1984), wastewater treatment stations (Wood & Marsh 1999), farm irrigation systems, water treatment facilities (Wood et al. 1998), and industrial intake sites (Gordon & Mawatari 1992), they are opportunistic, growing rapidly and producing abundant resistant statoblasts. *Plumatella* colonies can survive temperatures from 5°C to 37°C, though optimum growth is limited to spring and summer in most localities (Bushnell 1966). Disturbance by storms, floods, wind or drought is thought to help regulate natural populations; in a stable artificial environment such as Southern Reservoir, populations are not so regulated and can flourish unchecked. Such rapid growth, when coupled with the resistance of statoblasts (Wood 1983; Hutchinson 1993; Wood and Marsh 1999), make *Plumatella repens* a particularly pernicious biofouler.

3.3 Other bryozoans

It is possible, though unlikely, that one or more bryozoan species remained undetected throughout this survey. Wood et al. (1998) found two other freshwater bryozoan species in Otago: *Fredericella sultana* (Blumenbach, 1779) and *Plumatella emarginata* Allman, 1844. If these other species do occur in the microstrainer hall they are presently very rare. A similar survey at another time of the year might reveal a seasonally transient species, although this is again unlikely because most freshwater bryozoans bloom during summer. It is always possible that new fouling species of bryozoans may invade the system in the long-term.

During laboratory studies of germination (see section 7), a new type of statoblast was discovered at Southern Reservoir. These statoblasts have been tentatively identified as *Plumatella cf. velata* (Figure 3), the first report of the species in New Zealand. While no colonies of this species were found at Southern Reservoir, the statoblasts were successfully germinated in the laboratory.

4 FRESHWATER BRYOZOANS AROUND DUNEDIN

A survey of freshwater bryozoans in New Zealand (Wood et al. 1998) found five species occurring during the summer (January-February 1995), of which four were found in and around Dunedin. A detailed survey was carried out in 2002 by the present authors to elucidate the distribution of freshwater bryozoans around Dunedin, with a view to determining likely environmental controls on distribution.

At 16 of the 22 survey sites (see Figure 1), no bryozoans were found at any visit. Most of these sites were shady, fast-flowing streams with clear water. All four reservoirs and both wide slow rivers yielded some bryozoans, with a total of four species. *Plumatella emarginata* was the most widespread species, occurring at all six sites, and abundant at several. *Fredericella sultana* was found at both wide rivers and in Southern
Reservoir, mostly on rocks. Both these species were most abundant in summer and declined as autumn arrived. *Plumatella repens* and *Paludicella articulata* were found at Southern Reservoir, as expected, and nowhere else in the survey. Wood et al. (1998) found *P. repens* at Ross Creek in 1995, but there was no sign of it in 2002, despite searching in the same places. This is a surprising result, especially considering the effectiveness of dispersal of *P. repens* by floatoblasts. It seems unlikely that the resting stages were simply overlooked, as statoblasts of *P. emarginata* were identified at Ross Creek during the survey. No floatoblasts were found in the water from the borefield pump.

One of the reasons for studying small streams was to ascertain if these intakes were sources of freshwater bryozoans, carrying them into reservoirs. It appears that the opposite is true - reservoirs and slow rivers with their nutrient-rich eutrophic waters clearly provide an excellent environment for the growth of freshwater bryozoans, whereas clear shady rapid streams do not.

5 BRYOZOAN GROWTH, DEVELOPMENT, AND DENSITY AT SOUTHERN RESERVOIR

We know of no study in which a fouling population of freshwater bryozoans has been monitored over several years. Here we report on growth and development over 44 months at Southern Reservoir (Figure 4).

Young bryozoan colonies began to appear on settling plates each spring (mid to late October) as the water temperature exceeded 9°C. *Paludicella articulata* was found only on the upper sides of the plates, and *Plumatella repens* grew only on the undersides, indicating some degree of ecological partitioning. Strong summer growth was well established by January, with colonies up to 2 or 3 cm long on both surfaces. Peak size (about 5 cm) and coverage (100% of the plate covered) was reached in February to March (late summer), and all colonies were dead by May (as the water temperature dropped to below 9°C). No bryozoan growth occurred between May and October (winter to early spring) in any year. This seasonal pattern is similar to that found in northern hemisphere populations (Wöss 1996).

Growth of *Paludicella articulata* appears to be steady over the warmer months. It appears in spring and the same colonies grow and persist until autumn. The largest colony of *P. articulata* on a settling plate was 7 cm in diameter after 60 days immersion, a mean growth rate (in any direction) of 0.6 mm/day. In contrast, *Plumatella repens* is more opportunistic and more rapid-growing. It appears immediately after conditions improve, and spreads very rapidly, then the colonies die. Colonies of 12 cm in diameter developed in only 42 days, a mean growth rate of 1.4 mm/day.

Despite the artificial environment inside the microstrainer hall, a whole community is associated with surfaces there. We observed biofilm, larval insects, snails, and adult insects on our settling plates as well as in the hall. We also noted the ubiquity of bryozoan statoblasts. During the warmer months they are present in enormous quantities. In March 2001 we scraped a ‘tideline’ of statoblasts from one chamber and found it to be 10 cm wide and up to 3 mm thick - millions of the tiny resting stages can be found on a few square metres of wall.

![Figure 4. Coverage of settling plates by freshwater bryozoans at Southern Reservoir, November 2000 to June 2004. *Paludicella articulata* settles only on the upper surface of the plates (open circles), whereas *Plumatella repens* settles on the undersides (closed circles).](image-url)
In March 2001 the microstrainer chamber was drained for cleaning and we were able to determine the density of settlement on the chamber walls. Typical coverage by bryozoans was about 1.4 kg/m² (blotted wet weight); but in an area with particularly dense coverage, density was 4.2 kg/m². Given the surface area of the below-water microstrainer chamber walls (about 368 m²) available for bryozoan settlement, a single year’s crop of freshwater bryozoans could weigh from 515 to 1545 kg. About a tonne of bryozoan remains washing through pumps and filters during the autumn die-off is far more than the microstrainers, filters, and water treatment station can handle.

### 6 CONTROLLING SETTLEMENT OF FRESHWATER BRYOZOANS

Several possible strategies for management of biofouling are available. One can eradicate the pest species completely, try to limit adult growth, control reproduction, and prevent future infestation. In the case of freshwater bryozoans at Southern Reservoir, with resistant and abundant small resting stages, total eradication is unlikely. Colony growth might be limited or controlled by physical removal, chemical treatment, thermal, light or acoustic treatment, and dessication. Resting stages could be removed by filtration. Or, settlement could be physically or chemically inhibited.

In our study investigating ways to control settlement, most colonies growing in treated and control pipes were small (less than 50 zooids), with *Paludicella articulata* growing only on the upward-facing interior surface of the pipe, and *Plumatella repens* growing only on the downward-facing interior surface (as on the settling plates in the previous section). *P. articulata* was more abundant than *P. repens* in all pipes, both in terms of numbers of colonies and biomass.

None of the treatments resulted in total inhibition of settlement by freshwater bryozoans. Indeed, acidified water actually produced more bryozoan material (average wet weight 4.02 g) than the untreated control (average wet weight 3.1 g). Bryozoans in the high-velocity water showed somewhat less growth (average wet weight 2.49 g) than those in the control, and there were many ungerminated statoblasts. Ultra-sonicated pipes, too, contained fewer colonies (average wet weight 2.43 g) than in the control pipes. Much less bryozoan material was found in the UV-irradiated pipes (average wet weight 2.68 g), but there was quite a lot of other organic material (perhaps algal) in this treatment.

None of the colonies subjected to water treatment CIP solutions contained living polypides. There was well-preserved polypide tissue in many of the samples, including the control, suggesting they had not been dead for very long. While both Acid CIP and Caustic CIP left some intact polypides, the combination at high temperature resulted in total removal of polypide material. The tough chitinous zooid walls remained intact in all treatments, but the Acid CIP apparently weakened the walls, as they appeared thinner and paler than the control. Caustic CIP had little effect on the walls, but there were numerous bubbles inside the zooids, suggesting that some CO₃ production had occurred.

Statoblasts were abundant within *Plumatella repens* colonies, and at least some statoblasts had been released in all treatments. More statoblasts were released by colonies at high temperatures. Individual statoblasts showed no sign of degradation or change among the water treatments. A number of the control statoblasts germinated (mean of 12%), but Caustic CIP treatment reduced the germination rate to 5%, whereas Acid CIP and Acid & Caustic combined treatments resulted in no germination.

### 7 EFFECTS OF EXTREME CONDITIONS ON STATOBLASTS

The Dunedin City Council regularly shuts down and drains the microstrainer chambers, then waterblasts the walls to remove bryozoan cover. While this approach provides a temporary solution, it does not prevent new colonies forming in the summer. The long-term solution lies in controlling germination of reproductive units of the invading species, i.e., statoblasts and hibernacula. But how resistant are these resting stages?

Storing wet floatoblasts of *P. repens* resulted in decreasing germination (split valves and évagination (ancestrula formation). Germination showed significant (p = 0.000) decreases between 94 and 129 days of storage dropping by nearly half (49%) in 30 days and by another 69% with five further storage days. Storing air-dried statoblasts of *P. repens* caused an overall decrease in germination and évagination over time. No germinating activity occurred in any samples after 29 days of dry storage and évagination did not occur after 11 days. Regression analysis using a log-log linear line has a strong fit to the data (R² = 82.5%) predicting that the dry storage time for floatoblasts to reach zero total germination would be 54.6 days.

Floatoblasts were treated with the chemicals that compose the Clean in Place (CIP) treatment to be utilised in Dunedin City Council water treatment at a variety of combinations and pre-heating temperatures and soaking levels. Chemical components EDTA (0.14 and 0.05%), hydrogen peroxide, and Memclean C (citrus based cleaner) had no effect on total germination. Caustic CIP and a combination of Acid and Caustic CIP sharply decreased total germination. Acid CIP, sodium hydroxide and sulphuric acid treatments prevented any germination.

Heating Acid CIP to 35°C and 50°C produced the lowest total germination results. A log-log regression
analysis for each of the soaking predicts the temperature necessary to prevent total germination using Acid CIP is between 42.5°C and 43.7°C (R² between 80.1 and 84%). Short soaking times in Caustic CIP at 35°C caused total germination to drop sharply, but Caustic treatment at very high temperatures (50°C) or with long soaking times at 35°C (90 minutes) produced higher mean total germinations than that of the untreated controls.

8  FUTURE STUDIES

Paludicella articulata is the only gymnolaemate freshwater bryozoan found in New Zealand, and has been identified at only one site in the southern hemisphere. This distribution suggests that it may be introduced to southern New Zealand, perhaps early in European settlement. Used pipes or equipment from Europe, infested with resistant hibernacula, may have been used in construction of the Ross Creek Reservoir in the 1900s. Subsequent transfer to Southern Reservoir could easily have occurred, though it is not clear why P. articulata is now absent from Ross Creek. Alternatively, it may be that P. articulata is found elsewhere in the southern hemisphere (where very few freshwater bryozoan surveys have been carried out), but is yet to be recorded in the scientific literature. For example, a recent survey of freshwater bryozoans in central Chile has just provided the first record of Plumatella repens in Chile (Orellana 2003).

In an attempt to understand the genetic affinities of the P. articulata population at Southern Reservoir, nine samples were obtained from Europe and North America for comparison with eight New Zealand examples and three out-groups. To investigate phylogenetic relationships between these samples, a region of the mitochondrial cytochrome c gene was amplified and sequenced. This gene proved to be uninformative as all sequences were near-identical (Wyeth 2002). Work to identify a more informative marker is on-going.

9  DISCUSSION AND CONCLUSIONS

Two species of freshwater bryozoans, Paludicella articulata and Plumatella repens, are responsible for biofouling at Southern Reservoir, Dunedin, New Zealand. Paludicella articulata, a northern-hemisphere temperate species, has been recorded only at two sites in the southern hemisphere, both in Dunedin and both in drinking water reservoirs. This persistent biofouler is tolerant of a range of environmental conditions, but limited by low temperatures (<9°C), low pH (<5.9), disturbance and drying. Its resting stages, hibernacula, on the other hand, tolerate at least some degree of drying, starvation, cold, and disturbance.

The world’s most widespread and abundant freshwater bryozoan, Plumatella repens grows rapidly, doubling in size every 4 to 7 days (Bushnell 1966), though colonies rarely persist longer than 3 months. Recorded from tropical to temperate latitudes in both hemispheres, the New Zealand distribution of P. repens ranges across New Zealand, from lakes, rivers, ponds and ditches. Plumatellids are extremely tolerant of various environmental conditions (surviving temperatures from 5°C to 37°C), which makes them persistent and effective biofoulers.

Four species of freshwater bryozoans were found in a summer/autumn survey of waterways and reservoirs around Dunedin, all in slow-moving turbid waters. No bryozoans were found in shady, fast-flowing streams with clear water. Plumatella emarginata was the most widespread species, and along with Fredericella sulcata was abundant in summer and declined as autumn arrived. Plumatella repens and Paludicella articulata were found at only Southern Reservoir.

Monitoring over 3.5 years in the microstrainer hall at Southern Reservoir shows that new young bryozoan colonies appear on settling plates each October as the water warms up (above 9°C) in spring. Strong summer growth is well established by January, with colonies up to 2 or 3 cm long on both surfaces. Some ecological partitioning occurs, with Paludicella articulata growing on the tops of settling plates, while undersides were covered with Plumatella repens. It would be interesting to determine whether this distribution is determined by interspecific competition or simple ecological preferences.

Peak size and coverage is reached in February to March (late summer), and all colonies are dead by May. No bryozoan growth occurs between May and October (winter to early spring) in any year. P. articulata grows steadily at about 0.6mm/day. In contrast, Plumatella repens is more opportunistic and more rapid-growing, reaching a mean growth rate of 1.4mm/day. Bryozoan density on microstrainer tank walls is 1.4kg/m² (blotted wet weight) with a maximum of 4.2kg/m², thus providing a potential annual crop of 515 to 1545 kg.

While sonication, acidification, ultra-violet irradiation, and increasing water flow do not result in total inhibition of settlement and germination by freshwater bryozoans, some degree of reduction of settlement did occur in high velocity, ultra-sonicated and UV water treatments. Chemical water treatment involving both acid and caustic chemicals affected polypides, especially at high temperature, and reduced statoblast germination rate. Storing statoblasts dried and/or refrigerated decreased germination significantly but neither treatment method is practical for the control of establishment of colonies. A more workable solution is likely to be the use of Acid CIP chemical solution at temperature over 35°C and Caustic CIP.
solutions for soaking periods of 10 and 20 minutes and temperature of 20°C or less.

A study aimed at elucidating the genetic affinities of the \textit{P. articulata} population at Southern Reservoir is on-going.

Biofouling freshwater bryozoans \textit{Paludicella articulata} and \textit{Plumatella repens} grow throughout Southern Reservoir and the associated water treatment station in Dunedin, New Zealand, causing considerable inconvenience and expense. The multi-staged research approach adopted by the Dunedin City Council Water Department and AMS Research has allowed the Dunedin City Council Water Department to understand better the scope of the infestation, to limit the potential for further colonisation by freshwater bryozoans, and to design management strategies for controlling the problem in future.

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Ovicell pores and frontal wall pore sieve plates in eastern Pacific

Microporellidae

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ABSTRACT: Twenty one species, formerly placed in *Microporella* or newly described from the eastern Pacific, south of Alaska to the Galápagos Islands and Colombia and west to the Hawaiian Islands and American Samoa all have numerous pores in the ovicell hood, placing them in *Microporelloides* Soule, Chaney & Morris, 2003. *Microporella* spp. from the eastern Atlantic, Mediterranean and polar regions have few or no central ovicell hood pores. Seven of 10 *Microporelloides* species from British Columbia to California also bear calcareous sieve plates deeply set in frontal wall pores which are absent in other temperate species and in those in south of California in the eastern tropical Pacific. Pore sieve plates were not seen in Pleistocene specimens but may be visible in Recent material using light microscopy. In other Microporellidae, *Fenestrulina* spp. and *Fenestruloides* spp. have imperforate ovicell hoods with distal areolae only, and easily visible surficial frontal wall pore sieve plates rather than deeply set ones.

1 INTRODUCTION

Descriptions of the Family Microporellidae Hincks, 1880 and the genus *Microporella* Hincks, 1877 were not changed substantively between those publications and that of Osbum (1952), although some subsequent authors (e.g., Gordon 1984) expanded the familial definition to include a number of other genera characterized by the presence of ascopores. Hayward & Ryland (1999) defined the Family Microporellidae as follows: ‘Primary orifice semicircular, ascus opening via an ascopore, proximal to the orifice. Frontal shield with scattered pores. Ovicell present. Oral spines and avicularia present or absent.’ The genus *Microporella* they defined as: ‘Colony encrusting. Primary orifice semicircular, ascopore distinct on a raised base. Oral spines present. Ovicell hyperstomial, ascopore distinct on a raised base. Oral spines present. Ovicell hyperstomial, imperforate, closed by zooidal operculum. Frontal shield with scattered pores. Avicularia adventitious, with acute or setiform mandibles. Basal pore-chambers large and distinct.’

To these characters we add that ascopores may be borne on an umbo or not; ascopores may be round or lunate, with smooth or denticulate rims, often with a distal uvulate process of various sizes and shapes or filled with a cribrate plate. Frontal wall pores are numerous, smooth and rounded or irregular in shape, with or without a cribrate sieve plate. Ovicell hoods in a new genus, *Microporelloides* Soule, Chaney & Morris, 2003, contain numerous pores which may be similar to frontal wall pores or smaller or larger. The basal wall in both *Microporella* and *Microporelloides* usually, but not always, consists of an uncalcified membranous central area with flattened calcified margins varying in width according to species.

Osbum’s (1950, 1952, 1953) treatise on eastern Pacific bryozoans predated use of scanning electron microscopy (SEM), as did Soule’s (1959,1961,1963) studies of the Gulf of California and Soule & Soule’s (1964) studies of Scammon’s Lagoon (=Ojo de Liebre) on the western coast of Baja California. Osbum’s identifications also reflected the philosophy then current that Atlantic and Mediterranean species were expected to occur in similar temperature zones in the eastern Pacific (Soule, Soule & Morris 2002) but in some cases he incorporated a wide range of variability in species descriptions to compensate for differences observed.
Soule, Soule & Chaney 1995 indicated that *M. ciliiata* (Pallas, 1766) apparently does not occur in the eastern Pacific, and that Osburn's material identified as that species included at least one new species with single avicularia, *M. catalinensis* Soule, Soule & Chaney, 1995 and one with two avicularia, *M. planuta* Soule, Soule & Chaney, 1995. Five species that contain pore sieve plates were discussed in that paper: *M. californica* Busk, 1856, *M. cribrosa* Osburn, 1952; *M. infundibulipora* Soule, Soule & Chaney, 1995; *M. planuta* Soule, Soule & Chaney, 1995 and *M. setiformis* O'Donoghue & O'Donoghue, 1923. All have a denticulate ascopore rim with a variously shaped, denticulate, uvulate process, except for *M. setiformis* which has only a small round, smooth ascopore. The more southern microporellids had not been examined by SEM at that time.

2 MATERIALS AND METHODS

2.1 Collections studied

Microporellid specimens studied are largely from the collections of the University of Southern California (USC) Allan Hancock Pacific Expeditions (AHF), obtained primarily by trawl and dredge in the 1930s and 1940s from California, Baja California, the Gulf of California, and extending to Colombia and the Galápagos Islands (Osburn 1952). These are accessed to the Santa Barbara Museum of Natural History (SBMNH) but presently retained at USC. Other collections were made by Soule & Duff (1957) of Pleistocene material from Santa Barbara and the greater Los Angeles area, and J.D. Soule collected specimens intertidally and by trawl and dredge during the Puritan-American Museum Expeditions to Baja California and the Gulf of California in the mid-1950s (Soule, 1959, 1961, 1963). Morris collected by snorkel and scuba in the Mazatlán Harbor area, Sinaloa, Mexico during water quality surveys by USC’s Harbors Environmental Projects in the 1970s, directed by D.F. Soule. Hawaiian specimens were collected in the late 1960s by snorkel and scuba under NSF grants to Soule and Soule. American Samoa specimens were collected by Soule and Soule in the course of water quality studies for the tuna canneries.

2.2 Methods

Dry specimens were prepared for SEM by sonifier for the few specimens on algal substrates and/or by cleaning with sodium hypochlorite if on shell or stone. Loose specimens were mounted with water soluble white glue on copper pennies which were temporarily mounted on stubs or glass slides. Specimens already permanently mounted on glass slides were surrounded by aluminum foil. All were sputter-coated with gold for scanning, and examined with a Cambridge 360 SEM, usually at 10kv.

3 RESULTS

3.1 Recent eastern Pacific microporellid research

Soule, et al. (2003) created the genus *Microporelloides* based on the occurrence of numerous small to large pores in the ovicell hood, often similar to the frontal wall pores, in all of the eastern Pacific forms found from British Columbia south to the Galápagos Islands and Colombia, South America, and west to the Hawaiian Islands. Soule, Chaney & Morris (2004) added further species from southern California and American Samoa to total 21 species. In contrast, Polar and eastern Atlantic-Mediterranean *Microporella* spp. have few or no pores in the central hood, although the hoods may be bordered by areolae.

Our first reaction was to postulate that this might simply be a temperature/oxygen solubility relationship in which more large pores might be valuable as oxygen is reduced in warmer waters, but water temperatures where eastern Pacific species in which ovcicells with pores occur range from cool temperate to warm temperate and tropical. In contrast, over similar temperature ranges in the eastern Atlantic, species with ovcicells have few or no pores. We then looked at the literature for reports of species with and without ovcicell pores in other geographical areas to see if similar patterns occurred. Instead we found such species occurring together or in the same general region, within similar temperature ranges. We have called these regions transition areas.

We conclude that the presence or absence of ovcicell pores may be an evolutionary characteristic worth evaluating since the type species of *Microporella*, ‘*M. ciliata* sensu lato’, has been reported from the Miocene to Recent but that has not been confirmed and the species is apparently absent in the northeastern Pacific and eastern tropical Pacific. Some *Microporelloides*, such as *M. californica*, *M. umbonata* and *M. vibraculifera* have been recorded from the Pleistocene in southern California (Osburn 1952. Soule & Duff 1957, Soule et al. 1995).

3.2 Transitional areas

It was not our intent to examine the multitude of records of *Microporella* spp., *sensu lato*, worldwide, as did Taylor & Mawatari (this volume) in their excellent studies of *Microporella* spp. Instead we focused on the northeastern and eastern tropical Pacific species (Soule et al. 1995, 2003, 2004). We discuss below some geographic regions wherein we noted various species with and without ovcicell pores that co-occur.
3.3 Northern and southern Alaska

Examination with SEM of specimens from the Arctic MacGinitie collections made under the auspices of the U.S. Navy off Point. Barrow, northern Alaska, and identified by Osburn (unpublished) as *Microporella arctica* Norman, 1903, show that indeed it has no central ovicell hood pores but has a small umbo (see Figs 1-4 for comparison of ovicell hood pores). The species also has a small umbo proximal to the ascopore which is surrounded distally and laterally by large areolae, and frontal wall pore sieve plates. Kluge (1962, translation 1975) referred to Norman’s species as a variety of *M. ciliata*, which has scarce single avicularia with acute mandibles, whereas Point Barrow specimens have a few zooids with small, widely oval avicularian rostra. It is probably an undescribed species. The scarce avicularia are generally more distally placed than those of *M. ciliata*, sensu stricto.

Dick & Ross (1988) described two new *Microporella* species, *M. germani* Dick & Ross, 1988 and *M. neocribroides* Dick & Ross, 1988 from the Kodiak vicinity intertidal, as having imperforate granular ovicells with only small marginal pores, and one, *Microporella alaskana* Dick & Ross, 1988, as having marginal pores and a few scattered pores on the hood surface, which would place the last named in the genus *Microporelloides*. Their *M. californica* Busk, 1856 has many small ovicell pores and radiating ridges extending up to an umbo typical of that species. Their material was not reexamined by SEM for pore plates.

*Microporella speciosa* Suwa, Dick & Mawatari (1998), was described from the subtidal of Kodiak Island and western Alaska as having a single avicularium with a short acute mandible directed laterally, differing from the oval of our Point Barrow material. Their species has ovicells without frontal hood pores but with areolae around the base of the hood. It resembles *M. trigonellata* Suwa and Mawatari 1998 from Hokkaido, Japan except that the single acute avicularium in the latter is directed distally. The Kodiak Island, Alaska vicinity thus seems to be a transitional area.

3.4 Japan


Mawatari & Suwa (1998) described two new species of *Microporella* from Sagami Bay in Japan, found in the Döderlein Collection in the Musée Zoologique in Strasbourg, France. One, *M. serrata* Mawatari & Suwa, 1998, has an oovicell imperforate except for large distal areolae, and a cribrate ascopore such as that in *Microporelloides cribrosa* from California and *Microporella neocribroides* from the Kodiak vicinity. The other, *M. unca* (Mawatari & Suwa 1998), has a completely porous oovicell, placing it in *Microporelloides*. It has a thick, raised avicularium rostrum somewhat similar to that in *Microporelloides vibraculifera* (Hincks, 1883), described from British Columbia and reported in California and western Baja California, but the latter has a much larger rostrum and vibraculum. Thus Japan also appears to be a transitional area, seemingly having about an equal number of species with few or no mid-frontal oovicell pores and species with them, and in having species with and without cribrate frontal wall pore plates.

3.5 Chile

*Microporella areolata* Moyano, 1983 was described from central Chile as having a few very small frontal wall pores with larger oovicell pores and marginal pores, placing it in *Microporelloides*. Moyano (1991) also found *Microporellapersonata* (Busk, 1854) with an imperforate hood, in central Chile, extending its range northward from the Strait of Magellan and Falkland Islands. Thus the central Chilean coast seems to be another transitional area.

3.6 Other areas that support *Microporelloides* spp.

There are other areas that support *Microporelloides* spp. For example, Marcus (1937) illustrated oovicells with pores in his ‘*M. ciliata*’ from Brazil, apparently making it an undescribed *Microporelloides*. Other references indicate that the Caribbean hosts *Microporelloides* spp. rather than, or in addition to, *Microporella* spp.

In much literature prior to SEM it is not possible to be certain whether pores are present in the oovicell hoods, so the character may be more widespread than confirmed to date. However, it is important to note the total absence of ‘*Microporella*’ spp. which lack oovicell hood pores in the northeastern and tropical
Figures 1-4. Comparison of ocell structures. Figure 1. *Microporella arctica* (?), Point Barrow, Alaska, imperforate ocell 530 pm in diameter. Figure 2. *Microporelloides mazatlanica*, Mazatlán, Mexico, untreated, raised, perforate ocell 300 pm in diameter, avicularia mandibles 240-300 pm in length from hinge bar. Figure 3. *Microporelloides catalinensis*, off Santa Catalina Island, CA, large frontal wall pores, distal frontal wall blending into ocell hood, hood 300 pm in diameter. No frontal wall sieve plates. Figure 4. *Microporelloides setiformis*, off Santa Rosa Island, CA, ocell, 350 pm in diameter; frontal wall, ocell hood with small pores 8-13 pm in diameter, tiny pore sieve plates present.
4 SIZE OF PORES IN OVICELLS AND FRONTAL WALLS

Microporelloides ovicell pores are generally, but not always, similar in size to those in the frontal wall. For example, ovicell pores in *M. hawaiiensis* Soule, Chaney & Morris, 2003, while numerous, are small, about 2.5-5 pm in diameter, whereas frontal wall pores are about 7-10 pm. In some northeastern Pacific species such as *M. umboniformis* Soule, Soule & Chaney, 1995 from southern California, ovicell pores are about 5 pm and frontal wall pores about 10-15 pm in diameter. Frontal wall pore sizes are similar in *M. vibraculifera*, described from British Columbia and identified in southern California from the Pleistocene to the present, and 8-13 ptm in *M. setiformis*, described from British Columbia and found in the California Channel Islands.

Both ovicell and frontal wall pores in *M. catalinensis* from southern California are much larger, about 18-20 pm, sometimes merging or forming even longer slits or irregular pores in both the ovicell hood and frontal wall. Pores are similarly large but round in *M. infundibulipora* from southern California. *M. galapagensis* Soule, Chaney & Morris, 2003 has frontal wall pores 10-20 pm in diameter sunken in pits tapering until the frontal wall appears rugose; ovicell pores are similar but rapidly become covered with heavy secondary calcification.

5 CONTINUITY OF OVICELL ECTOOECIUM WITH DISTAL FRONTAL WALLS

The appearance of ovicelled zooids differs among species in their association with the next distal zooid in northeastern Pacific species. In some species ovicells appear to be distinctly separated from the next distal frontal wall surface, while in others the distal frontal wall surface is continuous with the mature ovicell hood.

5.1 Separation of ovicell hoods from distal zooid frontal walls

The ovicell ectooecium, even when porous, seems well separated from the next distal zooid frontal wall as marked by larger marginal areolar pores in *Microporelloides cribrosa*, *M. californica*, and *M. planata* from southern California; *M. mazatlanica* Soule, Chaney & Morris, 2003 from Mazatlán, Sinaloa, Mexico; *M. pontifica* (Osbum, 1952) from the Gulf of California; *M. gibbosula* (Canu & Bassler, 1930) from the Gulf of California and the Galápagos Islands; and *M. galapagensis* Soule, Chaney & Morris, 2003 and *M. hawaiiensis* Soule Chaney & Morris, 2003 from their respective localities. Whether separation of ovicell hoods from distal zooid frontal walls is a developmental criterion distinguishing these species from others is not known.

5.2 Continuity of ovicell hoods with distal zooid frontal walls

Ovicell ectooecium seems to be confluent with that of the next distal frontal wall in *Microporelloides setiformis* from British Columbia and California, *M. catalinensis* from the Channel Islands, *M. tractabilis* (Canu & Bassler, 1930) from the Galápagos Islands, Panama and Colombia, and *M. coronula* Soule, Chaney & Morris, 2003 from Mazatlán, Mexico. Whether continuity of ovicell hoods with distal zooid frontal walls is of taxonomic or developmental significance is unknown but it is consistent within these species.

The primary ovicell disk is laid down distal to the maternal apertural rim, recumbent on the next distal frontal wall. The outer wall of the ovicells in *Microporelloides* spp. is similar in structure to adjacent zooid frontal wall, and never forms an imperforate or clearly separated ovicell hood such as occurs in *Microporella* spp. Taylor & McKinney (2002) discussed the evolutionary origins of cheilostome ovicells from spines borne on distal zooids, which might be consistent with the latter type of development, although as they point out, there may be other modes of formation.

6 ASCOPORE SIZE AND SHAPE

Ascopores range from being almost round without denticulation, with an opening about 16 p.m in diameter, to round, ovoid or lunate shapes from 20 to 60 p.m in diameter, often with a median distal uvulate projection and with or without denticulate margins. Figs 5-7 illustrate different ascopores. In both the genera *Microporella* and *Microporelloides* there are no frontal wall pôrês between the proximal apertural lip and the ascopore as there are in the genera *Fenestrulina* and *Fenestruloides*.

Only one species in the eastern Pacific south of Kodiak, Alaska has a cribrate plate occupying the entire ascopore space, *Microporelloides cribrosa* (Osbum, 1952). Canu and Bassler (1930) indicated that *M. tractabilis* had a ‘perforate lamina’ over the ascopore, but Osbum described that ascopore as large, with a projecting shelf (our uvulate process) leaving a lunate opening, as illustrated in Soule et al. (2003). Other species have been reported to have
cribrate ascopores, such as *M. neocribroides* from Kodiak and Japan and *M. serrata, M. elegans* and *M. pulchrafcom* Japan. *M. discors* Uttley and Bullivant, 1972 from New Zealand waters as illustrated by Gordon (1984) shows a variably complete merger of a strong denticulate uvulate process with ascopore rim denticles instead of a completely cribrate plate. Cribrate ascopore plates in *M. cribrosa* are more elaborately
s sculpted and fused (Fig. 7). The cribrate ascopore reported by Soule (1961) in a Gulf of California specimen and re-examined by SEM is actually composed of tiny denticular debris particles and calcareous epibionts accumulated on the ascopore.

7FRONTAL WALL SIEVE PLATES

Cribrate frontal wall pore sieve plates are much smaller than cribrate plates present in ascopores. Cribrate sieve plates in some species then included in the genus *Microporella* were illustrated in Soule et al. (1995). Figs 8-10 show examples of some cribrate pore sieve plates. So distinctive in some of the southern California species, pore sieve plates are absent altogether in all species examined from south of the California-Baja California border, with Tanner Bank off San Diego, CA the southern limit as exemplified by *Microporelloides franklini* (Soule, Chaney & Morris, 2003). The more southern islands and banks west of Baja California have not been as thoroughly sampled, however.

Species with cribrate pore sieve plates included in *Microporelloides* are *M. cribrosa*, and *M. californica* from southern and central California coastal waters, *M. setiformis*, from British Columbia and southern California, *M. planata* and *M. infundibilipora* from the southern California Channel Islands and *M. franklini* from off Tanner Bank near San Diego, CA. These species were placed in the subgenus *Cribri­porella* Soule, Chaney & Morris, 2003 as was *M. santabarbaraensis* Soule, Chaney & Morris, 2004. The type of *M. californica* BMNH 1899.7.1.1399, was not available for SEM during this study; it is labeled ‘California collected by Dr. Gould’. The presence of pore plates in it could not be verified.

Soule et al. 2003 listed three previously described species of eastern Pacific *Microporelloides* which lack pore plates: *M. tractabilis*, *M. gibbosula* Canu & Bassler, 1930, and *M. pontifica* Osbum, 1952 from the Gulf of California and the Galápagos. They described five new species lacking them: *M. mazatlanica*, from Sinaloa, Mexico, *M. coronula* and *M. peschongi* Soule, Chaney & Morris, 2003 from Baja and the Gulf of California; and *M. galapagensis*, and *M. hawaiiensis* Soule, Chaney & Morris, 2003, from their respective localities. Soule, Chaney & Morris, 2004 added *M. lepueana* Soule, Chaney & Morris, 2004 from American Samoa, and created the new subgenus *Microporelloides* Soule, Chaney & Morris, 2004 for this group, with *M. mazatlanica* the type species, suppressing the ineligible subgenus name *Patorporella* Soule, Soule & Chaney, 2003. They added new species *M. wrigleyi* Soule, Chaney & Morris, 2004 and *M. sanmiguelensis* Soule, Chaney & Morris 2004 from southern California, to the genus *Microporelloides*, subgenus *Microporelloides* at that time.

8DEVELOPMENT OF PORE SIEVE PLATES

IN *MICROPORELLOIDES*

Cribrate pore sieve plates originate in an interior frontal wall layer as minute calcareous projections which grow to anastomose in the center of the pore. Examination of the interior surface of the frontal wall shows no indication of separation of the projections from the frontal wall nor any rims on the pores (Figs 11,12). From the exterior, subsequent secondary frontal wall calcification is seen to build up around the pores, which generally retain their symmetry in spite of the depth of calcareous layers of the thickening frontal wall and, usually, the lack of a discrete rim.

In contrast, in pores lacking sieve plates, the pore rim is distinct as viewed from the interior frontal wall surface (Fig. 13). Succeeding layers of frontal wall calcification can be seen, as well as the exterior rim beneath the intact frontal membrane.

8.1 Potential stimuli for developing pore sieve plates

One can speculate about what the stimuli might be for formation of the pore sieve plates, their presence confirmed in some species along about 800 km of California coastal waters, perhaps extending northward to British Columbia, but apparently not south of southern California. Epizooites browse on bacteria, fungi or protists growing on the bryozoan frontal membranes or walls (e.g. Harvell 1984, Soule et al. 1995) and probably enjoy the tissue in the frontal wall pores. If the pores are occluded by sieve plates, breaching the barrier to the interior of zooids would be more difficult.

The geographic range of the sieve plate character encompasses cold Alaskan waters and cool temperate to warm temperate waters in the eastern Pacific, but seemingly not to subtropical or tropical waters to the south. Depths ranged from intertidal to about 150 m, which could include considerable temperature difference, but temperature data are not available for most stations so temperature gradients cannot be accurately determined. No Microporellidae were found in the very warm, shallow, high saline waters of Scammons Lagoon (Soule & Soule 1964) on the west coast of Baja California.

Suwa and Mawatari (1998) illustrated deeply set cribrate pore plates in *M. neocribroides* from Alaska and Hokkaido, Japan, and *M. elegans*, *M. pulchra* and *M. serrata* from Hokkaido. They maintained cultures of collected species at 12°C in their laboratory, which is a temperature similar to lower limits of temperatures in shallow waters in southern California in winter and deeper waters in summer.

Gulf of California waters are tropical, although the west coast Baja California waters may be subtropical in summer, when the California Current is dominant
Figures 11-14. Interior view of developing frontal wall pores with and without sieve plates. Figure 11. *Microporelloides cribrosa*, off San Pedro, CA, interior frontal wall, developing cribrate sieve plates, spaces 12-13 pm at widest (subgenus *Cribriporella*). Figure 12. *Microporelloides franklini*, Tanner Bank off San Diego, CA, developing sieve plates 10-12 pm in diameter. Figure 13. *Microporelloides mazatlanica*, Guaymas, Gulf of California, interior of frontal wall pores 10 pm in diameter, without sieve plates (subgenus *Microporelloides*). Figure 14. *Fenestruloides morrisae*, Tiburon Island, Gulf of California, interior of frontal wall with surficial pore plate.
and upwelling may occur, than in winter periods when the countercurrent flows northward more strongly inshore, carrying tropical waters. Hawaiian waters are subtropical and American Samoa tropical. Physical or biological factors which control formation of cribrate pore sieve plates might limit the distribution of the pore sieve plate character to some cold and temperate regions, excluding such plates from species in the tropical/subtropical eastern Pacific. Five species in California waters lack pore sieve plates but all the tropical/subtropical species examined lack them.

Among *Microporelloides* species that lack sieve plates, some have smaller frontal wall pores but others do not, and some have thinner frontal walls than those with sieve plates but others do not. Species with and without pore sieve plates can co-occur in the same general thermal regime in cooler waters, although they may have found different microhabitats, but do not co-occur in the eastern Pacific warmer waters.

Many microporellids seem to colonize small shell fragments and stones that are tumbled about on the bottom, and those on algae are subjected to suspended sediments, but the frontal wall pores are generally smaller than sand grains that might breach the frontal membrane. Predators that breach the small pores would not seem to be limited to cooler waters and excluded from the warmer waters but it is a possible hypothesis that could be examined.

### 9 COMPARISON OF *MICROPORELLOIDES* WITH *FENESTRULINA* AND *FENESTRULOIDES*

The family Microporellidae is represented in the eastern Pacific by the genera *Microporelloides*, *Fenestrulina* and *Fenestruoides*, with several characters in common: the presence of an ascopore, frontal wall pores and ovicells. However, there are subtle differences in development that need to be further examined in living material.

#### 9.1 Ovicells

Ovicells appear to develop differently in *Fenestrulina* and *Fenestruoides* species examined as compared to *Microporelloides* from the same area in the northeastern Pacific. As the primary gymnocystal disk in the fenestruidins is deposited distal to the spines and apertural rim of the proximal zooid, calcareous ribs fan out atop the next distal frontal wall to form buttockes extending to the disk (Fig. 17). A rim is formed by adjacent frontal wall, and the spaces between the buttockes become the areolar pores which rim the mature imperforate hood. No buttockes have been seen in the northeastern Pacific *Microporelloides* spp.

#### 9.2 Frontal wall pores

Fenestruoidins in southern California are represented by one species of *Fenestruoides* and several species of *Fenestruoides* (Soule et al. 1995). All *Fenestruina* spp. have a well defined gymnocystal rim, with frontal wall pores confined mostly to the margins, to the area between the apertural and ascopore, and to the area distal to the apertural rim. Eastern Pacific *Microporelloides* spp. lack frontal pores between the ascopore and the apertural and distal to the aperture. Many specimens worldwide have been included in *Fenestrulina malusi sensu lato* (see Soule et al. 1995). *Fenestruoides* spp. have very little gymnocytopl showing, and frontal wall pores in mature zooids are distributed more or less evenly over the frontal wall except in species having an umbo. Pores are absent around the inflated base of an umbo that bears the ascopore or is just proximal to it. Pores are easily visible with light microscopy in fenestruidins because of the surficial position of the pores (Fig. 14).

Fenestruinid pore sieve plates appear to originate in the surficial layers of the frontal wall, in contrast to the sieve plates in *Microporelloides* which originate in a primary calcified layer and become sunken as calcification of the frontal wall increases. Scanned from the interior, *Fenestruoides* pore plates are not immersed in multiple layers of calcification as are the pores in *Microporelloides*.

#### 9.3 Fenestruoides illustrated worldwide in the literature

Examples of species that belong in the *Fenestruoides* have been illustrated earlier in the literature from widely disparate areas. Examples include: Jersey, U.K. (Soule et al. 1995); Arctic (Kluge 1962, trans.1975); south Atlantic (Hayward 1980); Antarctic (Hayward & Thorpe 1989, Hayward & Ryland 1990); Indian Ocean, Mauritius (Hayward 1988) and Indonesia (Winston & Heimberg 1986); western Pacific, New Zealand (Gordon 1984, 1989); Great Barrier Reef (Hastings 1932, Ryland & Hayward 1992); Philippine Islands (Canu & Bassler 1929); eastern Pacific, from the Kodiak Islands vicinity (Dick & Ross 1988) and British Columbia (O’Donoghue & O’Donoghue 1926), to California and Mexico (Gabb & Horn 1862, Canu & Bassler 1923, Osbum 1952, Soule et al. 1995); and Chile (Moyano 1983, 1991). Thus *Fenestruoides* spp. are represented worldwide.

#### 9.4 Avicularia

Some authors have used absence/presence of avicularia to define the difference between fenestruidins and microporellids, but that is not valid in the eastern Pacific. A distinct, raised, acute avicularium at the
Figures 15-18. 15-16 Differences in proximal apertural rims. Figures 17-18 Development of *Fenestruloides* ovicell. Figure 15. *Microporelloides mazatlanica*, Mazatlán, Mexico, aperture with almost straight proximal lip, 90 p.m wide, two small condyles at ends. Figure 16. *Microporelloides hawaiensis*, Molokai, Hawaiian Islands, aperture with almost straight proximal lip, 106 jim wide, strongly denticulate ledge characteristic of some western Pacific species. Figure 17. *Fenestruloides morrisae*, Tiburon Island, Gulf of California, developing ovicell with buttresses that will separate distal areolar pores. Figure 18. *Fenestruloides morrisae*, Anacapa Passage, southern California, complete ovicell with distinct rim separating it from next distal zooid.
proximal end of one zooid was found in the type species of *Fenestruloides, F. morrisae* Soule, Soule & Chaney 1995, although no other avicularia have been found. This does indicate a potential in the genus to produce marginal avicularia.

9.5 Differences in position of microporellid avicularia

Although we have divided microporellids on the basis of the presence or absence of central ovicell pores, microporellid species might alternatively have been divided on the basis of the presence of either one or two frontal avicularia. The problem in so doing is that in at least one species from off Baja California, *Microporelloides peschongi*, typically has a single avicularium except in large zooids that give rise to two zooids as does *M. lepueana* from American Samoa. Some other species also show variability in number, ranging from no avicularia to one or two.

The placement of the single avicularium can be significant. It can be located distolaterally, in the position of one of paired avicularia, with the avicularium probably derived from a distolateral pore. However, in *Microporella ciliata*, the avicularium seems to originate at a more medial proximolateral pore and comes to lie more proximally on the frontal wall than it does in *Microporelloides franklini, M. pontifica, M. gibbosula* and *M. hawaiiensis*. There is considerable variation in placement and the characteristic is not sufficiently definitive for taxonomic division in our opinion.

9.6 Character of the proximal apertural rim

Another character that might be used to separate microporellid species in the Pacific is the nature of the proximal apertural rim. In all of the coastal eastern Pacific species, the proximal rim is always nearly straight and smooth, sometimes with blunt condyles (cardelles) at the corners lying slightly behind the proximal rim (Fig. 15). However, *Microporelloides hawaiiensis* (Fig. 16) and *M. lepueana*, which have a straight, denticulate proximal apertural rim, are more closely allied with the western Pacific species *Microporella orientalis*, as figured by Ryland and Hayward (1992), although the denticulate proximal apertural rim they figured was much more finely denticulate. All are unlike the Tizard Reef specimen of *Microporella* from the South China Seas figured by Soule et al. 2003 which has very large condyles as well as the denticulate proximal rim.

The denticulate proximal apertural rim appears in several species in diverse Pacific locations (e.g. Harmer 1957, Gordon 1984, Tilbrook et al. 2001) and is probably sufficiently distinctive to create subgroups of species with and without the denticulate proximal rim but doing so would require an extensive review of western Pacific specimens not presently available to us. Suwa & Mawatari (1998) recorded two *Microporella* species as having a denticulate proximal apertural rim, but their other five species have smooth proximal apertural rims. This seems to be another indication of Japan as a transition zone. Moyano (pers. com.) indicates that *Microporella hyadesi* Jullien, 1888, a southeastern Pacific-southwestern Atlantic species, also has a denticulate apertural rim.

10 CONCLUSIONS

10.1 Ovicell pores in Microporelloides

The taxonomic situation for the northeastern and tropical eastern Pacific microporellids has changed greatly with further examination by SEM of extensive collections from southern and Baja California. All 21 species known from British Columbia south to Colombia and the Galápagos Islands and west to the Hawaiian Islands and American Samoa have extensive ovicell pores in the central (frontal) area of the hood placing them in *Microporelloides*. None have imperforate ovicell hoods, with or without areolae, in contrast to those in species previously reported from the Arctic, Antarctic, northern and eastern Atlantic and Mediterranean. Thus no *Microporella sensu stricto* occur in the northeastern Pacific.

Transition areas exist in the Pacific, specifically in Japan, Alaska and Chile, in which *Microporelloides* spp. show central frontal ovicell pores, usually like those in the frontal wall whereas *Microporella* spp. do not. Other transition areas, or areas populated with both genera, may well exist.

The trend toward ovicells with numerous pores was discussed in Soule & Soule (2002) and Soule, Soule & Morris (2002) in a different genus, *Parasmittina*, in which the distribution of species with numerous pores was approximately the same in the northeastern Pacific as that in *Microporelloides*. In the *Parasmittina*, however, all ovicells had at least a few pores in the central hood, even in Arctic environments. The gradual increase in number and size of pores in eastern Pacific *Parasmittina* species from temperate to tropical waters might well be linked to temperature/oxygen solubility and the gradation left no possibility of division of the genus on that basis.

10.2 Frontal wall pore sieve plates

Seven of the 12 species of *Microporelloides* occurring in central and/or southern California bear complex frontal wall pore sieve plates (Subgenus *Cribriporella*), a characteristic that does not seem to extend to species to the south in Baja California, the Gulf of California, Colombia or the Galápagos.
Islands, or west to the Hawaiian Islands and American Samoa (Subgenus Microporelloides).

10.3 The importance of emphasizing species differences

The characters discussed illustrate consistent differences observed in eastern Pacific microporellid genera and species. Such differences are important to zoogeographic and evolutionary perspectives, perhaps involving isolation and speciation after the closing of the Panamanian isthmus. Other influences might be alterations in eastern Pacific circulation by the Aleutian Islands during periods of changing eustatic sea levels. It is certainly clear that Recent speciation has occurred in the Gulf of California, the coast of California and in the California Channel Islands.

Recognition of invertebrate species diversity in the eastern Pacific is important to coastal zone protection. Pressure for coastal development and concomitant degradation by coastal zone populations is severe, with more than ten million people in the greater Los Angeles area, for example. Federal and State regulations require industry and public agencies to report on at least the megafauna to be impacted in a proposed development. However, if biologists continue to portray the local invertebrate species such as bryozoans as mere representatives of common species found elsewhere in the world, no pressure will be exerted to preserve local coastal and Channel Island shallow water species and habitats. So little research is being funded for smaller invertebrate groups that they are largely ignored in environmental surveys in the United States, in part for lack of specialists to make timely determinations, but causing a false perception of lower species diversity. Development may have already eliminated habitat at many of the stations collected in earlier years, so it is critical that the unique character of some of the smaller invertebrates that are important in the local food web be recognized.

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REFERENCES


Freshwater Bryozoa of Italy. A survey of some species from the Italian bryozoan collection of A. Viganò with new records

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ABSTRACT: The survey of a part of the Viganò collection has supplied interesting information about the distribution of freshwater bryozoan species in Italy. The morphological analysis of the micro-architecture of statoblasts, performed by scanning electron microscope, has permitted the correct classification of the specimens, previously identified by Viganò as Plumatella repens and Plumatella emarginata. Plumatella rugosa, Plumatella reticulata, and Plumatella geimermassardi must be added to the ten species already known in Italy. In addition, Tanganella miilleri, a brackish-water species, has been recorded in Lake Trasimeno (Umbria, Perugia), which has a high salt content.

1 INTRODUCTION
Research on Italian freshwater Bryozoa was interrupted with the death of Prof. Antonio Viganò in 1972. Because of this, many problems regarding the taxonomy, the ecology and the biogeography of these animals have remained unsolved. Because of the recent discovery that some Phylactolaemata can be alternate hosts of Tetracapsuloides bryosalmonae (Canning et al., 2002), the etiological agent of Proliferative Kidney Disease (PKD) of salmonids (Canning et al., 1999), these invertebrates have gained importance.

2 MATERIALS AND METHODS
We continue the research on Italian bryozoans after a gap of thirty years (Caffara et al., 2002). In addition, both the previously unidentified and the classified samples of the Viganò collection are being re-examined. After verification using a scanning electron microscope (SEM) of statoblast superficial micro-architecture the samples are being classified. Viganò’s samples were collected in Italy between 1963 and 1971 and were from rivers, small alpine lakes, lakes located in the Po Valley, lakes in central Italy, artificial ponds and barrage lakes. Of the about one hundred samples, some have been preserved in 10% formalin, while others are dried or preserved in 70% ethyl alcohol. Slides have been prepared for the light microscope examination of most of them. The Viganò collection samples, together with the newly collected samples, are preserved in the private collection of M.I. Taticchi. With the reorganization of the collection a database will also be created.

The species recorded in Italy up until now are (Viganò 1964a, 1964b, 1965, 1966, 1969):

- Fredericella sultana (Blumenbach, 1779)
- Plumatella fruticosa (Allman, 1844)
- Plumatella emarginata (Allman, 1844)
- Plumatella casmiana (Oká, 1907)
- Plumatella repens (Linnaeus, 1758)
- Plumatella fungosa (Pallas, 1768)
- Hyalinella punctata (Hancock, 1850)*
- Lophopus crystallinus (Pallas, 1766)
- Cristatella mucedo (Cuvier, 1798)
- Paludicella articulata (Ehrenberg, 1831)

*Only in a small spring-water alpine lake (2640 m above sea level) (Viganò, 1965).

Our aim is to identify the bryozoan species that were present in Italy thirty years ago, in particular in Lake Trasimeno (Umbria, Perugia). Although the entire national territory has not been investigated, it is important to study and compare the species distribution thirty years ago with the present distribution. This study might represent the starting point for investigating whether the changes of the trophic condition of the water bodies investigated have produced appreciable effects on the bryozoan fauna. In this sense, the bryozoan fauna can be considered a good bio-indicator. Moreover, the reliable information about the taxonomy of these invertebrates permits us to gain some biogeographical knowledge. This will be the starting point to accurately study the species, which are the preferred alternate hosts of Tetracapsuloides bryosalmonae.
3 RESULTS AND DISCUSSION

The sample labels, the locations, the dates and the identified species found are recorded in Table 1. Several of these species are recorded from Italy for the first time and these together with other interesting taxa are discussed below.

3.1 Plumatella rugosa (Wood et al., 1998)

In Lake Alserio the colonies have the form of a bush, the tubules are packed with statoblasts; they are transparent, shiny and not encrusted. In Lake Trasimeno the colonies adhere to the substrate, the tubules are amber-coloured and transparent, the septa are clearly visible (Fig. 3E). In Lake Cogolli the colonies adhere to the substrate and the fine mineral material, which encrusts the tubules, makes evident the keel and the emargination (Fig. 3F). P rugosa collected from the Italian localities shows the reticulation, which covers the whole floatoblast (Fig. 1A) in accordance to the description of Wood for this species (Wood et al., 1998 and Wood, 2001a). However, some differences can be noted: a) the polygonal cells of the annulus are slightly bigger than the fenestra ones; b) the interstitial tubercles of the fenestra, on both dorsal and ventral valves, are very flattened in the central part of the fenestra (Fig. 1 A, C); c) on the annulus only the first two or three series of cells next to the fenestra show interstitial tubercles; d) distally, little scattered nodules are noticed on both the valves (Fig. 1B, D) and their density is variable according to the locality; in Lake Alserio (Fig. IF) they are more abundant. The presence of nodules on the annulus contrasts with Wood’s description (Wood, 2001a, b) for this species. On the medial rib (Fig. IE, F) beads and incomplete demarcations can be seen. In the parasutural zone there are two rows of alternate tubercles and lateral ribs, more evident in floatoblast from Lake Alserio. The total length (L) and the length of the capsule of the dorsal valve (1) are generally smaller than those of the ventral valve, while the total width (W) and that of the capsule (w) are on average the same size on both valves (Table 2). However, the various parameters have a large range of variability in the three localities. On average the floatoblasts from Lake Alserio are the largest, followed by those of Lake Trasimeno and Lake Cogolli. The statoblasts collected from Lake Cogolli are more roundish. The dorsal fenestra is slightly wider than long (Fig. 3A, B). The mean dimensions (L and W) and the suture of the Italian floatoblasts are similar to those reported by Geimer & Massard (1986) for P repens from Luxembourg; but the P rugosa floatoblasts of our samples have the ratio L/W higher than those of P. repens (1.36 and 1.34, respectively). Moreover, as Viganò had observed (note not published), the floatoblast of P. rugosa is more rectangular than that of

Up until now, about half of the Viganò collection samples have been examined. Here we refer to the samples, which were labelled by Viganò: 'Plumatella repens' and 'Plumatella emarginata'. The samples were collected from the following locations:

- Lake Candia (Piemonte, Torino), 226 m above sea level, average depth of 5.9m, surface area of 21.35 km², average pH 7.5, a eutrophic lake (Gaggio & Cappelletti, 1984).
- Lake Alserio (Lombardia, Como), 260 m above sea level, surface area of 1.23 km², average depth of 5.32 m, average pH 7.4, a very eutrophic lake (Gaggio & Cappelletti, 1984).
- River Staffora (Lombardia, Pavia), a right tributary of the River Po. Sampling site: located at about 250 m above sea level, current speed 1.8 km/h, odour H₂S, low transparency.
- Lake Trasimeno (Umbria, Perugia), 258 m above sea level, surface area of 124.30 km², conductivity 900-1000 S (sodium chloride ions are up to 60% of total anions) (Hamza et al., 1995), average depth of 4.72 m, pH > 8; during summer months pH may reach 9.5-10, a eutrophic shallow lake (Taticchi, 1992).
- Lake Cogolli (Umbria, Perugia), 265 m above sea level, pH 7.5, an artificial pond about 5 km from Lake Trasimeno which receives its outflow.
- Lake Corbara (Umbria, Terni), a barrage lake on the River Tevere, 138 m above sea level, surface area of 15 km², a eutrophic lake (Di Giovanni & Prosperini, 1966).

From each colony, zoecial tubules, the richest in statoblasts, floato- and sesso-blasts, were isolated in order to ensure sufficient material for both light microscope and SEM. In this way the observed statoblasts surely belong to the same species. Some statoblasts, after treatment with KOH, were observed with an Olympus CX41 phase contrast microscope. The statoblasts were measured with image analysis Olympus DP soft system. The measures on the dorsal and ventral valves were: L = whole length; W = whole width; f = fenestra width. Moreover, the ratios calculated are the following: L/W, 1/w for both dorsal and ventral valves; for Prugosa also F(vent.)/F(dors.) and A/a for dorsal and ventral valves; for P. reticulata A/F for dorsal and ventral valves. The remaining statoblasts were treated with KOH for 30 seconds and washed in deionized water, freeze-dried in a freezer (Wood & Wood, 2000), fixed to aluminium stubs and sputter-coated with gold-palladium and viewed in a Philips XL 30 SEM. As to the classifications, the taxonomic key to freshwater Bryozoa of North America (Wood, 2001b) was also consulted and with regard to the description of the floatoblast sutures, the nomenclature of Reynolds (2000) was followed.
Table 1. The examined samples, labels, locations, the dates and the identified species in the collection of A. Viganò.

<table>
<thead>
<tr>
<th>Label</th>
<th>Location</th>
<th>Date</th>
<th>Species</th>
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<tr>
<td>tp 49</td>
<td>Lake Candia*</td>
<td>15-06-1968</td>
<td>P. rugosa</td>
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<tr>
<td>tm 14</td>
<td>Lake Alserio</td>
<td>27-06-1971</td>
<td>P. geimmermassardi</td>
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<td></td>
<td>P. rugosa</td>
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<td>tm 28</td>
<td>River Staffora*</td>
<td>01-10-1970</td>
<td>P. geimmermassardi</td>
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<td>s 231</td>
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<td>19-11-1963</td>
<td>P. rugosa</td>
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<td>s 232</td>
<td></td>
<td></td>
<td>P. rugosa</td>
</tr>
<tr>
<td>s 91 b</td>
<td></td>
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<td>P. reticulata</td>
</tr>
<tr>
<td>s 92</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>s 94, s 95</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>tm 27</td>
<td></td>
<td>24-09-1969</td>
<td>P. reticulata</td>
</tr>
<tr>
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<td></td>
<td>29-01-1971</td>
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</tr>
<tr>
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<td>01-09-1965</td>
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</tr>
<tr>
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<td></td>
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</tr>
<tr>
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<td>19-06-1967</td>
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</tr>
<tr>
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<td></td>
<td>27-07-1967</td>
<td>P. rugosa</td>
</tr>
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<td>28-05-1969</td>
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</tr>
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<td>12-05-1968</td>
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</tr>
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<td>tp 55</td>
<td></td>
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<td>P. rugosa</td>
</tr>
<tr>
<td>tp 50</td>
<td>Lake Corbara</td>
<td>15-07-1966</td>
<td>P. emarginata</td>
</tr>
</tbody>
</table>

* In the sample there were only floatoblasts collected throwing a net (mesh size 350 p.m) on the surface layer.

P. repens. Even Toriumi (1970), who received the Italian material from Lake Trasimeno by Vigano, defined it as 'special form' of P. repens like the Japanese one. The sessoblast (Table 3) is oval in shape, the frontal valve is crowded with single or fused papillae; the lamella, almost 50 mm wide, is reticulated with interstitial tubercles, larger near the inner than on the external margin; on the basal side the lamella is also reticulated and faintly tuberculated (Fig. 2A, D).

P. rugosa has been described here for the first time for Europe. It is noteworthy that according to Wood et al. (1998) this species has been found in River Reno and described as Stiolella indica by Franz (1992). All measures published by Franz (1992) (L, W, LAV) are larger than those of the Italian P. rugosa.

3.2 Plumatella reticulata Wood, 1988

Up until now, the presence of this species has not been reported from Europe. In this study it was found only in Lake Trasimeno. In the samples, only fragments of zoecial tubules containing floato- and sessoblasts are present. These fragments were found together with those of P. emarginata, P. casmiana and P. rugosa. The samples 91 b was isolated from an original sample (tg 4) in which there were also Paludicella articulata (Ehremberg, 1831) and Tanganella miilleri (Kraepelin, 1887). Ectocyst is pale-yellowish and encrusted with fine mineral particles; the keel is not always evident; septa are present. The floatoblast is oval in shape with parallel lateral sides (Fig. 3C). The dorsal valve is longer and less wide than the ventral one (Table 4). The SEM analysis shows an annulus paved with a very lumpy appearance (Fig. 4A); the inner series of annulus cells forms something like a ring round both the fenestrae. The dorsal fenestra is smooth (Fig. 4B), the ventral one has scale-like features with a tubercle in the centre of each of them (Fig. 5A, B); this feature is unique for P. reticulata. The medial rib is single with a sharpened edge (Fig. 5C, D); the lateral ribs are hardly visible. The frontal valve of the sessoblast has a double reticulum (Fig. 5E); the higher one is larger and thicker than the inner one. The lamella is smooth; the lateral side of the sessoblast is reticulated (Fig. 5F). P. reticulata of Lake Trasimeno corresponds to the Wood’s description (Wood, 1988, 2001b) for North America specimens, both for the floatoblast dimensions and the ratios L/W, 1/w, while the dorsal and ventral fenestra appear more roundish in the Italian specimens.
Figure 1. Scanning electron micrographs of *Plumatella rugosa* floatoblast. (A) Lake Trasimeno, whole dorsal valve of floatoblast, scale bar = 100 μm; (B) detail of photo A, scale bar = 50 μm; (C) floatoblast ventral valve, scale bar = 100 μm; (D) detail of photo C, scale bar = 20 μm; (E) floatoblast suture (Lake Trasimeno), scale bar = 20 μm; (F) Lake Alserio, suture, scale bar = 10 μm.

*P. reticulata* from Israel, which was found by Massard et al. (1992), shows a ventral fenestra bigger than that of the Italian specimens. *P. reticulata* and *P. emarginata* are very similar but the following differences can be noticed: a) *P. emarginata* is oval, while *P. reticulata* is quite rectangular in shape; b) *P. emarginata* shows a lengthened dorsal fenestra, while in *P. reticulata* is quite roundish; c) sessoblast surface uniformly
granular in *P. emarginata*, roughened by network of raised lines in *P. reticulata*.

The characteristic sessoblast had already been observed by Viganò (data not published) who identified the species as *P. emarginata* Pony Creek form, according to Bushnell (1965). It is interesting to notice that, up until now, *P. reticulata* in Italy has always been found associated with *P. emarginata* (as in sample tp 56). However, *P. emarginata* can also be found not associated with *P. reticulata* (as testified by the sample collected in Lake Corbara).

### 3.3 Plumatella geimerassardi Wood & Okamura, 2004

Wood & Okamura (2004) described this species on the basis of specimens found in England, Ireland, Germany, Norway, and Italy. The Italian specimens come from the Viganò collection samples (from Lake Alserio) and from samples collected more recently (from Lake Piediluco, Umbria, and from an oxbow of the River Po). Table 1 reports two additional locations (Lake Candia and River Staffora) where this species has been found. For a description of *Plumatella geimerassardi* we refer readers to Wood & Okamura, 2004.

### 3.4 Tanganella miilleri (Kraepelin, 1887)

In the original sample tg 4, which had not been examined by Viganò, Wiebach in 1974 found some fragments of a ctenostome species, which he identified as *Victorella pavida* Saville Kent, 1870 (unpublished data). Following Jebram’s suggestions, in 1976 one of us (M.I.T.) collected some living specimens from Lake Trasimeno, which had eight tentacles and lacking the intertentacular organ. This species was not found subsequently in this lake. However, also considering Jebram’s observations on the presence of *Tanganella miilleri* in brackish lakes near Naples (Jebram, 1976), we think these specimens can be considered *Tanganella miilleri* owing to the distinctive character, which is the absence of the intertentacular organ (Braem, 1951).
Table 2. *Plumatella rugosa*. dimensions (|xm|) of dorsal and ventral valves of floatoblasts from Lake Alserio, Lake Trasimeno and Lake Cogolli (mean, standard deviation - SD, minimum - Min, maximum - Max, number of measurements - N).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Dorsal</th>
<th>Ventral</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>L. Alserio</td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>363</td>
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</tr>
<tr>
<td>1</td>
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<td>F</td>
<td>150</td>
<td>7</td>
</tr>
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<td>a</td>
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<tr>
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<td>L</td>
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</tr>
<tr>
<td>1</td>
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<tr>
<td>Fv/Fd</td>
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</tr>
</tbody>
</table>

This is important for being the first reference to the finding of a ctenostome bryozoan in Lake Trasimeno. It should be noted, however, that other brackish-water planktonic and benthonic species (*Bacillaria paradoxa*, *Navicula salinarum*, *Palaemonetes antennarius*) have been observed in this lake (Taticchi, 1968).

3.5 *Plumatella sp.*

Few statoblasts of a Plumatellidae were found in the samples 30, but due to the poor number of statoblasts it is impossible to make any sure classification (Fig. 6A, B). In this material the dorsal annulus presents an incomplete reticulation (only on the external margin) and large convex cells; the nodules and tubercles are completely missing. The dorsal fenestra is reticulated and the interstitial tubercles are more evident near the annulus. The reticulum cells have the same dimension on both the annulus and the fenestra. The floatoblast dimensions are very similar to those of *P. rugosa*.

On the frontal lamina of the sessoblast (Fig. 6C, D) the papillae are cuspidate; the lamella is reticulated only near the external margin, which is rather linear. The sessoblast is smooth on the lateral side.

Further investigations on this species and on the specimens of the sample tp 47 (in which we identified another Plumatellidae, possibly *Plumatella casmiana*) are needed.
Figure 3. Light microscope photos. (A) Dorsal valve of *Plumatella rugosa* from Lake Trasimeno and (B) from Lake Alserio; (C) dorsal and ventral valves of *Plumatella reticulata*; (D) dorsal and ventral valves of *Plumatella* sp; (E) Lake Trasimeno, zoecial tubule with septa (narrow) and (F) Lake Cogolli, zoecial tubule with keel (narrow) and emargination (narrow) of *Plumatella rugosa*. Scale bar = 200 pm for photos A, B, C, D, E; scale bar = 500 pm for photo F.
4 CONCLUSION

Up until now, the survey of the Viganò collection has allowed identification of thirteen Italian freshwater bryozoan species, including *Plumatella rugosa*, *Plumatella reticulata*, and *Plumatella geimeir-massardi*. In particular, it appears that *Plumatella repens* was completely absent in the 1960s in Lake Trasimeno and its ecological niche could have been occupied by *P. rugosa*, a very similar species. In addition, it is important to note that in Lake Trasimeno, for which some brackish-water planktonic and bentonic species have already been evidenced, *Tanganella mulleri*, a brackish-water species, has also been found. The presence of this species is coherent with the high salinity content of the large Umbrian Lake.

Table 3. *Plumatella rugosa*: dimensions (pm) of sessoblasts from the three localities (mean, standard deviation - SD, minimum - Min, maximum - Max, number of measurements - N).

<table>
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<tr>
<th></th>
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<td>47</td>
<td>8</td>
<td>34</td>
<td>63</td>
<td>20</td>
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Table 4. *Plumatella reticulata*: dimensions (pm) of dorsal and ventral valves of floatoblasts from Lake Trasimeno (mean, standard deviation - SD, minimum - Min, maximum - Max, number of measurements - N).

<table>
<thead>
<tr>
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<tr>
<td>a</td>
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</tr>
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</table>

Figure 4. *Plumatella reticulata* from Lake Trasimeno. (A) Whole dorsal valve of floatoblast with smooth fenestra, scale bar = 100 pm; (B) detail of the dorsal valve fenestra, scale bar = 50 pm.
Figure 5. *Plumatella reticulata* from Lake Trasimeno. (A) Floatoblast ventral valve, scale bar = 100 μm; (B) detail of ventral valve fenestra with tuberculated scales, scale bar = 20 μm; (C) floatoblast lateral view, scale bar = 100 μm; (D) detail of floatoblast suture, scale bar = 20 μm; (E) whole reticulated frontal valve of sessoblast, scale bar = 100 μm; (F) sessoblast lateral view, scale bar = 100 μm.

ACKNOWLEDGEMENTS

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support. We are grateful to Pierluigi Rondoni for his assistance in the preparation of the scanning micrographs.

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Preliminary overview of the cheilostome bryozoan *Microporella*

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**ABSTRACT:** *Microporella* is a lepralioid cheilostome with a widespread distribution at the present day and a geological range stretching back to the Early Miocene. Almost 150 species have been assigned to *Microporella* but approximately one-third of these belong elsewhere. Species identification can be difficult because differences between species are often subtle, sometimes not preserved in fossils, and are seldom recorded in original species descriptions. Several supposedly cosmopolitan species, including the type species *M. ciliata* (Pallas), comprise more than one species, while recent studies have shown that regional diversities of *Microporella* species can be much higher than is at first apparent. In order to clarify the taxonomy of *Microporella* and to investigate evolutionary, biogeographic and morphological patterns in the genus, we have undertaken a global survey of living and fossil *Microporella*. A cladistic analysis of nine genera belonging to the *Microporellidae* shows the inferred position of *Microporella* within this family.

1 INTRODUCTION

One of the most distinctive of all cheilostome genera is *Microporella* Hincks, 1877. While identification of the genus *Microporella* is usually uncontroversial, identifying species of *Microporella* has become increasingly difficult as ever more new species have been introduced. This taxonomic proliferation is largely due to the application of scanning electron microscopy (SEM) which, as with several other ascophoran genera (e.g. Soule et al. 2002), has revealed significant, yet often subtle, differences between geographically distinct ‘populations’ of what were formerly regarded as cosmopolitan species. The lack of a monographic synthesis is now beginning to impede progress in *Microporella* systematics. Not only do taxonomists working on bryozoan faunas find it difficult to access the widely-scattered primary literature with which to compare their own material, but older, pre-SEM publications seldom provide adequate descriptions of species morphology.

*Microporella* was established by Hincks (1877, p. 526) who gave *Lepralia ciliata* Pallas, 1766 as type species and diagnosed the genus thus: ‘*Zoarium encrusting; zoecia* with a semicircular aperture, the lower margin straight and entire; a semilunar or circular pore below it.’ Since Hinck’s time, and especially with the recognition of *Fenestrulina* Jullien, 1888 as a separate genus, *Microporella* has come to be used for lepralioid ascophorans in which the cryptocrystal frontal shield is porous all over, apart from between the semielliptical orifice and the ascopore, and all or some of the autozooids bear one or a pair of avicularia laterally or proximolaterally of the semielliptical orifice. The concept of the genus has also been expanded to include a few bifoliate erect species (see below).

We report here some preliminary results of a global survey of *Microporella* species. A database under construction has enabled biogeographical and temporal patterns in species and character distributions to be explored. Inferred phylogenetic relationships between *Microporella* and other genera of *Microporellidae* are also reported - these may ultimately help us to understand how species within *Microporella* are inter-related.

2 DIVERSITY AND BIOGEOGRAPHY

A literature search revealed the existence of 157 living and fossil species that have been assigned to *Microporella* either by the original author or subsequently. Seven of these species are regarded as unrecognizable, and 52 species belong in other genera (notably *Fenestrulina* and *Calloporina*), leaving 98 species validly assigned to *Microporella*. An undetermined
number of these species are likely to be junior synonomys, although these probably represent only a small proportion of the total.

Coincidentally, the first named species of *Microporella* became the type species, *M. ciliata* Pallas, 1766. Figure 1 shows the number of new species now assigned to *Microporella* named during each 25 year period from 1750 onwards. For each such period between 1825 and 1974, a relatively constant number of new species (8-12) was introduced. However, a significant increase in the naming of new species occurred during the final full 25 year period (1975-1999) when 24 new species of *Microporella* were introduced, and the short period between 2000 and the end of 2003 has seen the naming of 15 new species. This upsurge is undoubtedly explained by the availability of SEM which has enabled distinctions to be made between species exhibiting differences in skeletal morphology that are too subtle to be fully appreciated with an optical microscope.

The latitudinal occurrences of 63 Recent species of *Microporella*, based on type localities, is summarized in Figure 2. Clearly evident is the broad latitudinal distribution of the genus, with species occurring at latitudes from the equator to 80° and being present in both northern and southern hemispheres. There is a concentration of species at mid-latitudes, the maximum number of species (21) occurring at 40°. Biogeographically, the greatest diversity of species occurs on the northern rim of the Pacific. The coast of western North America in particular seems to be a diversity hotspot for *Microporella* - 19 species have been described from this region. Relatively high diversities are also apparent in the north-west Pacific (including Japan and China) with 15 species. In contrast, only one species has its type occurrence in the Indian Ocean and one in Antarctica. The extent to which these differences in diversity are real or simply reflect monographic effort remains to be established. However, SEM undertaken in connection with the current project has revealed the existence of many additional undescribed species, even in supposedly well-known regions such as the north-east Atlantic and Mediterranean.

Biogeographical ranges of individual species of *Microporella* are in need of re-evaluation. As Hayward (1988) remarked, the near cosmopolitan distributions accorded to some species are almost certainly spurious. For example, *M. ciliata* has its type locality somewhere in the Mediterranean but occurrences have since been reported from the Red Sea, northwest Europe, the Arctic, the western North Atlantic, the Caribbean, Brazil, the eastern Pacific from Oregon to Galapagos and Chile, the Antarctic Peninsula, south-east Asia, Australia and New Zealand. Even allowing for the veracity of anthropogenic transportation, a distribution encompassing all major climatic regions and oceans of the world is scarcely credible. Indeed, our SEM investigations suggest that true *M. ciliata* may perhaps be a Mediterranean endemic.

### 3 MORPHOLOGY

#### 3.1 Colonies and skeleton

The majority of species of *Microporella* have multi-serial encrusting colonies, occasionally becoming multilamellar but more often remaining single layered.
However, *M. lineata* Canu & Bassler, 1929 has uniserial encrusting colonies, and *M. bifoliata* Ulrich & Bassler, 1904, *M. hyadesi* (Jullien, 1888) and *M. ordo* Brown, 1952 all have bifoliate erect colonies. Eschariform colonies of *M. ordo* from Spirits Bay in northern New Zealand may grow to a diameter of 70 mm. In contrast, encrusting species of *Microporella* often have very small colonies. For instance, colonies of *M. ciliata* encrusting Adriatic bivalve shells were found by McKinney (2000) to have a median colony area of only 2.89 mm².

Little is known of the skeletal mineralogy of *Microporella*, although Poluzzi & Sartori's (1975) analysis of *M. ciliata* from the Adriatic revealed that the skeleton comprised 53% calcite (with 7 mole% MgCO₃) and 47% aragonite. Aragonite in other biminaleralic cheilostomes is commonly secreted during ontogenetic thickening of frontal shields. It is often leached in fossils and the preservation of some fossil specimens of *Microporella* suggests loss of the outer parts of the frontal shield where aragonite may well have been concentrated. Uncalcified windows are common in the basal walls of encrusting species (see Suwa & Mawatari 1998) but otherwise the skeleton is well-mineralized in the great majority of species.

### 3.2 Autozooid size

In a subset of 50 Recent and 11 fossil species for which zooid length data has been published, mean/median zooid length ranged from 0.40 mm (*M. intermedia* Livingstone, 1929) to 0.94 mm (*M. pirikaensis* Hayami, 1975), with a mean value of 0.59 mm and standard deviation of 0.125 mm (Fig. 3). No correlation could be detected between zooid length and latitude of occurrence for the Recent species in this dataset, although the Recent species having the largest autozooids was the sole Antarctic species of *Microporella*, *M. stenopora* Hayward & Taylor, 1984.

### 3.3 Frontal shield

All species of *Microporella* have autozooids with a porous, cryptocyst frontal shield (Fig. 4A-H), occasionally with a very narrow rim of gymnycyst. Cryptocyst convexity and degree of ornamentation by structures described as pustules, tubercles or granules varies between species. A relatively flat frontal shield is found, for example, in *M. hyadesi*, whereas that of *M. marsupiata* (Busk, 1860) is highly convex. In some species, areolar pores around the perimeter of the frontal shield clearly differ from those on the interior, usually by being somewhat larger and more elongate. However, in other species, areolae are not well differentiated, especially in older zooids with thickened frontal shields. When distinct areolae are recognizable, they commonly range from about 6 to 15 per zooid. Pores are always absent between the ascopore and the orifice, and also tend to be lacking in that part of the cryptocyst covering the avicularium chamber. Soule et al. (1995) noted that the pores in some species are partly plugged by sieve plates, often composed of spoke-like rays. Subsequently, Soule et al. (2003) used this character as the basis of a new subgenus *Cribriloporella* (type species *M. cribrosa* Osbum, 1952). Substantial ontogenetic thickening of the frontal shield occurs in some species, e.g. *M. alaskana* Dick & Ross, 1988. This has the effect of deeply incising the sieve plates, making them difficult to observe and compromising their utility as taxonomic characters, particularly in fossils where preservational deficiencies cause further problems. Ontogenetic thickening in some species produces reticulations around the depressed pores.

The frontal shield immediately proximal of the ascopore is elevated to form a mucro or umbo in many species, e.g. *M. cribrosa* Osbum, 1952, *M. infundibulipora* Soule et al., 1995, *M. rogickae* Winston et al. 2000. The degree to which this structure is developed may, however, be variable even within a single colony. Occasionally, the umbo is prolonged distally so that it overhangs the ascopore (Fig. 4B), probably fulfilling a protective role. In addition to a strong umbo, *M. unbonata* Hincks, 1883 has thick spinose processes on either side of the orifice (Fig. 4D).

### 3.4 Orifice and oral spines

The orifice in *Microporella* is basically semieliptical, with a straight proximal edge that may be equipped with condyles at the comers (e.g. *M. catalinensis* Soule et al., 1995) or a row of small teeth extending along its entire length (e.g. *M. hyadesi*), occasionally both (Fig. 4B). In most species, the orifice is wider than high but in some it is more nearly equidimensional. Rarely the convex distolateral edge is beaded (e.g. *M. monilifera* Liu et al., 2003).
Figure 4. Scanning electron micrographs illustrating aspects of skeletal morphology in some Recent species of *Microporella*. A, *M. californica* (Busk, 1856), autozooids with paired avicularia and 3 or 4 oral spine bases; Commander Islands, NW Pacific, Grischenko Colin (Sapporo). B, *Microporella* sp., orifice with both teeth and condyles, ascopore overhung by a mucro, and inclined avicularium with an open-tipped rostrum; Algeria, NHM (London) 69.10.6.6 (a). C, *Microporella* aff. *arctica* Norman, showing orifice and subcircular ascopore set within a zone of smooth calcification; Sea of Okhotsk, NW Pacific, Grischenko Colin. D, *M. umbonata* Hincks, 1883, ovicellate zooid with tiny, crescent-shaped ascopore very close to the proximal edge of the orifice; Vancouver, Canada, NHM 21.11.17.15. E, *M. spectulum* Brown, 1952, orifice with 7 oral spine bases and crescent-shaped ascopore with cribrate morphology; NZOI Station M793, New Zealand, NIWA (Wellington). F, *M. diademata* (Lamouroux, 1825), ovicells with areola-like marginal pores and 'visors' formed by a faceted area of smooth calcification; New Zealand, NHM 1963.2.12.92. G, *Microporella* sp., autozooid (centre) with two avicularia on the left side, separated by a discontinuity in the frontal shield indicative of skeletal repair; Algeria, NHM 69.10.6.6 (a). H, *Microporella* sp., early astogeny showing unusual nontatiform, 'ascophoran' ancestrula (lower centre) and two periancistrular autozooids each with an avicularium on the left side; Sagami Bay, Japan, Grischenko Colin. Figs A, C and H are secondary electron images of coated specimens; the remainder are back-scattered electron images of uncoated specimens. Scale bars: A, H = 500 pm; B-G = 100 pm.
The majority of species possess articulated oral spines which generally break-off during early ontogeny (Fig. 4E). Spine number ranges from zero (e.g. *M. catalinensis* Soule et al., 1995) to eight (e.g. *M. marsupiata*), and commonly varies somewhat within colonies (Fig. 4A). Arranged in a crescentic row around the distal rim of the orifice, the oral spines are generally simple, although outer spines are bifid in *M. marsupiata*. There is some indication of a correlation between number of oral spines and latitude of occurrence among species of Recent *Microporella*, with a decline in spine number from equator to poles (Fig. 5).

### 3.5 Ascopore

Ascopore position, size and shape all vary considerably between species. In some species the ascopore is located very close to the proximal edge of the orifice (Fig. 4D), whereas in others it is well separated from the orifice (Fig. 4C). The ascopore is enclosed within an ovoidal area of smooth calcification (Fig. 4C) that is sometimes raised above the level of the surrounding frontal shield and/or enclosed by a rampart (Fig. 4E). In some species (e.g. *M. arctica* Norman, 1903) this ascopore field is confluent with the rim of the orifice but in others (e.g. *M. ciliata*) it is separated by an expanse of granular cryptocyst.

In a few species of *Microporella* the ascopore is small and subcircular (Fig. 4C) to transversely elliptical (e.g. *M. lineata*), but more often it varies from reniform to crescent-shaped with the concave face nearest to the orifice (Fig. 4D-E). Small teeth usually project into the ascopore. Sometimes these join at the centre of the ascopore, giving a spoke-like structure, as in *M. stel lata* (Verrill, 1879). Other species have a cribrate ascopore (Fig. 4E) covered by a plate bearing numerous small perforations, either scattered (e.g. *M. elegans* Suwa & Mawatari, 1998) or arranged biserially (e.g. *M. discors* Uttley & Bullivant, 1972).

The functional morphology of the ascopore deserves consideration. The ascopore serves as the conduit for water flow into the ascus when the tentacle crown is expanded, and out of the ascus when it is withdrawn. The volume of water flowing through the ascopore is equivalent to twice the volume of the tentacle sheath (Taylor 1981). Retraction of the tentacle crown in bryozoans can occur very rapidly, presumably necessitating high velocity expulsion of water through the ascopore. An ascopore of large surface area would presumably facilitate this flow. However, a wide ascopore may make the interior of the zooid vulnerable to the ingress of particles or to invasion by microorganisms. As long ago as 1880, Hincks hypothesized that the teeth projecting into the ascopore of *Microporella* may serve to guard the entrance. Likewise, both the reniform to crescentic shapes of many ascopores and the presence of cribrate plates have the effect of diminishing the width of the individual opening/s while maintaining a large overall surface area. Soule et al. (2003) noted the potential of cribrate ascopores in screening out invaders and debris. Modelling flow through ascopores of different morphology would be worthwhile in order to understand better the comparative functional morphology of this ubiquitous feature of *Microporella* and the Microporellidae.

### 3.6 Ovicells

Ovicells have been described in most though not all species of *Microporella*. They always have a cryptocrystal surface that is continuous with the frontal shield of the distal zooid and generally has a similar surface texture (Fig. 4D). Ovicell topography varies between species, from moderately flat to highly globular, as in *M. ordo* and *M. hyadesi*. A few species (e.g. *M. fimбриata* Ryland & Hayward, 1992) have an area of smooth calcification forming a rib along the proximal edge of the ovicell. In *M. diademata* (Lamouroux, 1825) this smooth area is raised vertically into a facet-like visor, giving the ovicell an extremely prominent proximal edge (Fig. 4F).

Ovicell porosity varies between species, ranging from those in which only a single row of areola-like pores are present (Fig. 4F) to others having pores distributed more-or-less evenly across the ovicell surface (Fig. 4D). Soule et al. (2003) used the presence of multiple, widely distributed pores, similar in size to or larger than frontal shield pores, as the principal...
character defining their new genus *Microporellloides* (type species *M. mazatlanica* Soule et al., 2003). Particularly in species with pronounced marginal pores, radial ribs may occur between these pores (e.g. *M. alas kana* Dick & Ross, 1988), fading towards the centre of the ovicell. As with frontal shields, calcification during later ontogeny may thicken the ovicell roof, burying and sometimes occluding the pores. Variably umbonate ovicells characterize certain species, e.g. *M. serrata* Mawatari & Suwa, 1998. Oral spines may be completely obscured in ovicellate zooids, although sometimes the outermost one or two pairs remain visible (Fig. 4F).

Personate ovicells occur in some species of *Microporella*. Here the proximal margin of the orifice of the maternal zooid has a low peristome that is confluent with the raised proximolateral edges of the ovicell roof. Normally this peristome is situated between orifice and ascopore but in *M. pontifica* Osbum, 1952 an extension of the peristome surrounds the ascopore (see Soule et al. 2003, Figs 30, 32-34). The degree of ‘personation’ can vary both between species and within colonies of *Microporella*. Some species (e.g. *M. agonistes* Gordon, 1984) have what might be termed ‘semi-personate’ ovicells in which lappets extend downwards from the proximolateral edges of the ovicell but do not meet to form a complete peristome.

### 3.7 Avicularia

By definition, at least some autozooids in all species of *Microporella* bear one or two avicularia proximolaterally or laterally of the orifice. While these avicularia at first appear to be adventitious, Hastings (1963, pp. 180-181) regarded them as interzooidal because: ‘...the avicularian chambers extend to the basal surface of the colony where each appears to replace one pore-chamber (dietella) in the series of pore chambers round the distal end of the zoecium.’ In general, species of *Microporella* can be divided between those having one avicularium (Fig. 4B, D, G, H) and those having paired avicularia (Fig. 4A, F), although some species exhibit variations. For example, many autozooids of *M. arctica* lack avicularia altogether, others having a single avicularium. Dick & Ross (1988) reported that 80% of avicularia in *M. alas kana* are paired but 20% are single. The sporadic paired avicularia found in *M. serrata* are unusual in often being asymmetrical in position, orientation and size. During the current research two examples were observed of autozooids bearing two avicularia on one side of the zooid. Scanning electron microscopy of one of these aberrant zooids (Fig. 4G) shows that it has been repaired, with one avicularium antedating the repair and the second, more distal avicularium formed during reparative growth of a new frontal shield (skeletal repair is a common feature in *Microporella*).

Apart from differences in size, especially of the avicularian chamber which is variably inflated, the skeletal structure of *Microporella* avicularia is comparatively uniform: the opesiae is semielliptical, the cross bar complete and simple, and the rostrum a high-sided triangular shape. Certain avicularia have a channelled, open tip and sometimes a rostrum with concave sides (Fig. 4B). In these instances, the mandible extends beyond the rostrum and is generally setose. Also the tip of the avicularium may be raised such that the plane of the rostrum is inclined relative to the frontal shield of the autozooid (Fig. 4B). The relative size of *Microporella* avicularia ranges from about 10% of autozooid length in *M. lineata*, to more than 25% of autozooid length in *M. agonistes*.

Suwa & Mawatari (1998) recognized three different types of avicularian mandibles in *Microporella*'. (1) simple, (2) setiform with a beak at the base, and (3) lanceolate with a pair of hooks at the base. Setiform mandibles can be extremely long, as in *M. vibraculifera* Hincks, 1883 where they are approximately the same length as the autozooids. Lanceolate mandibles are well seen in *M. harmeri* Hayward, 1988, a species in which Shirakawa (1999) recognised dimorphism in mandible morphology with narrow and more flabellate morphs.

Location and orientation of avicularia both vary according to species. In some species (e.g. *M. speculum* Brown, 1952), avicularia are located close to mid-length on the lateral perimeter of the autozooid, well proximally of the orifice. In other species, they are level (oralmost so) with the ascopore and, if large, may impinge on the ascopore causing its shape to be distorted (e.g. *M. agonistes*). Finally, some species (e.g. *M. donovani* Taylor & Foster, 1994) have avicularia laterally adjacent to the orifice. Orientations of avicularia vary from lateral (e.g. *M. pontifica*), through distolateral (the majority of species) to distal (e.g. *M. tractabilis* Canu & Bassler, 1930). The single avicularium of *M. ceramia* (MacGillivray, 1869) is unusual in apparently being directed proximally. Two ‘rules’ relate avicularium number, location and orientation. Firstly, species with paired avicularia generally have them located relatively distally. No examples have been found of paired avicularia positioned close to mid-length on the autozooid and, conversely, avicularia positioned laterally of the orifice are almost always paired. Secondly, orientation of avicularia depends on position: the most distally located avicularia are oriented approximately parallel to the long axis of the autozooid, proximally located avicularia are oriented almost transversely to this axis, while those in positions between have an intermediate orientation.

In species normally having only one avicularium per autozooid this can be placed either on the left or right side of the autozooid. The cormidia comprising an autozooid and its associated avicularium therefore
have a distinct handedness. A preliminary analysis of handedness has been undertaken in three colonies belonging to three different species of *Microporella*. In a fragment of the bifoliate Subantarctic species *M. hyadesi*, a total of 229 autozooids had avicularia, 150 (65.5%) on the left side and 79 (30.4%) on the right side. The hypothesis of even handedness (i.e. 50% left, 50% right) can be rejected for this specimen (chi-square = 22.013, P < 0.0000). Among 89 zooids from part of an encrusting colony of *M. ciliata* Auct., 51 (57.3%) had avicularia on the left side and 38 (43.7%) on the right side. In this case it is not possible to reject the null hypothesis of even handedness (chi-square = 1.899, P = 0.1681). Finally, all of the zooids in a small encrusting colony of *Microporella* sp. from Sagami Bay, Japan were surveyed. Fifty-nine (41%) were left-handed and 85 (59%) right-handed, suggesting a bias towards right handedness (chi-square = 4.694, P = 0.0302). The existence of handedness in two out of three colonies analysed suggests that further studies are warranted into the patterns and developmental processes involved in this asymmetry. For example, are there consistent differences between species of *Microporella*, and can the handedness of specific cormidia be related to that of the parental zooid and earlier zooids in the colony?

Functionally, the avicularia of *Microporella* remain as enigmatic as those in most other cheilostomes. The variety in mandible morphology, as well as position and orientation of avicularia, allows for the possibility of more than one function. Mawatari & Suwa (1998) considered that *Microporella* avicularia with beaked mandibles may play a role in predator defence, whereas those with long setae could have a cleaning function or be used in the tearing-off of fouling microbial mats. Unfortunately, few observations have been made on avicularium behaviour in *Microporella*. Winston’s (1991) study of the responses of avicularia to chemical stimulation in four bryozoans from Friday Harbor (Washington State, USA) provides some insight into possible function. Of the four species, the avicularia of *M. vibraculifera* displayed the strongest coordinated response to a mixture of amino acids as well as to alanine, glycine and acetylcholine. Amino acids are common feeding stimulators and are also liable to leak from predators and prey species when body walls are ruptured.

#### 3.8 Early astogeny

The ancestrula and early astogeny have been described in very few species of *Microporella*. In those species for which it is known, the ancestrula is tatiform, has between 9 and 13 mural spines encircling the opesiae, and often possesses a narrow proximal cryptocyst. Some ancestrulae are occluded by closure plates or contain intramurally budded autozooids of ‘ascophoran’ type. A primary, non-tatiform ancestrula has been observed in an unidentified Japanese species (Fig. 4H) and it is possible that such ascophoran ancestrulae are more widespread. Typically, the ancestrula buds two daughter zooids, left and right distolateral (Fig. 4H). Further budding completes the circle of periancestral zooids in multiserial species. Budded zooids in early astogeny resemble those from zones of astogenetical change but are smaller and quite often lack avicularia.

### 4 EVOLUTION

#### 4.1 Fossil record

Species of *Microporella* are frequently reported from the Neogene and Quaternary fossil record and at least 23 species are based on fossil occurrences. Unfortunately, the descriptions of most fossil species are inadequate by comparison with modern species - details of ascopore and ovicell morphology are seldom available. Apparent fossil occurrences of extant species require critical re-evaluation, including those of the 5 extant species (*M. ciliata*, *M. coronata* (Audouin & Saviugny, 1826), *M. hyadesi*, *M. lunifera* (Haswell, 1881), and *M. spicata* MacGillivray, 1889) that ostensibly range back into the Miocene.

There are several citations of Oligocène *Microporella* in the older literature but none of these could be confirmed through direct study of available material or examination of published figures. Rovereto (1939, p. 607) lists a ‘*Microporella papillosa*’ as being present in the Oligocène of Liguria, Italy but there is no figure and furthermore the author of the species is not given. Vigneux’s (1949, p. 67) claim that *M. ciliata* occurs the Oligocène of Germany is not borne out by examination of the references he cites. More recently, Braga & Bahr (2003, p. 255) have attributed an Oligocène fossil from Arabia to *Microporella*. Through the kindness of Prof. G. Braga we have been able to examine this material using SEM and show that it does not belong to *Microporella* but appears instead to be a hippocodind.

Possibly the oldest occurrences of *Microporella* comprise two poorly preserved species, both with unpaired avicularia, from the basal Miocene Tarakohe Mudstone of Nelson Province, New Zealand. One of these was recorded by Brown (1952, p. 256) as *M. hyadesi* although it does not in reality belong to this extant species. By the end of the Miocene *Microporella* had become widely distributed, with occurrences in Australia, Japan, the eastern USA, northern Africa and Europe.

Coarse-scale changes in the species diversity of *Microporella* through time are shown in Figure 6. Twenty species of *Microporella* have been recorded.
from the Miocene, 13 from the Pliocene, 20 from the Pleistocene and one from the Plio-Pleistocene. Average species richness for each of these time intervals is substantially less than for the Recent. However, this should not be taken as indicating a recent diversification of *Microporella* as the pattern is almost certainly an artefact of the paucity of SEM undertaken on fossil *Microporella* compared to that on Recent species, along with preservational factors that hinder detection of subtle differences in skeletal morphology.

There are as yet no indications of evolutionary trends through time in *Microporella* morphology. As at the present-day, the overwhelming majority of Miocene species were multiserial encrusters but even in the Miocene one species (*M. bifoliata*) had bifoliate erect colonies. The proportion of species with paired avicularia has remained approximately the same through geological time (Fig. 6).

4.2 Microporellid phylogeny

The Microporellidae Hincks, 1879 contains ten nominal genera: *Microporella*, *Adelascopora*, *Calloporina*, *Chronocerastes*, *Diporula*, *Fenestrulina*, *Fenestruloides*, *Flustramorpha*, *Microporelloides* and *Tenthredulina*. Phylogenetic relationships between these genera have not previously been analysed cladistically. We therefore undertook a preliminary analysis based on skeletal characters in order to shed light on the origin of *Microporella* and the primitive states of these characters that may have pertained in this genus, information which will be of value during future analyses of phylogenetic relationships between species of *Microporella*. Unfortunately, the genus *Microporelloides* Soule et al., 2003 was published too late to be included in this study. For the remaining nine genera, 37 skeletal characters were recognized, most binary but six multistate (Appendix); ten of these characters proved to be autapomorphies and therefore are uninformative in resolving the interrelationships between microporellid genera. Coding was based primarily on type species as these are definitive for the genera concerned. Two outgroup taxa - *Escharina waiparaensis* Brown, 1952 and *Chiastosella daedala* Brown, 1952 - were chosen to root the tree. Each shares a significant number of characters with the Microporellidae while lacking the ascopore that is apomorphic for the family (Harmer 1902, p. 326 suggested that the ascopore resulted from the distal closure of a schizoporellid sinus). Brown (1952, p. 219) remarked on the likelihood of a close relationship between *Chiastosella* and the microporellid *Calloporina*, while D.R Gordon (pers comm. July 2003) has pointed out the similarity between *Escharina waiparaensis* and *Microporella*.

The data were analysed using the standard parsimony program PAUR. A single most parsimonious cladogram of 66 steps was recovered (Fig. 7). This interprets *Calloporina* as the most basal microporellid, immediately crownward of which is a clade comprising the two similar genera *Fenestrulina* and *Fenestruloides*, followed by a clade of two flustriform genera, *Adelascopora* and *Flustramorpha*. The four remaining genera form a clade in which *Microporella* is the sister group of a clade consisting of *Diporda*.
and the New Zealand endemics *Tenthrenulina* and *Chronocerastes*.

One implication of the analysis is that *Microporella* probably originated before the Miocene, even though its confirmable fossil record starts in the Miocene as discussed above. A pre-Miocene origin can be inferred because *Tenthrenulina*, which occupies a more crownward position on the cladogram than *Microporella*, dates back to the Oligocene.

5 DISCUSSION

Almost one hundred species of *Microporella* are currently recognized. This number will inevitably increase as more and more bryozoan faunas, both fossil and modern, are studied in detail using SEM and, eventually, molecular techniques. A firm basis for recognising new species demands better knowledge of existing species of *Microporella* which are too often inadequately described in the literature. The large size of the genus is also making it unwieldy and difficult for taxonomists to use. A recent attempt (Soule et al. 2003) to subdivide the genus should be evaluated through phylogenetic analysis. Biogeographical, morphological and evolutionary patterns suggested by the preliminary survey presented here also need to be more thoroughly investigated. Much remains to be learnt about the functional morphology of the ascopore and avicularia, and of developmental asymmetry in the autozooid/avicularium cormidia.

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REFERENCES


APPENDIX

Data matrix and character coding used in the cladistic analysis of microporellid genera. *Chiastosella* and *Escharina* are outgroup taxa.

| Taxon        | Characters: 1, colony form: encrusting uniserial (0), encrusting multiserial (1), erect bifoliate (2), erect vincularian/cellariiform (3). 2, calcification: rigid (0), flexible (1). 3, pore chambers: absent (0), present (1). 4, basal window: absent (0), present (1). 5, marginal gymnocyst: absent (0), present (1). 6, cryptocyst granulation: absent (0), coarse (2). 7, umbo/mucro: absent (0), present (1). 8, paired spinose mucros: absent (0), present (1). 9, differentiated areolae: absent (0), present (1). 10, frontal pores: absent (0), restricted distribution in distribution (1), widely distributed (2). 11, frontal pores between ascopore and orifice: absent (0), present (1). 12, frontal pore morphology: simple (0), spinose/stellate/cribrate (2). 13, ascopore position: juxtaposed with orifice (0), separated from orifice by cryptocyst (1). 14, ascopore shape: ovoidal (0), crescentic (1), slit-like (2). 15, ascopore restrictions: absent (0), teeth (1), complete divisions (2), cribrate (3). 16, ascopore plane: flat (0), tilted towards orifice (1). 17, ascopore cup: absent (0), present (1). 18, orifice shape: semieliptical (0), with sunus (1). 19, condyles: absent (0), present (1). 20, denticulate proximal edge of orifice: absent (0), present (1). 21, denticulate distal edge of orifice: absent (0), present (1). 22, oral spines: absent (0), present (1). 23, branched oral spines: absent (0), present (1). 24, ovicell roof: simple (0), sectored (1). 25, ovicell topography: flush (0), prominent (1). 26, ovicell areolae-like marginal pores: absent (0), present (1). 27, ovicell frontal pores: absent (0), present (1). 28, umbo/mucro: absent (0), present (1). 29, ovicell personation: absent (0), present (1). 30, oral spines in brooding zooids: absent or concealed (0), present (1). 31, avicularia: absent (0), present (1). 32, avicularium location: proximal of orifice (0), with orifice (1). 33, avicularium orientation: distal (0), distolateral (1), lateral (2). 34, number of avicularia per autozooid: one (0), two (1). 35, avicularian rostrum: flat (0), lined significantly to frontal shield (1). 36, tip of rostrum tip: closed or channelled (1). 37, ancestrula: tatiform (0), ascophoran (1). |
A biogeographical analysis of Indo-West Pacific cheilostome bryozoan faunas

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ABSTRACT: A list of cheilostome bryozoan families, genera and species was compiled for a number of shallow Indo-West Pacific locations, using previously published bryozoan faunas and data recorded by the senior author. Totals of 67 families, 146 genera and 430 species were tallied from these locations. The resulting presence/absence matrices were subjected to Detrended Correspondence Analysis (DCA), to assess location similarity/dissimilarity, and allows for some preliminary observations to be made regarding the biogeographical distribution of Indo-West Pacific cheilostome bryozoans. Primarily, there is a split at all taxonomic levels between the Indian Ocean and Pacific Ocean bryozoan faunas. In the Pacific, a Hawaiian split is supported at both family and genus levels. Within the western Pacific faunas, at the family level the faunas of the Solomon Islands, the Philippines and the Great Barrier Reef group together loosely. Whilst at the genus level the Solomon Islands group with Tahiti, Fiji and the Philippines. At the species level the Solomon Islands sits firmly in a group with the Philippines and Indonesia. This difference in location grouping might be due to the respective timings of clado­genesis at the family, genus and species levels, with family and genus data reflecting older affinities. Some processes that may have led to the observed results are discussed; with the observed biogeographical patterns seen best explained by the integration of tectonic events, changes in sea level, as well as vicariant and dispersal events.

1 INTRODUCTION

Bryozoa have not been well studied biogeographically, except for recent work in Antarctica (Barnes & De Grave 2000, 2001) and surrounding areas of the South Pacific (Moyano 1991, 1996). These areas are particularly suited to such work owing to recent, extensive and thorough taxonomic studies (e.g. Hayward 1995). Whilst Seo (1996) recently published on the geographical distribution of cheilostome bryozoans from temperate Korean waters, only one paper has been written on the biogeography of the Bryozoa from the tropical western Pacific Ocean (Okada & Mawatari 1958). Soule & Soule (1967) dealt with the biogeographical affinities of 13 species of Hawaiian Bryozoa, all of which were noted as being rather cosmopolitan in their distributions. However, several are now known to be species complexes, e.g. Hippopodina feeegeensis (Busk, 1884) (see Tilbrook 1999) and Trypostega venusta (Norman, 1864) (Tilbrook unpubl. data), while others, as they note themselves, are possibly misidentified, e.g. Rhynchozoon rostratum (Busk, 1855) and Schizoporella unicornis (Johnston, 1847). Okada & Mawatari (1958) divided the entire Indian and Pacific Oceans into eight provinces; two in the Indian Ocean, three in the Western Pacific Ocean, and three in the Central and Eastern Pacific Ocean. Whilst most of the data used by Okada & Mawatari (1958) were gleaned directly from the existing literature, some of which may now be thought of as less than reliable, many of their broader conclusions make intuitively reasonable sense. In the Indo-West Pacific region, they note their Malayan Province (Malay Archipelago, South China Sea, the Philippines) appears more intimately connected with their Chinese Province (East China Sea, Yellow Sea, Southern Japan) than it does with their Papuan Province (Southern New Guinea, tropical Australia, Coral Sea). The Papuan Province in turn is intimately connected with their Polynesian Province (Polynesia).

The general lack of verifiable, and therefore useable, data in the form of scanning electron micrograph (SEM) illustrated bryozoan species lists from the Pacific Ocean, and the Indo-West Pacific in particular, has meant that a more comprehensive biogeographical...
analysis has not been possible. However, the relatively recent publication of a small number of SEM illustrated bryozoan faunal lists has allowed for some taxonomic/nomenclatorial continuity at a number of discrete, but Indo-West Pacific wide locations, making such a dataset amenable to biogeographical analysis, if somewhat preliminary in scope.

2 METHODS

A list of cheilostome bryozoan species was compiled for six shallow-water, mainly reefal, Indo-West Pacific locations: Mauritius (Hayward 1988), Indonesia (Winston & Heimberg 1986), The Philippines (Ristedt & Hillmer 1985, Scholz 1991), Vanuatu (Tilbrook et al. 2001), Heron Island (Ryland & Hayward 1992, Hayward & Ryland 1995) and the Solomon Islands (Tilbrook unpubl. data), resulting in a 430 species X 6 locations matrix. Additional species were included from the senior author’s personal observations of material from these locations. An additional four locations (Hawaii, Tahiti, Fiji and the Great Barrier Reef) were included, to compile a genus matrix of 146 genera X 10 locations: Hawaii (Soule et al. 1987, Ms Chela Zabin, Bishop Museum, Hawaii, pers. comm., 2001), Tahiti (d’Hondt 1995, Tilbrook unpubl. data), Great Barrier Reef (Tilbrook unpubl. data), and Fiji (Tilbrook unpubl. data). Due to the lack of illustrations in the Hawaiian fauna recorded by Soule et al. (1987) and in d’Hondt’s (1995) list of French Polynesian bryozoans we excluded them from any species-level analysis. The genus data matrix was used to produce a 67 families X 10 locations matrix. The Heron Island dataset was used only at the species level, being replaced at the genus and family level with the Great Barrier Reef data, in order to provide a more analytically acceptable geographical congruence. Biodiversity level attributes of these matrices are summarised in Table 1, including the numbers of ascophoran and non-ascophoran (‘anascan’) taxa.

The resultant data sets were subjected to Detrended Correspondence Analysis, an eigen-analysis ordination technique (DCA: Hill & Gauch 1980). DCA has several advantages over other ordination techniques as arch effects are eliminated by dividing the first axis into segments, then setting the average score on the second axis within each segment to zero. Similarly, the tendency to compress the axis ends relative to the middle is also corrected in DCA by rescaling the axis to equalize as much as possible the within-sample variance of species scores along the sample ordination axis.

In summary, DCA (and other ordinations) arranges the locations as points in multidimensional space, such that points close together correspond to locations with a similar taxic composition and points that are far apart correspond to locations with a dissimilar taxic composition. Owing to the low number of areas investigated, only 15 segments were used in the detrending process (see Hill & Gauch 1980). For analytical purposes, single-location endemics were excluded from any analysis, as they can be considered biogeographically uninformative in what is ostensibly a comparison of similarity. For ease of graphical interpretation, only the first two axes were extracted; nevertheless in all analyses they accounted for a minimum of 75% of the total variance explained.

3 RESULTS

3.1 Family-level analysis

The Solomon Islands group loosely with the Great Barrier Reef and the Philippines when the data set is taken as a whole (Fig. 1A). However, no clear locality groupings emerge, presumably because of the Indo-West Pacific wide distribution of the majority of families, a fact reflected in the low levels of endemicity recorded (Table 2). Equally, whilst 7% of the families, each from Hawaii and the Great Barrier Reef are endemic (the highest in the dataset and indication of

Table 1. Number of families, genera and species for the Indo-West Pacific locations analysed in this study.

<table>
<thead>
<tr>
<th>Taxon (Totals)</th>
<th>Mauritius</th>
<th>Indonesia</th>
<th>Philippines</th>
<th>Solomon Islands</th>
<th>Heron Island</th>
<th>Vanuatu</th>
<th>Great Barrier Reef</th>
<th>Fiji</th>
<th>Tahiti</th>
<th>Hawaii</th>
</tr>
</thead>
<tbody>
<tr>
<td>Families (67)</td>
<td>40</td>
<td>30</td>
<td>43</td>
<td>45</td>
<td>43</td>
<td>44</td>
<td>54</td>
<td>46</td>
<td>27</td>
<td>43</td>
</tr>
<tr>
<td>Ascophoran (43)</td>
<td>27</td>
<td>18</td>
<td>30</td>
<td>30</td>
<td>28</td>
<td>29</td>
<td>33</td>
<td>33</td>
<td>18</td>
<td>30</td>
</tr>
<tr>
<td>‘Anascan’ (24)</td>
<td>13</td>
<td>12</td>
<td>12</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>21</td>
<td>13</td>
<td>9</td>
<td>13</td>
</tr>
<tr>
<td>Genera (146)</td>
<td>63</td>
<td>43</td>
<td>69</td>
<td>78</td>
<td>67</td>
<td>65</td>
<td>97</td>
<td>75</td>
<td>36</td>
<td>70</td>
</tr>
<tr>
<td>Ascophoran (94)</td>
<td>45</td>
<td>27</td>
<td>50</td>
<td>52</td>
<td>44</td>
<td>43</td>
<td>60</td>
<td>54</td>
<td>24</td>
<td>48</td>
</tr>
<tr>
<td>‘Anascan’ (52)</td>
<td>18</td>
<td>15</td>
<td>19</td>
<td>26</td>
<td>23</td>
<td>22</td>
<td>37</td>
<td>31</td>
<td>12</td>
<td>22</td>
</tr>
<tr>
<td>Species (430)</td>
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<td>78</td>
<td>132</td>
<td>179</td>
<td>122</td>
<td>92</td>
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<td></td>
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<tr>
<td>Ascophoran (322)</td>
<td>79</td>
<td>46</td>
<td>97</td>
<td>133</td>
<td>91</td>
<td>68</td>
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<td></td>
</tr>
<tr>
<td>‘Anascan’ (108)</td>
<td>24</td>
<td>32</td>
<td>37</td>
<td>46</td>
<td>31</td>
<td>30</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
long separation), this is not reflected in the multivariate plots (except perhaps for the Great Barrier Reef in the ‘anascans’-only plot), as the faunas overlap substantially with the other areas. When the ascophoran and ‘anascan’ families are analysed separately (Figs 1B-C) the same lack of grouping is seen, only Indonesia separating from the other locations in the ascophorans-only plot, possibly a reflection of its low ascophoran/’anascan’ ratio (Table 3).

Further, the superfamilial make-up (ascophoran/‘anascan’ ratio) of the faunas is also worth documenting (Table 3). Whilst for the most part at the family level the modal ratio is 1.9 or 2, a number of faunas have a ratio higher (Fiji, Hawaii and the Philippines) or much lower (Indonesia and the Great Barrier Reef) than this.

3.2 Genus-level analysis

When all localities are included, Mauritius and Hawaii are clearly separated from the remaining western Pacific localities (Fig. 2A). This is most likely attributable to their prolonged isolation and resultant higher levels of generic endemism - Hawaii 13% generic endemism, Mauritius 17% (Table 2). These levels of endemism are much higher than those seen in the western Pacific locations, or as predicted by a plot of number endemic genera versus generic richness. For this, when all localities are included, there is no significant relationship (max. r$^2$ 0.102), however when Hawaii and Mauritius are excluded, a significant quadratic relationship exists (r$^2$ 0.91, pCO.01) between generic richness and endemism (Fig. 3). When Mauritius and Hawaii are excluded from the ordination analysis (Fig. 2B), the Solomon Islands sit firmly between Fiji, Tahiti and the Philippines (which in turn is closest to Indonesia). Indonesia and Vanuatu sit further from this main western Pacific group than the Great Barrier Reef. An analysis of ascophoran and ‘anascan’ genera separately, produces virtually identical location groupings. At the genus level, the modal ascophoran/’anascan’ ratio is 2.00, with Mauritius and the Philippines having a much higher ratio.

### Table 2. The proportion of endemic taxa at each location.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Mauritius</th>
<th>Indonesia</th>
<th>Philippines</th>
<th>Solomon Islands</th>
<th>Heron Island</th>
<th>Vanuatu</th>
<th>Great Barrier Reef</th>
<th>Fiji</th>
<th>Tahiti</th>
<th>Hawaii</th>
</tr>
</thead>
<tbody>
<tr>
<td>Families</td>
<td>0.0</td>
<td>3.0</td>
<td>0.0</td>
<td>2.0</td>
<td>0.0</td>
<td>0.0</td>
<td>7.0</td>
<td>0.0</td>
<td>0.0</td>
<td>7.0</td>
</tr>
<tr>
<td>Genera</td>
<td>17.0</td>
<td>5.0</td>
<td>3.0</td>
<td>9.0</td>
<td>6.0</td>
<td>2.0</td>
<td>7.0</td>
<td>1.0</td>
<td>0.0</td>
<td>13.0</td>
</tr>
<tr>
<td>Ascophoran</td>
<td>18.0</td>
<td>4.0</td>
<td>2.0</td>
<td>4.0</td>
<td>7.0</td>
<td>2.0</td>
<td>2.0</td>
<td>0.0</td>
<td>0.0</td>
<td>12.5</td>
</tr>
<tr>
<td>‘Anascan’</td>
<td>17.0</td>
<td>7.0</td>
<td>5.0</td>
<td>0.0</td>
<td>4.0</td>
<td>0.0</td>
<td>16.0</td>
<td>5.0</td>
<td>0.0</td>
<td>14.0</td>
</tr>
<tr>
<td>Species</td>
<td>31.0</td>
<td>23.0</td>
<td>37.0</td>
<td>40.0</td>
<td>42.0</td>
<td>29.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ascophoran</td>
<td>54.0</td>
<td>26.0</td>
<td>39.0</td>
<td>46.0</td>
<td>42.0</td>
<td>26.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>‘Anascan’</td>
<td>42.0</td>
<td>12.5</td>
<td>32.0</td>
<td>13.0</td>
<td>41.0</td>
<td>30.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3. Ratio of ascophoran/'anascan' components of each taxon for each location.

<table>
<thead>
<tr>
<th>Taxon (Overall)</th>
<th>Mauritius</th>
<th>Indonesia</th>
<th>Philippines</th>
<th>Solomon Islands</th>
<th>Heron Island</th>
<th>Vanuatu</th>
<th>Great Barrier Reef</th>
<th>Fiji</th>
<th>Tahiti Hawaii</th>
</tr>
</thead>
<tbody>
<tr>
<td>Families (1.8)</td>
<td>2.1</td>
<td>1.5</td>
<td>2.5</td>
<td>2.0</td>
<td>1.9</td>
<td>1.9</td>
<td>1.6</td>
<td>2.5</td>
<td>2.0</td>
</tr>
<tr>
<td>Genera (1.8)</td>
<td>2.5</td>
<td>1.8</td>
<td>2.0</td>
<td>2.0</td>
<td>1.9</td>
<td>2.0</td>
<td>1.6</td>
<td>2.6</td>
<td>2.0</td>
</tr>
<tr>
<td>Species (3.0)</td>
<td>3.3</td>
<td>1.4</td>
<td>2.6</td>
<td>2.0</td>
<td>2.9</td>
<td>2.3</td>
<td>2.6</td>
<td>2.0</td>
<td>2.2</td>
</tr>
</tbody>
</table>

3.3 Species-level analysis

The Solomon Islands are closely associated with the Philippines throughout these analyses (Figs 4A-C), indicative of a more recent connectivity between these locations. The other locations are removed from these core locations, with the position of Mauritius in the total and ascophoran-only analysis indicative of an old Indian Ocean/Pacific Ocean separation. The tight grouping of Heron Island and Vanuatu in the ascophoran-only analysis (Fig. 4B), a possible indication of recent connectivity, is in stark contrast to their positions in the ‘anascan’-only analysis (Fig. 4C). The observed differences in the ascophoran-only versus ‘anascan’-only analysis relating to the position of Indonesia (Figs 4B-C) are assumed related to the relative paucity of ascophorans in the Indonesian dataset (Table 3).

The modal ascophoran/'anascan' ratio is 2.9 at the species level, with Mauritius exhibiting a much higher ratio (3.3) and Indonesia a much lower one (1.4) (Table 3). The level of species endemism is highly correlated with species richness (Fig. 5; r² 0.83, p < 0.05) for all species combined, which is also reflected in an ascophoran-only analysis (r² 0.62, p < 0.05), but not in an ‘anascan’-only analysis (r² 0.08, not significant).

4 DISCUSSION

Following the break-up of Gondwana in the Mesozoic, by the early Tertiary the Earth’s tectonic plates were still positioned far differently from the way they are today. This break-up has been hypothesised as increasing marine diversity, primarily because of the separation...
and fusion of tectonic plates (Valentine & Moores 1970). It was between the Miocene and Pliocene (15-5 Ma) that the Australian/New Guinea plate and the Eurasian and Asian (Sundaland) plates collided, resulting in the contemporary alignment of land and sea in the Indo-Australian region (Fleminger 1986). The closing of the Indonesian seaway (and the effective separation of the Indian and Pacific Oceans) during the Pliocene was finally brought about by the emergence of Halmahera as New Guinea finished its northwards progress (Hall 2001). It is thought that this closing effectively triggered a regional climate change not only locally (Indo-Malaysia) but also further afield by stopping ingress of the warmer southern Pacific water into the Indian Ocean in favour of the cooler northern Pacific water (Cane & Molnar 2001). This region then underwent a number of eustatic sea-level changes (in the region of 100-200 m) during the Pleistocene (2 million-10,000 years ago) due to several glacial and interglacial stages, each lasting for tens of thousands of years (Fleming 1986).

Today Wallacea (a term often used for the region around the Indonesian Seas) acts as the tropical seaway between the Pacific and Indian Oceans, with throughflow, varying seasonally (Waworuntu et al. 2001, Gordon et al. 2003). During the Pleistocene glacial stages, the Torres Strait and the Timor Sea would have become exposed and many of the island groups in the region became single landmasses. This would have had an obvious effect on the direction of the prevailing oceanic currents throughout the area. Sea-surface temperatures during glacial times are thought to have been 6-8°C lower than those of interglacial stages, with unusually cool (<21°C) surface temperatures seasonally, particularly in the area of the eastern Indonesian Seas (Fleminger 1986). Today the southern Pacific water is warmer and more saline than that of the northern Pacific and Indian Oceans (Cane & Molnar 2001).

The presence of localised upwelling plumes off western New Guinea cooling the surface water (Fleminger 1986) would have an influence on the distribution of stenothermal organisms influencing, if only
locally, the distribution of certain cheilostome bryozoan species. The Pleistocene glacial-stage upwellings, which covered a far greater area than those of Recent plumes, could have had quite a severe effect on the bryozoan fauna of the area.

All modem bryozoan families are thought to have been in place by the late Eocene, even if there is no fossil evidence as yet for some (D.P. Gordon, NIWA, New Zealand, pers. comm., 2003). A brief analysis of the known geological and geographical ranges of the bryozoan families used in this study shows two noteworthy features. Firstly, on average ‘anascan’ (non-ascophoran) families are older (52% Mesozoic, 95% pre Oligocene) than ascophoran families (20% Mesozoic, 70% pre-Oligocene). Secondly, ascophoran families show more cosmopolitanism (52%) and lower endemism (9%) than do non-ascophoran families (37% and 25% respectively).

Although there were no clear groupings to emerge from the family-level analysis, the loose grouping of the Solomon Islands, the Great Barrier Reef and the Philippines has been noted previously. Benzie & Williams (1997) grouped them together in their study of the genetic relationship of giant clam, Tridacna maxima (Röding, 1798), populations. Their Fijian population was a sister-group to these three populations, with the four populations grouped into a ‘West Pacific’ group; a sister-group to a ‘Central Pacific’ group, comprising populations from the Marshall Islands, Kiribati, Tuvalu and the Cook Islands.

Within the Pacific Ocean bryozoan faunas, the Hawaiian fauna appears very different from the others, particularly in terms of its endemism. This is most probably a consequence of the long geological history of Hawaii and the Hawaiian-Emperor Seamount Chain; the Emperor segment ages from 80-43 million years, the Hawaiian segment aged less than 43 million years (Gordon 2000). Although the results are not strictly comparable because of analytical differences, De Grave (2001), in his analyses of Indo-Pacific pontoniid shrimps, found that Hawaii formed the basal sister-area to all the remaining Pacific areas he analysed. Equally, Bernardi et al. (2001) separated a Hawaiian clade of coral-reef damselfish from other Pacific clades.

The grouping of the locations based on bryozoan genera is similar to those seen in other marine invertebrates. The similarity of the Philippines and Indonesian faunas has been noted previously in shrimps (De Grave 2001); equally, gene flow between Linckia starfish populations is unrestricted owing to the prevailing ocean-current patterns (Williams & Benzie 1997). However, as Benzie & Williams (1997) indicated in three giant clam species, there may be gene flow by a ‘stepping-stone’ process along island chains and between archipelagos. They found levels of gene flow dominant along three routes that radiated from (or terminated in) the Philippines. These gene-flow routes, i.e. the Great Barrier Reef-Philippines (via Torres Strait), Fiji-Solomon Islands-Philippines, and Central Pacific (Cook Islands-Tuvalu-Kiribati-Marshall Islands)-Philippines, were found to be perpendicular to the prevailing sea-surface currents, e.g. the South Equatorial Counter Current and the North Equatorial Counter Current (Benzie & Williams 1997).

The level of gene flow along these three routes was an order of magnitude greater than the levels of gene flow recorded between routes. Using Parsimony Analysis of Endemicity, De Grave (2001) found a related pattern in pontoniid shrimps with Melanesia (including the Solomon Islands, Vanuatu and Fiji) consistently appearing as the sister-area to a group comprised of the Indo-Philippine area, Queensland, NW Australia and the western Indian Ocean. Concurring with Benzie & Williams (1997), De Grave (2001) describes Melanesia as a string of ‘stepping-stones’, sat at the margin of the Pacific plate. During the Pleistocene glacial stages there was no connection between the western Pacific locations and Indo-Malaysia, the Torres Strait and Timor Sea becoming episodically dry. Such sea-level changes have been cited as the cause of cladogenesis in a number of marine organisms, e.g. the sea urchin Diadema (Lessios et al. 2001). The possible changes in current direction that accompanied these land barriers may have resulted in changes in strength and direction of the sea currents south of Melanesia, further isolating Melanesia and its fauna from Queensland. For the more stenothermal taxa ranging across the Indo-West Pacific, each glaciation would have interrupted their distribution, providing the mechanism and opportunity for allopatric subpopulations to diverge. The speciation of five planktonic copepod species groups, discussed by Fleminger (1986), suggests that Wallacea constituted a geographic barrier during the course of their cladogenesis. Thus the intermittent physical barrier between the Indian and Pacific Oceans could have reinforced the difference between the two faunas over geological time, as well as connectivity amongst the Pacific locations.

Both Benzie & Williams (1997) and De Grave (2001) conclude that the South Equatorial and South Equatorial Counter Current Systems provide a good means of dispersal between western Pacific locations, the observed patterns thought to be representative of past connectivity and dispersal at times of lower sea levels, which had not been erased by subsequent dispersal by present-day circulations.

The isolation of the Pacific plate locations (Solomon Islands, Fiji and Vanuatu) because of geographical distance during plate movements and episodic lowering of sea levels means that these faunas lie intermediate to those of the Philippines/Indonesia and the eastern Coral Sea, grouping with one or other dependent on the taxon level analysed.
The species-level grouping of the Solomon Islands and the Philippines, itself closely grouped with Indonesia, was noted by Williams & Benzie (1997). Today there is a relatively easy explanation for the unrestricted gene flow between these locations recorded by Williams & Benzie (1997). There are two main pathways of Pacific water throughflow into the Indonesian Seas, the western route and the eastern route (Waworuntu et al. 2000). The western route is the primary route (Waworuntu et al. 2001) and carries water down to 500 m mainly from the North Pacific, via the Mindanao Current, through the Makassar Strait, Flores Sea and Banda Sea, before exiting into the Indian Ocean via the Timor Sea (Waworuntu et al. 2000). The eastern route carries water mainly from the South Pacific, via Halmahera, past Ambon to the Banda Sea and Timor Sea. The Solomon Islands are positioned in the boundary zone of the North and South Pacific Central Gyre faunal provinces (McGowan 1986).

Uthicke & Benzie (2001) found unrestricted gene flow between Torres Strait and the Solomon Islands in populations of the sea cucumber Holothuria scabra Jaeger, 1833. It is possible then that the Solomon Islands bryozoan fauna would be more similar to the northern Great Barrier Reef fauna than it obviously is to the Heron Island fauna at the southernmost tip of the Great Barrier Reef. Such a fine-spatial-grain biogeographical analysis is, however, beyond the currently available datasets.

A reasonable explanation of the difference in location groupings seen between the genus and species analyses might result from the timings of cladogenesis at genus and species levels. Quite clearly, genus-level geographical affinities reflect older linkages, more indicative of Pacific plate links, than species-level affinities, which reflect more recent, perhaps Pleistocene, current-mediated and/or other dispersal events.

In this, it is worth noting that whilst Mauritius has the highest proportion of endemic species, 51% (Table 2), its ratio of endemic species to endemic genera is the lowest seen, at 3% (Table 4). Endemic genera can consist only of endemic species, but it appears that there is a higher ratio of endemic species to endemic genera in locations with the lower proportions of endemic genera, i.e. the Philippines (12.3%) and Vanuatu (14.5%). Therefore, it appears that more widespread genera have a greater propensity to diversify, common genera giving rise to many endemic species, for instance Parasmittina, Celleporaria and Rhynchozoa. Although species of these genera do produce large conspicuous erect colony forms, most of the endemic species have some ecological and colonial attributes in common; i.e. they produce small ‘spot’ colonies (sensu Bishop 1989).

The ascophoran/anascan ratio results show Mauritius and the Philippines consistently have ratios at all taxonomic levels higher than the other locations, whilst Indonesia consistently has ratios far lower than the others. It could be said that the ascophorans are more prone to diversification than the ‘anascans’. Or, maybe just that more taxonomic untangling has been attempted on the ascophorans than the ‘anascans’.

Whilst most of the available Indo-West Pacific biogeographical data sets (some are cited above) are from taxa with a presumed relatively high dispersal-potential, this is not necessarily the case for cheilostome bryozoans. In fact the larvae of aclonal animals typically disperse farther than those of clonal animals (Jackson 1986). Most cheilostome bryozoan species produce a brooded coronate larva that is of a relatively short-lived, non-pelagic, benthic larval type and so less able to disperse as readily as the fully planktonic larvae of many marine molluscs for instance (Watts et al. 1998). There are two main pathways of Pacific water throughflow into the Pacific Ocean and its potential influence on dispersal because of rafting. Indeed DeVantier (1992) did record Bryozoa amongst rafting organisms; as such rafting

<table>
<thead>
<tr>
<th>Genera/Families</th>
<th>Mauritius</th>
<th>Indonesia</th>
<th>Philippines</th>
<th>Solomon Islands</th>
<th>Heron Island</th>
<th>Vanuatu</th>
<th>Great Barrier Reef</th>
<th>Fiji</th>
<th>Tahiti</th>
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<td>1.7</td>
<td>0.0</td>
<td>4.5</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.9</td>
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<tr>
<td>Species/Genera</td>
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<td></td>
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</tr>
</tbody>
</table>
dispersal of mature colonies cannot be discounted as a potential means of dispersal in Indo-West Pacific bryozoans, even if larval dispersal is thought to be limited.

This biogeographical analysis of cheilostome bryozoans may be of broader interest as the region around Indonesia, Malaysia, the Philippines and New Guinea has long been known to harbour a greater number of marine species than any other oceanic region; species richness declining outwards from this region (Roy et al. 2001). Originally this area was thought to represent a centre of radiation, or centre of origin, as indicated by the fact that many marine families exhibit their greatest diversity there. Using a cladistic biogeographical technique of fish, coral and nudibranch mollusc distributional data, Santini & Winterbottom (2002) split the Indo-West Pacific region into 18 areas, mostly corresponding to tectonic plates. They concluded that the diversity of marine organisms seen in SE Asia is the result of the convergence of many continental and volcanic land fragments, each with its own endemic species, SE Asia thus acting as a centre of accumulation for lineages originating in the western Indian Ocean, circum-Australian region or the south-western Pacific.

Biogeographical studies are contingent upon reliable information regarding the species composition and distribution of taxa across the area being analysed. As a study like the present one heavily relies on published data, a prime consideration is the completeness of the faunal inventory for each location. Gosliner & Draheim (1996) established that the apparent inventory of Hawaiian opisthobranch molluscs (arguably a more visible group) increased by more than 75% in just three years. This apparent under-recording may have played a role in the fact that Tahiti and Indonesia occupy positions in the family-level analysis, which are not congruent with their present-day geographical proximity to other localities (Fig. 1A-C). At the species level, Indonesia has the smallest proportion of endemics, closely followed by Vanuatu, perhaps another incidence of under-recording. Indeed, it is surprising that the Vanuatu fauna is not more similar to that of the Solomon Islands as it is part of the same oceanic ridge, bounded by a series of narrow oceanic trenches (Huber & Baines 2000), and has been close throughout the tectonic evolution of the area.

The addition of other bryozoan faunas, at the species level, from the Indo-West Pacific (e.g. the northern Great Barrier Reef or Torres Strait, Fiji, Tahiti, Hawaii or Western Australia) to a future analysis may help to clarify some of the uncertainties that the present analyses have produced. A more detailed regional assessment of both the Indonesian and Philippines faunas would be highly profitable, as these larger areas are capable of subdivision (Santini & Winterbottom 2002). At present, such finer-grained studies are impossible, given the general paucity of reliable bryozoan data sets from the larger part of the Indo-West Pacific.

The observed biogeographical patterns appear to be a consequence of changing patterns in dispersal and connectivity over time. Both Mauritius and Hawaii have been separated from the western Pacific locations for a prolonged period. The western Pacific locations appear to have gained and lost connectivity and resultant faunal associations over geological time, owing in the most part to tectonic events and eustatic sea-level changes and concomitant oceanic currents. It appears under these conditions that more widespread (common) genera have a greater propensity to diversify relatively more rapidly than less widespread (endemic) genera.

In conclusion it seems that, for the most part, the observed biogeographical patterns seen in the Indo-West Pacific cheilostome bryozoans can be explained by the integration of tectonic events, changes in sea level, vicariant events and dispersal events.

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Some remarkable Bryozoa from the Neogene of Moravia (Czech Republic)

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ABSTRACT: A preliminary overview concerning bryozoan faunas from the Badenian (Middle Miocene) of various localities in Moravia (Czech Republic) is given. Some of these faunas belong to the northern part of the Vienna Basin; most of them however, occur in the Miocene of the Carpathian foredeep. These studies aim to provide a better and more detailed understanding of the spatial and temporal distribution of bryozoan taxa for the Central Paratethys at least. For this reason biostratigraphical studies have been included in this project too. 12 taxa of Bryozoa have their type localities in Moravia. The 'classical' locality Bischofswart (= Hlohovec) has been rediscovered, and as a consequence Cellepora polythele Reuss, 1847 has been restudied on the basis of topotypes. The morphology of its zoarium yielding an optimum of water flow is discussed.

1 INTRODUCTION

'Moravia' being the eastern part of the Czech Republic will in this paper be used in the present meaning of this term; one has to realize that borders in Central Europe have often changed considerably, especially during the last century. Mistakes and misunderstandings in connection with geographical terms are therefore nearly inevitable; to mention but one example: Canu & Bassler (1925) described Bryozoa from three different localities: Steinebrunn (Austria), Eisenstadt (Austria), and Porzteich (at this time: Czechoslovakia, now Czech Republic), giving 'Bryozoa from Austria and Hungary' in the title, but only one species from Kroisbach (= Fertőrakos) representing actual Hungarian material.

Even authors in the 19th century had occasionally a few 'geographical' problems: the locality Garschenthal (Uvaly, 8 km SE Mikulov) was mentioned by Reuss (1874) as situated in Styria and in Hungary; the latter opinion had been shared also by Manzoni (1878). Such mistakes can probably easily be explained by the fact, that these authors got their material from local collectors, whose names are frequently mentioned in their publications. This is also similar for material from Moravia studied by Reuss (1847); he mentions in this connection three names: Mr Poppelack (an architect from Feldsberg = Valtice, Moravia), Dr J. Eitlberger from Brünn (= Brno, Moravia) and Mr Rubesch, curator of the mineralogical collections at Bilin (= Bílina, Bohemia, Czech Republic).

2 GEOLOGY AND BIOSTRATIGRAPHY

In respect to the geological and biostratigraphical setting only a few general remarks are given here. Anything more would definitely be far beyond the scope of this paper.

Moravian bryozoan localities are situated either in the Molasse Zone, the Subcarpathian Miocene foredeep or within the northern resp. northeastern part of the Vienna Basin. The Subcarpathian foredeep is equivalent to the Molasse Zone, there is however one important difference: Molasse sediments consist largely of Early Miocene sediments whereas in the Carpathian foredeep of Moravia and Poland also sediments from the Badenian (Middle Miocene) occur. The Vienna Basin is a rather small, tectonical 'pull-apart basin' extending from SSW (Gloggnitz, 47°40'N, 15°57'E; Lower Austria) towards NNE (Napajedla = Napajedl, 49°10'N, 17°32'E; situated near Zlín, Moravia) across a distance of about 200 km. The width of the basin is 55 km at its maximum and contains Neogene sediments up to 5,500 m thickness in the Austrian part (Tollmann 1985). For a modern summary concerning depositional systems, sequence stratigraphy, and regional as well as global sea-level changes see Kovac et al. (2004). The sediments especially the full-marine development during the Middle Miocene, include a considerable variety of sands, clays and corallineaceous limestones ('Leithakalk') which are of great interest in connection with bryozoan studies.
In respect to biostratigraphy one can confirm that all the localities mentioned in this paper can be attributed to the Badenian stage (= Middle Miocene) of the Paratethys. Unpublished studies of foraminiferal and calcareous nannoplankton assemblages by K. Holcová (Charles University, Praha) have confirmed distinctly ‘Lower Badenian’ faunas from three localities (Podbrezice-reef, Podbrezice-village, and Kralice).

3 BRYOZOAN LOCALITIES IN MORAVIA

In the introduction to his extensive 1847 publication Reuss mentioned seven localities from the Czech Republic: one of them in Bohemia and six situated in Moravia. From four of these localities Bryozoa were studied by Reuss: Kostel (= Podivín), ‘Satschan bei Austerlitz’ (= Zatecany near Slavkov), Bischofswart (= Hlohovec), and Austerlitz (= Slavkov). In his revision Reuss (1874) added two more bryozoan localities from Moravia: Nikolsburg (now: Mikulov) and Porzteich (a lake, close to Voitelsbrunn = Novy rybník near Sedlec). Manzoni (1877, 1878), who continued this revision after the death of Reuss added the localities Grussbach (= Hrušovany) and Raussnitz (= Rousínov). Prochážka (1894) gave a detailed study of an invertebrate fauna from the Miocene of Kralice nad Oslavou and included also many bryozoan taxa.

Canu & Bassler (1925) described 26 different bryozoan taxa from ‘Porzteich’; David & Pouyet (1974) in the course of their detailed revision of the Cheilostomata from the Vienna Basin included also a considerable number of specimens from Moravia in their studies. In the course of recent studies during the last two years bryozoan faunas have been collected by K. Zágorsek (Národní Muzeum, Praha) and the author from various Moravian localities partly situated in the northernmost part of the Vienna Basin or (more often) in the southern part of the Carpathian foredeep. There would be no sense giving faunal lists or short overviews of all the material and data collected up to now. Instead a few localities and a few taxa of special interest for various reasons will be discussed here.

A locality of special interest, the bryozoan reef of Podbrezice, is described elsewhere Zágorsek & Holcová (this volume).

An additional item of interest in respect to the study of Miocene bryozoans is the fact that 26 taxa of the Paratethys bryozoan fauna have their type localities in Moravia. Four of these taxa (Cellepom marginipom, Cellepom pulupa, Escham semitubulosa, Hemieschara tubigem) are according to our present state of knowledge not recognized any more, seven would urgently need a revision (coll. Prochážka, material not available for study), two (Lepmlia micmstoma, Defmncia Orbignyana) are regarded as junior synonyms. Type material from Moravian localities in the collections of the Museum of Natural History, Vienna is listed in Table 1.

Table 1. Bryozoan type material from Moravian localities. Repository: Museum of Natural History, Vienna (Department of Geology and Palaeontology).

<table>
<thead>
<tr>
<th>Name of species</th>
<th>Type locality</th>
<th>Author</th>
<th>Inv. No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calpensia leptosoma</td>
<td>Bischofswart</td>
<td>Reuss(1847)</td>
<td>type probably lost</td>
</tr>
<tr>
<td>Cellepora polythele</td>
<td>Bischofswart</td>
<td>Reuss(1847)</td>
<td>1859.45.653</td>
</tr>
<tr>
<td>Cribella cyclocephala</td>
<td>Kostel</td>
<td>Reuss(1874)</td>
<td>1878.1.1.88</td>
</tr>
<tr>
<td>Hippadenell regularis</td>
<td>Kostel</td>
<td>Reuss(1874)</td>
<td>1878.11.60</td>
</tr>
<tr>
<td>Hippoporellifer hypsostoma</td>
<td>Kostel</td>
<td>Reuss(1874)</td>
<td>1878.11.43</td>
</tr>
<tr>
<td>Hippoporella pauper</td>
<td>Kostel</td>
<td>Reuss(1874)</td>
<td>1878.11.49</td>
</tr>
<tr>
<td>Lepralia microstoma ( = Microporella ciliata)</td>
<td>Kostel</td>
<td>Reuss(1847)</td>
<td>1878.11.29</td>
</tr>
<tr>
<td>Schizoporella microstoma</td>
<td>Satschan</td>
<td>Reuss(1847)</td>
<td>1867.40.228</td>
</tr>
<tr>
<td>Schizoporella tetratoga</td>
<td>Bischofswart</td>
<td>Reuss(1847)</td>
<td>1867.40.35</td>
</tr>
<tr>
<td>Smittina chelopora</td>
<td>Satschan</td>
<td>Reuss(1847)</td>
<td>1867.40.191</td>
</tr>
<tr>
<td>Smittipora platystoma</td>
<td>Satschan</td>
<td>Reuss(1847)</td>
<td>1867.40.190</td>
</tr>
<tr>
<td>Steginoporella manzonia</td>
<td>Porzteich</td>
<td>David &amp; Pouyet (1974)</td>
<td>1859.19.150</td>
</tr>
</tbody>
</table>
4 MATERIALS AND METHODS

Material studied in the course of this investigation includes the bryozoan collections housed in the Museum of Natural History at Vienna, material kept in the collections of the Department of Palaeontology at the University of Vienna and samples recently collected in the course of field work done by Kazmér, Zágorsek and the author. The specimens kept at the University of Vienna and samples recently collected in the collections of the Department of Palaeontology, University of Vienna, material kept in the collections of the Department of Palaeontology, University of Vienna, includes specimens collected by P. Svacek (then of Brno) and by the author. The most extensive collection of bryozoan from the Miocene of Moravia has been assembled by Zágorsek: more than 17 different localities have been successfully sampled and for most of these localities the taxonomic work has nearly been finished. Publications concerning these faunas are in preparation.

5 RESULTS

5.1 A few remarkable taxa from Moravian localities

5.1.1 Bobiesipora fasciculata (Reuss, 1847) (Fig. 1, A)

Diagnosis: Basis densely covered with kenozooecia, ramifying branches originating from it, apertures with ‘pseudolunularia’ arranged in radial, meandering fascicles on lower side of branches, ridges on back side, branches densely covered with kenozooecia, gonocyst dorsally, situated in ramification of branches, very rare.

Under the name Apsendesia fasciculata Reuss (1847) described a cyclostome bryozoan from Miocene limestone at Mörbisch (Austria). Further studies resulted in the establishment of a separate genus for this taxon (Vávra 1978) and increased the number of localities at which this species occurs in the Austrian Miocene considerably: Baden, Eisenstadt, Freibühel, Mörbisch, Steinebrunn, Stotzing, and Weissennegg have been mentioned in a recent summary of data (Vávra 2002); the only one Miocene locality outside Austria in which it had been found was Korytnica (Poland). Zágorsek (2001, 2003) has found Bobiesipora fasciculata also in the Eocene of Austria and Hungary. In the course of his collecting P. Svacek (then of Brno, Masaryk University) found well-preserved material of this species in the Badenian of Kralice nad Oslavou (Moravia).

It is worth mentioning that Procházk a (1894) was the first to discover this species in the Miocene of Moravia. Under the name Defrancia Orbygniana he described a new species from a bryozoan stratum at Kralice. He gave only a rather short description, a few details and some illustrations (pi. 40, figs. 14a, b); they are rather convincing however. To confirm my suspicion that his Defrancia Orbygniana represents a junior synonym of Bobiesipora fasciculata would require a study of the type material. While the Procházk a collection has been rediscovered, the bryozoan material is unfortunately still missing (pers. comm. Dr Růžena Gregorova, Moravian Museum, Brno, via Zágorsek). The material in our collection contains among others also a rather well-preserved larger part of a zoarium (Fig. 1, A); usually only single branches or their fragments are found.

A well-preserved complete zoarium has been figured by Vávra (2002) from the Miocene of Stotzing (Burgenland, Austria). It consists of a circular to oval-shaped base covered with kenozooecia. Branches develop in radially arranged fascicles with various bifurcations; the ovicell situated on the dorsal side in
a bifurcation of such a branch of this species (Rauchstallbrunngruben, Baden, Lower Austria) has only once been found until now (Prof. E. Voigt, coll. Hamburg) which has been pictured by Vávra (1978: pi. 1, fig. 7). The generic attribution of this genus is however still under discussion - possible lichenoporid affinities cannot be ruled out. In any case these finds (5 specimens, among them a complete basal
with protuberances. The term ‘mamillata’ is for a palaeontologist of course somewhat reminiscent of ‘mamelon’ meaning protuberances covering the surface of colonies of stromatoporoida or sclerospongea. The term is derived from the Latin word mamma, meaning nipple - from which were derived terms like ‘mammals’ or the French word ‘mamelon’. According to Lehmann (1985) this term is a synonym of monticuli (Latin for ‘small mountains’, or in English ‘monticules’). Kühn (1955: 242) has probably been the first author suggesting a biological interpretation of these protuberances. He understood these ‘warzenförmigen Erhebungen’ (= wart-like peaks) as strategy of faster colony growth. Regarding celleporids as fast-growing forms of Quaternary and Pleistocene seas he suggested Cellepora polythele to be some ‘Über-Holoporella’ (= super-Holoporella) - statements remaining within the realm of speculation however.

Pouyet (1973) who used the terms protuberances and mamelons in her revision of the celleporids gave no suggestion as to the possible function of this rather specialized surface pattern. Following suggestions based on studies of Palaeozoic and Recent taxa Banta & al. (1974) and Taylor (1979), regarded monticules as possible excurrent water outlets, an idea confirmed later by observations of Recent colonies and their water current systems by Cook (1977; see also McKinney & Jackson 1989: 134) one can easily apply this idea to Cellepora polythele. Careful observations yield additional evidence for this interpretation: Banta & al. (1974) listed a number of facts concerning the occurrence of such monticules, criteria being largely valid for Cellepora polythele too: (1) Distance between monticules: remarkably constant; (2) Monticules: arranged in a rhombic (hexagonal) pattern; (3) Diameters of monticules nearly constant; (4) Monticules rather common in many taxonomically unrelated Bryozoaa with robust colonies. One additional item that describing monticules as being modifications of the exozone - applies of course for Palaeozoic stenolaemate Bryozoaa only (Banta & al. 1974). In this connection Shunatova & Ostrovsky (2002) contributed essential new details to this idea based on observations of Recent marine taxa from the White Sea and Barents Sea. Following their results one should regard monticules no longer as places of excurrent water flow: they argue such monticules were often places of incurrent water flows and changed their function from incurrent to excurrent after polypide degeneration only. Various similar studies have also been summarized recently by Ostrovsky & Shunatova (2002); the only one study containing observations for Recent Celleporaria until now was that of Winston (1978), who stated for Celleporaria albirostris that the knobs mark the excurrent channels. A specimen with well-preserved surface has meanwhile been found at Hlohovec, showing even a number...
Figure 2. *Cellepora polythele*. Badenian (Middle Miocene) of Hlohovec (= Bischofswart, Moravia), Topotypes. A: Rather well-preserved zoarium showing the evenly-spaced monticules; B: Heavily calcified zoarium, average preservation; C: Basal view, showing the shape of some unknown substratum; D: A ‘twinned’ colony, a zoarial type not very uncommon at Hlohovec; E: Section showing the monticules of earlier growth stages; F: Section showing repeated growth stages of the zoarium. A-F; scale bar = 1 cm. Material in the collections of the Department of Palaeontology, University of Vienna (Accession No.: 3560/ 6-7).
of ovicells (Vávra, in press): most of the ovicells are situated at the top of the protuberances supporting thus the idea that these mamelons can be regarded as places of excurrent water flow. The water current may thus also have been useful during the setting free of the larvae.

Thin sections of Cellepora polythele from South Moravia have yielded additional details: these section show some type of growth rhythms (Fig. 2, E, F) which seem to confirm the occurrence of monticules for each stage of zoarial growth including even juvenile and some sort of twinned colonies (Fig. 2, D). The formation of these monticules seems to correlate with a special budding pattern; given the poorish state of preservation on account of a high degree of calcification makes any further studies rather difficult.

For a satisfying redescription of Cellepora polythele a considerable number of criteria would need a careful restudy. Unfortunately the unsatisfactory state of preservation makes any closer investigation rather difficult, zoaria have obviously been heavily overgrown by thin sheets of algae, and calcification and other events have occurred during diagenesis. Based on material collected during our own field work at Hlohoevec and by using material from one additional Moravian locality (hill situated south of the fish-pond Nesyd near Lednice, near to the Austrian border; Lednice = Eisgrub, situated 14.5 km ESE Mikulov = Nikolsburg), some further observations can be added however.

One of the morphological features described already by Reuss (1847) concerns a dimorphism of zooecia: ostiolis inaequalibus rotundatis, interpositis minimis. This statement - also confirmed in more detail in the my own observations I confirm the different size of ovicells supports the occurrence of some dimorphism. Kühn (1925) has mentioned ovicells in one specimen from Gaudenmdorf (Early Miocene, Lower Austria) but has unfortunately not given any detailed description. Quite recently among our 44 specimens collected at Hlohoevec one specimen has been found which showed a rather well-preserved surface. It has even a number of ovicells situated mostly at the top of the protuberances; the type of ovicells as well as the shape of apertures and other details of morphology have now enabled to attribute this material to the Genus Cellepora [type species: Cellepora pumicosa (Pallas, 1766)].

Pouyet (1973) has interpreted interzooecial, rather large, oval-shapes pores as being bases of interzooecial avicularia. This interpretation could not be confirmed after studying this above-mentioned topotypic specimen with well-preserved surface.

Further results concerning Cellepora polythele will be published in near future (Vavra, in press).

5.1.3 Metrarabdotos maleckii Cheetham, 1968
(Fig. 1,C)
Diagnosis: bifoliate, erect zoaria. pisciform zooecia in longitudinal, alternating rows, small areolae, sub-circular apertures, mostly two small avicularia. situated symmetrically to aperture, ovicells large, nicely ornamented, rather rare.

This well-known taxon has been described from the Vienna Basin - under the names Eschara punctata Philippi resp. Eschara imbricata m. by Reuss (1847). It has been reported to occur not only in Austria but also in the Miocene of Poland, Rumania, Ukraine, and Czech Republic (Vávra 1977). From Moravia three localities were known: Podivín (= Kostel), Porzlech and Rousinov (= Raußnitz). Recently it has been found also at most of the Moravian localities, e.g. at Zidlochovice, Podbrezice etc. This species being rather wide-spread throughout the Paratethys is a representative of the subgenus Pommetra, which represents an offsprings of the New World subgenus Rhabdotometra, which has been reported from the United States (Eocene - Lower Miocene) as well as from the Oligocene (Stampian) of France (Cheetham 1968).

Metrarabdotos maleckii a common and wide-spread taxon, has been described from a rather high number of Austrian localities of Badenian age (= Middle Miocene): Baden, Ehrenhausen, Eisenstadt, Forchtenstein, Freibühel, Mörbisch, Niederleis, Nußdorf, Steinebrunn, Weßenegg, Wildon, Wurzing. According to Cheetham (1967) the genus Metrarabdotos is a reliable indicator for tropical areas. The significance of its occurrence in the Central Paratethys as an important climatic indicator has been already discussed (Vávra 1980, 2000).

5.1.4 Tremopora radicifera (Hincks, 1881)
(Fig. 1,B)
Diagnosis: bifoliate zoaria, elliptical zooecia, opesia occupying most of frontal side, one or two lateral
avicularia, hyperstomial, globular ovicells, scuta very rare in fossil specimens.

Only one species of this genus, Tremopora radiifera, occurs in Austria at different localities: Baden, Ehrenhausen, Eisenstadt, St. Margarethen. In the Austrian Miocene it is always among the rare faunal elements: quite in contrast to the very rich material from the Miocene of France (cf. Musée d’Histoire Naturelle, Paris; Balavoine Coll.). The first find of a rather well-preserved zoarium from the Badenian of Kralice nad Oslavou in Moravia (P. Svacek, then of Brno) confirms the presence of this rare taxon which is rather wide-spread in the area of the Central Paratethys. This species is regarded as a possible Indopacific faunal element (Vávra 2000), the confirmation of its occurrence in Moravia now, therefore deserves some notice.

5.1.5 Umbonula spinosa (Procházka, 1894) (Fig. 1,D,E)

Diagnosis: bifoliate zoaria, zooecia in strictly alternating rows, prominent, spine-like umbos, additional small umbos situated closely to aperture, areolae, ovi­cells hyperstomial, rather rare, morpholohy often simi­lar to Umbonula macrocheila (Reuss, 1847; Fig. 1, F), transitions possible.

This species was first described by Procházka (1894) from Kralice nad Oslavou, the type locality. Further reports of this taxon are rather rare in the literature: Svacek (1996) in the course of his studies of the bryozoan fauna from Kralice and Vávra (2002) who redescribed the topotypes collected by Svacek and first finds of this species from the Austrian Miocene. For a detailed modern restudy of the Umbonulids from the Paratethys area this species will be of rather great interest as it is morphologically rather similar to Umbonula macrocheila (Fig. 1, F) it deserves some interest. As U. endlichen as well as U. scarabaeus have been regarded as junior synonyms of U. macrocheila by some authors (Schmid 1989, Pouyet 1997) a careful revision of this whole group is needed.

6 CONCLUSIONS

Studies of bryozoan faunas from different localities in Moravia (Czech Republic) situated in the northern part of the Vienna Basin and in the Carpathian fore­deep (Badenian, Middle Miocene) offered opportunities for taxonomic studies and have yielded also a considerable amount of data concerning spatial and temporal distribution of single bryozoan taxa. Detailed informations concerning a few species being of special interest for various reasons (Bobiesipora fasciculata, Cellepora polythele, Metrarabdotos maleckii, Tremopora radiifera, Umbonula spinosa) are given.

ACKNOWLEDGEMENTS

The study of bryozoan faunas from the Neogene of Moravia has been supported by the “Fonds zur Förderung der wissenschaftlichen Forschung” within the project “Bryozoan sediments in Cenozoic tropical environments” (Project P 15600). A donation of some specimens of Cellepora polythele from the area of Lednice by Prof. E. Kusel, University of Vienna, is gratefully appreciated; bryozoan material has also been made available by the collecting activities of P. Svacek (then of Bmo) and K. Zágorské (Narodni Muzeum, Praha). A. Ostrovsky has contributed to this paper by discussing the morphology of Cellepora polythele, K. Holcová (Charels University, Praha) by biostratig­raphical studies. Photographical work done by A. Ostrovsky and K. Zágorské (stereoscan) and M. Vávra is gratefully appreciated.

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The higher phylogeny of Phylactolaemate bryozoans inferred from 18S ribosomal DNA sequences

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ABSTRACT: Freshwater bryozoans (Phylactolaemata) are organized among five distinct families. Comparative morphology of these families suggests a linear series, from simple to complex, which is generally interpreted as an evolutionary trend. We sought to test this widely accepted hypothesis by analysis of partial 18S rDNA sequences from 9 species representing the five families, rooted with 2 species of cnidarians. Genetic variation among the bryozoan species was small. The two monotypic families, Cristatellidae and Pectinatellidae, displayed twice the amount of variation as all other species combined. Because of the lack of sufficient informative sites parsimony analysis could not be used in the analysis. Maximum likelihood and distance matrix analyses both suggest a new phylogenetic tree that runs contrary to the traditional view. At the base of the tree nearest the outgroup are all globular colonies with large, hooked statoblasts and large lophophores. At the top of the tree are the branching, tubular colonies, with relatively smaller statoblasts and lophophores. These results cloud the already subjective view of phylactolaemates being related in some way to the ancient marine Stenolaemates or Ctenostomes, both of which exhibit tubular colonies. They also suggest unexpected evolutionary trends among phylactolaemate statoblasts: spiny, self-inflating statoblasts of Pectinatellidae and Cristatellidae appearing early, followed by the general morphological simplification of Plumatellidae and Fredericellidae.

1 INTRODUCTION

Freshwater bryozoans (Class Phylactolaemata) constitute a well-defined group of sessile invertebrates. With about 80 described species inhabiting a wide range of freshwater habitats, they are among the most common metazoans living on submerged substrates. Like their marine counterparts, phylactolaemates are exclusively modular in structure, composed of many identical zooids all freely sharing a common coelom (Wood 2001 ). The group displays an impressive diversity of colony morphology, ranging from diffuse branching tubules to compact, globular masses. Freshwater bryozoans often cause serious fouling of irrigation pipes and water cooling systems (Wood & Marsh 1998, Smith et al. this volume). Several species are implicated as final hosts to a serious myxozoan parasite of salmonid fish (Canning et al. 1999).

Among all of the so-called lophophorate animals (bryozoans, phoronids, and brachiopods) only the phylactolaemates and a handful of ctenostome bryozoan species occur in fresh water. One of their adaptations to a freshwater habitat is the asexual production of dormant structures called statoblasts. These enable populations to survive drought, cold temperatures, and other unfavorable conditions; they also serve as effective disseminules. Statoblast morphology is distinctive for each family and often provides diagnostic features for species identification.

Phylactolaemate bryozoans have long been regarded as the most primitive of the living bryozoans (Hyman 1959, Rvland 1970). This view is based on features believed to pre-date modern marine species: cylindrical zooid shape, muscular body wall, bilateral lophophore symmetry, and monomorphic zooids. From this standpoint, evolutionary trends within the class seem fairly clear. Fredericellids, with their diffuse tubular structure, and structurally simple statoblasts would be closest to the ancestral type (Corsi 1941, Brien 1960, Lacourt 1968, Ryland 1970, Willmer 1990). With this starting point, the evolutionary trends shown in Table 1 would include:

- Increased compactness of colonies leading to a consolidation and fusion of zooids.
- Lophophores with steadily increasing tentacle numbers.
- Increased complexity of statoblasts, starting with simple, bean-like structure of freidericellids, followed by development of two functional types in plumatellids, finally leading to the appearance of spiny, dual-function types in the globular colonies.
Table 1. Summary of morphological features distinguishing the five families of Phylactolaemata. The traditional view of phylactolaemate evolution assumes progression from left to right.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Fredericellidae</th>
<th>Plumatellidae</th>
<th>Pectinatellidae</th>
<th>Lophopodidae</th>
<th>Cristatellidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colony form</td>
<td>Branched tubes, diffuse</td>
<td>Branched tubes, diffuse to appressed</td>
<td>Sac-like, thick walled, zooids crowded</td>
<td>Sac-like, thick walled, zooids crowded</td>
<td>Sac-like, thick walled, zooids crowded</td>
</tr>
<tr>
<td>Zooid spacing</td>
<td>Widely spaced</td>
<td>Widely spaced to compact</td>
<td>Compact</td>
<td>Compact</td>
<td>Compact</td>
</tr>
<tr>
<td>Tentacle</td>
<td>Circular arrangement</td>
<td></td>
<td>U-shaped</td>
<td>U-shaped</td>
<td>U-shaped</td>
</tr>
<tr>
<td>Statoblasts</td>
<td>Simple, bean-like</td>
<td></td>
<td>2 types: Floating (self-inflating or sessile with peripheral spines)</td>
<td>Floating only (not self-inflating) with spines radiating from center</td>
<td>Floating only (self-inflating);</td>
</tr>
<tr>
<td>Approximate number of known species</td>
<td>4</td>
<td>70</td>
<td>1</td>
<td>5</td>
<td>1</td>
</tr>
</tbody>
</table>

This scheme is tacitly acknowledged in most recent books and articles where phylactolaemate bryozoans are described. Typically, Fredericellidae is treated first, followed by Plumatellidae, the progression always ending with Cristatellidae (Lacourt 1968, Bushnell 1974, Geimer & Massard 1986, Wood 1989, Smith 1989, Ricciardi & Reiswig 1994).

Among the three non-tubular families (Cristatellidae, Lophopodellidae, Pectinatellidae) there is no clear indication of the most likely lineage. All three families produce relatively large, free statoblasts with projecting hooks or spines. In Cristatellidae the spines originate from a central area (fenestra) while in other families they originate along the periphery. Statoblasts of Lophopodidae become buoyant only after desiccation, while those of Pectinatellidae and Cristatellidae are inflated to achieve buoyancy prior to their release. Unfortunately, the two latter families are each represented by only a single species, so the systematic information they can provide is limited.

This study is based on 18S ribosomal DNA extracted from nine species of phylactolaemate bryozoans. There were two components of the work. First, we wanted to see to what extent molecular data could contribute to an understanding of family relationships in phylactolaemate bryozoans. Second, we sought to explore the relationship of phylactolaemate bryozoans to other lophophore-bearing invertebrates based on their 18S ribosomal DNA sequences.

For the phylactolaemates specifically, we wanted to test the idea that fredericellid species lie closest to the common ancestor. In addition, we hoped for clarification on the systematic position of the Hyalinella punctata, a species that shares important features with both Plumatellidae and Lophopodidae (Wood 2001).

Finally, we sought a better understanding of the relationships among Pectinatellidae, Lophopodidae, and Cristatellidae, the so-called >higher = phylactolaemates (Mukai & Oda, 1980).

2 METHODS

Nine bryozoan species were used in this study, representing the five major families: Fredericellidae (Fredericella sultana and F indica), Plumatellidae (Plumatella reticulata, P. fitngosa, and Hyalinella punctata), Lophopodidae (Lophopodella carteri and Asajirella gelatinosa, Pectinatellidae (Pectinatella magnified), and Cristatellidae (Cristatella mucedo). All were collected in England except Pectinatella, which came from Ohio, USA. We placed specimens in filtered water to clear the gut of contaminants, then narcotized them with menthol and preserved them in 100% ETOH. Several polypides were removed from each colony for DNA extraction using Qiagen Qiap DNA mini kit.

Oligonucleotide primers for amplification (as synthesized, 5' to 3', F = forward, R = reverse) were as follows: 18S fragment 1 F, TCCCAGCTCCAATA-GCG; R, GCAGCAACTTTAATATACGC; fragment 2 F, ATTCTTAGATCGTCGCAAG; R, AGAGT-CTCGGTTATCG. The following PCR master mix (lx) was used: 5.2 1 ddH2O, 2.0 1 IOX buffer, 2.0 1 DNTP (2 M), 2.41 MgCl (25 M), 1.0 1 primer #1, 1.01 primer #2, and 0.4 1 TAQ. A 20 1 PCR reaction was run comprising of 14 1 of the master mix and 6 1 of DNA. The reaction mixture was then placed into a thermocycler and run through 32 cycles of the following program: 93°C denaturing (45 seconds), 55°C annealing (45 seconds), 72°C extension (2 minutes),
4°C holding. Amplified samples were then electrophoresed using a 0.8% agarose gel at 120 volts (lx TBE), stained, then cut from the gel. The DNA was purified from the gel using Qiagen QIAquick Gel Extraction Kit, concentrated, and sent to a third party sequencing house for direct sequencing.

To build a tree based on the 9 phylactolaemate species we used Phoronis australis (GenBank AF119079) and Phoronis hippocrepia (U08325) as a combined outgroup. Sequences were initially aligned by ClustalW, and further alignment was done manually using BioEdit (Hall 1999). The analyzed data set had 1454 to 1459 nucleotides depending on the species. Approximately 1352 (92.9%) of these were constant, 80 (5.5%) were parsimony uninformative, and only 23 (1.6%) parsimony informative. By including the outgroup species the number of parsimony-informative sites rose to 95 (6.5%). The sequences did not differ significantly in basic composition (t = 1.200, df = 22, P value = 0.2430).

To compare the phylactolaemates with other lophophore-bearing phyla we selected DNA sequences from 4 phylactolaemate species, each representing a different family. These were aligned together with 18S data from other lophophorates acquired from GenBank. Listed by taxon along with GenBank accession numbers, these included 3 phoronids: (Phoronis australis (AF119079), Phoronis hippocrepia (U08325), and Phoronis psammophila (U36271); 2 brachiopods: Terebratulina retusa (U08324), and Megerlia truncata (U08321); 3 cheilostome gymnolaemates, Caberea borvi (AF 119082), Electro bellula (AF499744), and Schizoporella (AF499743); and 1 ctenostome gymnolaemate, Alcyonidium gelatinosum (X91403). Two cnidianian species were selected to serve as a combined outgroup: Aurelia auritus (AY039208) and Anemonia sulcata (No. X53498).

Alignment was performed with ClustalW and BioEdit as described above. The alignment had 1402 to 1439 characters of which 59% were constant, 23% parsimony uninformative, and 18% parsimony-informative.

We conducted phylogenetic analyses using PAUP* 4.0b8 (Swofford 2000). For maximum parsimony 1000 heuristic searches were performed using random addition sequence. Characters were weighted equally and unordered, and gaps were treated as missing. For the phylactolaemate species Modeltest version 3.5 (Posada & Crandall 1998) indicated that sequence data best fit the K80 model with discrete approximation of the gamma distribution (K80+G, shape parameter 0.2047; Kimura 1980). The best fit for combined lophophorate data was the TrN model with discrete approximation of the gamma distribution (TrN+G, 4 rate categories, shape parameter 0.3807; Tamura & Nei 1993).

3 RESULTS

3.1 Phylactolaemates

In a comparison of the 5 phylactolaemate families the number of exclusive nucleotide substitutions was highest among the Lophopodidae (16) and Pectinatellidae (13) and lowest among the Fredericellidae (0) and Plumatellidae (4). Of course the phoronid outgroup had many more with 69.

The exclusion of all sites with insertions or deletions left 189 variable sites. Removing the phoronid species left only 23 sites that could be informative for parsimony analysis. Eighteen of these 23 sites involved base substitutions occurring exclusively in the two lophopodid species. Among the 23 sites there was not a single substitution involving Pectinatellidae, Cristatellidae, or Pectinatellidae, which together comprise 60% of the phylactolaemate families under consideration. Consequently these sequences were not accessible to parsimony analysis, and the tree shown in Fig. 1 reflects the failure to distinguish these families by parsimony. However, the phylogenetic tree in Fig. 1 does clearly separate lophopodid and plumatellid species, placing Hyalinella solidly among the plumatellids. Bootstrap numbers involving the three inaccessible families are understandably low.

Distance matrix analysis using UPGMA suggested a somewhat different phylogenetic tree (Fig. 2). Here Lophopodidae and Pectinatellidae are positioned at the base of the tree, with successive nodes leading to Cristatellidae, and finally a Plumatellidae-Fredericellidae complex. As expected, the two
3.2 Lophophorates

In a rough comparison of lophophorate sequences both brachiopods and phoronids had the greatest number of nucleotides matching the phylactolaemate bryozoans (93%). Phylactolaemates were 91% similar to Cheilostomes and 85% to the cnidarian outgroup.

Parsimony analysis clustered all species solidly within their respective groups (Fig. 3). However, the majority-consensus tree could not suggest lineages among them at the 50% level. Distance matrix methods were consistent in suggesting a tree that places phylactolaemate bryozoans close to phoronids and brachiopods and quite distant from Gymnolaemata (Fig. 4).

4 DISCUSSION

4.1 New interpretation of phylactolaemate phylogeny

This is the first attempt to study family phylogeny in freshwater bryozoans using the tools of molecular genetics. Interpretation of the data is somewhat complicated by the fact that two of the five families, Cristellidae and Pectinatellidae, are each represented by only a single species. This effectively precludes parsimony analysis, because none of the variations in their sequences are shared with other species in the study.

Pectinatellidae and the combined species of Lophopodidae had by far the greatest number of exclusive nucleotide substitutions. This suggests a long, isolated history for each group, which is consistent with their placement at or near the base of the distance matrix trees. By contrast, the plumatellids and fredericellids, all showing little genetic variation, are interpreted as being more recently evolved.

The revised scheme of family relations within the Phylactolaemata runs contrary to systems previously proposed (Hyman 1959, Ryland 1970, Wood 1983).

They suggest that:

- Early phylactolaemate bryozoans could have been compact and thick-walled colonies with relatively large zooids. Diffuse colonies of branching tubules would have appeared later, together with a general reduction in zooid size.
- The earliest statoblasts were uninflated, of course, but they were lophopodid, not fredericellid statoblasts. Statoblast self-inflation appeared with Pectinatellidae, and was subsequently lost in Fredericellidae (along with the statoblast annulus) and Hyalinella punctata.
Implications of this scheme are discussed below with respect to colony and statoblast morphology.

4.2 Colony morphology

Among the marine (gymnolaemate) bryozoans, branching tubules and cylindrical zooids are typical of Stenolaemata and Ctenostomata. Both of these are ancient groups, represented in marine deposits from the Ordovician (Boardman et al. 1983; Cheetham & Cook 1983). They pre-date the calcified, box-like zooids of Cheilostome bryozoans which erupted in the late Cretaceous and are still dominant today. It may be this progression from diffuse, branching tubules to a more compact colony form that has driven the notion of a similar trend in phylactolaemate bryozoans.

However, there is otherwise no reason to consider compact colonies any more advanced than diffuse, tubular ones. If the ancestral phylactolaemate were a solitary animal, then the development of modular form might well have begun with tightly clustered units. New zooids, formed by asexual budding and failure to separate, could remain together in close proximity, perhaps generating a colony-wide pattern of feeding currents as in modern Pectinatella (Mukai 1998).

One danger to tightly clustered zooids in fresh water habitats is the risk of losing the entire colony to desiccation if water levels drop. Those phylactolaemate colonies with the most closely knit zooids (Pectinatella, Lophopodella, Cristatella) reduce that risk somewhat with colony motility. In laboratory studies, for example, Lophopodella carteri can move downward as much as 1 cm/day ahead of a falling water level (Riley, pers. com.). More diffuse colonies are permanently sessile, but can grow long branches in any direction, extending the life of at least a portion of the colony when the water level drops.

4.3 Statoblasts

The phylogenetic trees suggested by 18S rDNA data indicate that the lophopodid statoblast is the most primitive. Although it sinks upon release from the colony, the wide annulus of sclerotized chambers traps air upon drying, providing effective buoyancy when the statoblast is returned to water. It had been proposed by Wood & Marsh (1996) that the initial lack of buoyancy was an adaptation protecting statoblasts from harsh tropical sunlight and warm surface water. While this may still be true, the new phylogenetic tree offers a different explanation for the absence of self-inflation.

Until recently the sharp differences between the statoblasts of fredericellid and plumatellid species appeared to support close proximity of these families. In fredericellids the statoblast is a simple capsule, while the plumatellid statoblast adds elegant sclerotized structures that either provide buoyancy or else cement the capsule firmly to the substratum. However, new studies on living colonies of the fredericellid Internectella bulgarica confirm that this species also produces free statoblasts capable of self-inflation and buoyancy, much like those of plumatellids (Wood, unpublished). A second type of statoblast in this species is sessile with a distinct annulus similar to the plumatellid sessoblast. (Gruncharova, 1968, Wiebach, 1974). In all other respects, Internectella retains the classic features of a fredericellid, with sparse colonies of stringy tubules, widely spaced zooids, and circular lophophores. A common species in Southeast Asia, Internectella bulgarica represents a compelling link between Fredericellidae and Plumatellidae.

In all other fredericellid species, the sessile, bean-like statoblast has been thought by some to represent a primitive condition (Corti 1941, Brien 1960, Lacourt 1968, Ryland 1970, Willmer 1990). In our interpretation, this simplification is derived. The outer peri­blast of fredericellid statoblasts is gone or at least reduced. The minutely jagged, keel-like basal ring that helps secure some fredericellid statoblasts to the substratum could well be a remnant of the basal peri­blast of plumatellid sessoblasts.

The proposed new tree places Pectinatellidae and Lophopodidae in some proximity. These are the only two families in which the statoblast periphery is adorned by various sizes of hooks, and so the adjacent lines are not surprising. Cristatellidae also has peripheral hooks, but they originate from centrally located spines, so their presence is apparently independent in this line. Minute peripheral hooks are seen in statoblasts of the plumatellid, Swarupella andamanensis (Rao et al. 1985) but the significance of this feature is not apparent.

4.4 Phylactolaemata, phoronids, and brachiopods

The suggestion of significant evolutionary distance between phylactolaemate and gymnolaemate bryo­zoans is not novel. Hyman (1959) noted similarities between phylactolaemates and Phoronis ovalis, the only modular phoronid species. Jebram (1973) added a supporting argument based on the similar adorai orientation of new buds in these two groups, exactly opposite from gymnolaemates. Mundy et al. (1981) nicely summarized these points, listing true body wall musculature and details of lophophore ontogeny as features not shared by gymnolaemates. Backus & Banta (2002) further noted the parallel between yolk-bearing peritoneal cells forming fat bodies in phoronids and the yolk peritoneal cells that accumulate in phylactolaemate statoblasts. Finally, Zimmer (1997) described the unusual lecithotrophic larva of P. ovalis, which appears to be more similar to the phylactolaemate larva than to the typical actinotroch.
of other phoronids. Taken together, these diverse observations build an interesting case for a common ancestry of phoronids and phylactolaemate bryozoans. The 18S rDNA analysis offered here links Phylactolaemata to a phoronid-brachiopod ancestor, but provides no further detail.

If phylactolaemates were derived from phoronids or a phorndon root why is there no evidence from previous, well-documented molecular studies? The answer could lie in the selection of species and methods. The 18S rDNA analysis by Halanych et al. (1995) chose a single phylactolaemate (Plumatella repens) to represent all bryozoans; Cohen & Gawthrop (1996) included only one species of gymnolaemate (and found the phylactolaemates genetically closer to priapulids). Other studies have used a variety of assumptions and methods of analysis producing widely different phylogenetic trees.

The findings presented here are far from conclusive. The small number of species in most phylactolaemate families does not allow much resolution. In retrospect, the 18S region of rDNA proved to be rather uniform and may not have been the best place to explore bryozoan phylogeny, (although it was an area where good lophophorate data were available). Certainly a complicating factor here may be the inhibition of meiotic crossing over in certain phylactolaemates, leading to an accumulation of favorable mutations and variable rates of rDNA evolution in different parts of the genome (Bachus & Banta 2002).

Additional kinds of evidence need to be explored, including new regions of the genome and chromosome morphology. For example, Bachus & Banta (2002) noted that morphology of the NOR chromosome in Fredericella appears to be more similar to that of Cristatella than that of Plumatella. They also saw a heteromorphism in the Pectinatella chromosome in which suggested links to either Fredericellidae or Plumatellidae, or to both (B.T. Bachus, pers. com.).

5 CONCLUSIONS

Analysis of about 1,450 sequential nucleotides in 18S ribosomal DNA of phylactolaemate bryozoans suggests that compact, gelatinous colonies with large zooids and spiny, free statoblasts are closest to the ancestral type. Diffuse colonies with branching tubules and sessile statoblasts appear to be more recent. In a comparison of rDNA from species representing cheilostomes, ctenostomes, phoronids, brachiopods, and phylactolaemates, the latter group was more closely linked with the phoronids/brachiopod line than with any of the others. While far from conclusive, this result adds to a growing list of diverse reports distancing phylactolaemates from gymnolaemate bryozoans.

REFERENCES


Smith, D.G. 1989. *Keys to the freshwater macroinvertebrates of Massachusetts (No. 4): Benthic colonial phyla, including the Cnidaria, Entoprocta, and Ectoprocta (colonial hydrozoans, moss animals)*. Westborough, Massachusetts: Massachusetts Dept of Environmental Quality Engineering, Division of Water Pollution Control.


The distribution of freshwater bryozoans in Austria

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Department of Limnology, Institute of Ecology and Conservation Biology, University of Vienna, Vienna, Austria

ABSTRACT: This survey deals with the geographical distribution of freshwater bryozoans in Austria. Nine of the ten species recorded so far belong to the class of Phylactolaemates and within this group the majority can be assigned to the Family Plumatellidae (Plumatella casmiana, P. emarginata, P. fruticosa, P. fungosa, P. repens and Hyalinella punctata). The Fredericellidae and Cristatellidae are each represented by one species (Fredericella sultana and Cristatella mucedo). However, rare freshwater bryozoans such as Lophopus crystallinus (Lophopodidae) are reported as well. The class Gymnolaemata is represented exclusively by Paludicella articulata. As freshwater bryozoans normally do not overwinter, colonies can usually only be found during a limited period of the year. In this study findings from colonies as well as from overwintering stages such as various forms of statoblasts are included and the different sampling methods will be discussed. In the case of floating statoblasts results from plankton sampling are compared with the species lists gained on the basis of collecting aufwuchs material in 23 backwaters of a Danubian riverine forest region. Non-floating resting stages were investigated through benthos sampling in the Danube River.

1 INTRODUCTION


Until recently in Austria freshwater bryozoans have never been a special target of interest; only scattered reports about the group have been published, such as on occurrence in lakes on the northern edges of the Alps (Corti 1898, Micolzéky 1912, Haemppel 1918, Brech & Rutten 1926, Zeitlinger 1928 and Foissner 1979) or in the Danube River (Lepold 1967). This might be due to the fact that in general colonies of this animal group cannot be found all year round. During unfavourable conditions, e.g. in the winter months, only resting stages such as different kinds of statoblasts and hibernaculae, can survive in the water bodies. Moreover, some species of the most common genus Plumatella are difficult to identify, if statoblasts are missing, as only the resting stages offer decisive criteria for species distinction. The variety of statoblasts can be divided into three different categories (Wöss 1996): the first group (floatoblasts) possessing a gas-filled swim-ring which enables them to float, while the two other groups are either lacking (piptoblasts) or only showing remnants of swim-rings (sessoblasts). Piptoblasts will sink in the water column after the decay of the colony, whereas sessoblasts can stick to the substrate due to an attachment apparatus on one side of their valves. While primarily intact floatoblasts are a typical component in plankton samples, different kinds of resting stages can be present in benthos samples.

In the last two decades there has been considerable research, some quantitatives on bryozoans in different biogeographical areas of Austria (Troyer-Mildner & Mildner 1987, 1992, Wöss 1989a, b, 1990, 1991, 1994-2002, Humpesch & Moog 1994, Fesl et al. 1999, Weidmair 1999). Furthermore, in some cases the determination of bryozoans have been included in standard limnological investigations of benthos samples and water quality (Butz 1985, Augustin et al. 1987, Moog & Grasser 1992, Müller 1993, Wöss 1995). This study aims at giving a general overview of the geographical distribution of the different species by gathering information from literature as well as from different databases (University of University of Natural Resources and Applied Life Sciences, Vienna; Natural History Museum Vienna and Museum of the Province of Carinthia). Additionally special focus is given to different sampling methods and the associated results.

2 METHODS

In many studies reporting species occurrence, the methods of sampling are not described in detail, but in
many cases they refer only to colony findings. The sampling methods differ if colonies or resting stages are the target of investigation. Therefore such methods will be described in the present study. The methods of sampling colonies and floating statoblasts have been applied by the author and have been used in shallow water bodies, such as in backwaters and ponds or on littoral and benthic zones of lakes to a depth of 3 m.

Colony collection took place by investigating natural substrates (submerged logs, branches, roots, aquatic plants and rocks) as well as artificial objects (e.g. plastic and styrofoam) for aufwuchs. The sampling was carried out either by wading along the shore or by working from a rubber boat and occasionally by diving. A long rake was used for thoroughly combing the bottom of the water body in search for substrates. In deeper water bodies the rake was fastened to a rope and weighted down with lead. Small pruning-shears were used for cutting the smaller branches or twigs of wooden substrates and aquatic plants, while a handsaw was used for thicker branches. In the case of massive logs or other objects, where no parts could be removed out of the water, the colonies were scratched carefully from the substrate with a knife. Colonies were either identified in the field, with the help of hand lenses or a field stereo-microscope or, in most cases, transported in water-filled 10 litre containers into the laboratory for further investigation.

Sampling of floatoblasts was usually carried out during the periods when colonies were not available (November to March). Drifting floatoblasts were collected with a modified plankton net where the gauze could be exchanged easily in the field. As statoblasts often adhere to the gauze it was necessary to change the gauze before continuing the work at a different site. Different mesh sizes from 50 µm to 300 µm were tested, but mostly the smallest mesh size was used, such as in the example discussed below.

Benthos samples were taken in the course of several projects dealing with macroinvertebrate communities of the Danube River, samples being collected at four sites, in a transect in the river, several times a year for about a decade. Quantitative sampling was carried out with a modified Peterson grab (Humpesch et al. 1990) and by a freeze-corer device (Humpesch & Niederreiter 1993). Animals were washed into a sieve (mesh size: 200 µm), hand sorted under a stereo-microscope and stored in 70% alcohol. Species were identified later on by the author based on the collected statoblasts and/or colony fragments.

### 3 RESULTS

A total of ten freshwater bryozoan species are known for Austria (Table 1). At present the total records for number of freshwater bryozoan findings in Austria is 409, but due to missing or non-comprehensible species determination the actual number of records amounts to 363. The detailed list of all localities with further parameters, such as coordinates and bioregion will be published elsewhere.

#### 3.1 Investigation area

The water bodies studied include stagnant water bodies such as lakes, natural and artificial ponds, as well as rivers and streams with backwaters in riverine forests and floodplain areas. Most of the records come from riverine forests and floodplain areas in Lower Austria (from the rivers Danube, March and Thaya) and Upper Austria (Danube River), smaller water bodies around Vienna as well as from lakes, ponds, smaller rivers and backwaters in the provinces of Carinthia, Upper Austria, Salzburg and Styria (Fig. 1).

The benthos samples of the transect in the Danube River were taken at river kilometer 1,889.9 (about 40 km east of Vienna). This part of the Danube is one of the only two stretches left free-flowing in Austria.

#### Table 1. Freshwater bryozoan species present in Austria.

<table>
<thead>
<tr>
<th>Gymnolaemata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ctenostomata</td>
</tr>
<tr>
<td>Paludicellidae</td>
</tr>
<tr>
<td><em>Paludicella articulata</em> (Ehrenberg, 1831)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Phylactolaemata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fredericellidae</td>
</tr>
<tr>
<td><em>Fredericella sultana</em> (Blumenbach, 1779)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Plumatellidae</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Plumatella casmiana Oka, 1907</em></td>
</tr>
<tr>
<td><em>Plumatella emarginata Allman, 1844</em></td>
</tr>
<tr>
<td><em>Plumatella fruticosa Allman, 1844</em></td>
</tr>
<tr>
<td><em>Plumatella fungosa</em> (Pallas, 1768)</td>
</tr>
<tr>
<td><em>Plumatella repens</em> (Linnaeus, 1758)</td>
</tr>
<tr>
<td><em>Hyalinella punctata</em> (Flancoc, 1850)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Cristatellidae</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cristatella muceda</em> Cuvier, 1789</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Lophopodidae</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lophopus crystallinus</em> (Pallas, 1768)</td>
</tr>
</tbody>
</table>

Figure 1. Sites with freshwater bryozoans in Austria. 1 = Vienna, 2 = Danube River, 3 = Salzburg and Upper Austrian region, 4 = Carinthian region.
with the flood plain areas north and south of this site belonging to the National Park Donau-March-Auen. In total, nine species were recorded; the samples contained mainly statoblasts and within this group piptoblasts were dominant, followed by various floatoblast types as well as sessoblasts. Colony fragments were also present, mostly of *F. sultana* and *P. articulata*, but fragments of *Plumatella* sp. were also found.

### 3.2 Detailed presentation of species (number of recordings in brackets)

#### 3.2.1 *Paludicella articulata* (15)
The only gymnolaemate species present in Austria is noted in a few entries in the data bases. It is recorded for stagnant bodies (Saissersee and Weissensee, two lakes in Carinthia) as well as for running water. The majority of findings have been made in the backwaters east of Vienna. In the benthos samples of the Danube River no overwintering stages (hibemaculae) have been found but fragments of colonies with protruded lophophores were recovered.

#### 3.2.2 *Fredericella sultana* (58)
*F. sultana* has only been found in Austrian lakes north of the Alps (Hallstätter See, Lunzer Untersee). There are numerous reports of occurrence in backwaters (of the rivers Danube, Emns, March and Thaya) and colonies have also be found in running water (Wöss 1994), such as in the rivers Danube and Mur. The vast majority of resting stages and colony fragments in the benthos samples of the Danube River can be assigned to *F. sultana*. As this species does not produce any floating forms of statoblasts, it is usually absent in plankton samples.

#### 3.2.3 *Plumatella casmiana* (15)
*P. casmiana* is one of the less common species of the Family Plumatellidae in Austria. It has been recorded in two lakes (Saissersee and Weberssee in Carinthia), nine smaller water bodies (mostly ponds) and it is very rare in the backwaters of the Danube riverine forests east of Vienna and in the floodplain area of the March River. It is the only species not to be found in the benthos samples of the Danube River. However, in the Laxenburg Pond *P. casmiana* has proliferated colonising artificial substrates and is the most abundant of seven bryozoan species in this pond (Wöss 2000).

#### 3.2.4 *Plumatella emarginata* (45)
This species has been recorded south of the Alpine ridge (Hafnersee and one pond in Carinthia). It is generally rare in lakes, but can be nearly as common in some riverine forests and floodplain areas as *P. fungosa* (see below), although its colonies never get as massive and dominant. *P. emarginata* is tolerant to very nutrient rich or even polluted water (such as in a waste water canal in the riverine forests of the Danube near Maria Eilend and in several fish ponds). Colonies have been recorded for the Danube River and its floatoblasts and sessoblasts are found very often in the benthos samples at the Danube transect of kilometre 1,889.9.

#### 3.2.5 *Plumatella afruticosa* (26)
This species has been predominantly found south of the Alps, in ponds, but above all in Carinthian lakes (Faakersee, Fiatschachersee, Grünsee, Hafnersee, Langsee, Magdalenensee, Rauschlesesee, Waidischsee and Weissensee), and also in Styria (Mur River area). Sometimes *P. afruticosa* is also present in sites of the riverine forests of the Danube (predominantly in Althenwörth/Grafenwörth). Here it occurs mainly in gravel ponds where it can be found on submerged macrophytes (Wöss 1991). It is quite rare in the floodplain areas of the Danube east of Vienna and has not been recorded in Upper Austria and Salzburg.

#### 3.2.6 *Plumatella fungosa* (69)
*P. fungosa* is the most abundant bryozoan in the riverine forests and floodplain areas in Austria (Wöss 1991, 1994, 2002). It often occurs in very nutrient rich water bodies and can also be found in a variety of natural and artificial stagnant water bodies, such as fish ponds. This species can typically reach enormous colony size, e.g. up to a metre long where enough substrate is available. *P. fungosa* is less frequent in lakes (Traunsee and Trümmer See north of the Alps and Egelsee, Hafnersee and Seiser See south of the Alpine ridge), but in summary it is the most prominent bryozoan species in Austria.

#### 3.2.7 *Plumatella repens* (65)
*P. repens* is the most abundant species of Bryozoa in Carinthia and it occurs in a great variety of water body types. *P. repens* is found in lakes (Afritzer See, Fiatschacher See, Grünsee, Hafnersee, Langsee, Magdalenensee, Maltaeschacher See, Ossiacher See, Seiser See, Weberssee in the south of the Alps and Zellsee in the north as well as in ponds and is also common in the riverine forests of rivers, although it is never as abundant in backwaters as is *P. fungosa*.

#### 3.2.8 *Hyalineellapunctata* (23)
The majority of the sites containing this only gelatinous species of the Family Plumatellidae are stagnant water bodies. *H. punctata* has not been recorded in lakes in the north of the Alps, but occurs in the Sonneggersee and the Ossiacher See in Carinthia. It is recorded in a smaller number of ponds and in several backwaters of the Danube River, mainly east of Vienna.

#### 3.2.9 *Cristatella mucrode* (45)
*C. mucrode* is often recorded in Alpine lakes (Traunsee, Wallersee, Fuschlseee and Lunzer Untersee in the north and Hafnersee, Magdalenensee, Saissersee
and Grünsee in the south of the Alpine ridge). Furthermore, this species is present in a great number of smaller water bodies in riverine forests and floodplain areas, with higher abundance in nutrient poor sites, such as gravel ponds (Danube backwaters of Althenwörth/Grafenwörth and east of Vienna). The presence of colonies is often limited to a shorter period of the year than other species, but then, however, colonies can occur in enormous abundances (Foissner 1979, Wöss 2002). In the Laxenburg Pond which has been regularly monitored since 1991, it was not detected until summer 2001.

3.2.10 Lophopus crystallinus (2)
Colonies of this species, which is generally described as being very rare, can only be recorded in one locality, the Pommersee, a backwater in the floodplain area of the March River. The Pommersee, a shallow water body, is characterised by high fluctuations in water level and can dry out during the summer months. L. crystallinus has been found repeatedly at this site since 1992, but is characterised by erratic occurrences. Significantly, this species has now been recorded a second time in Austria: floatoblasts were discovered in benthos samples from the Danube River.

3.3 Comparison of two collecting methodologies
A direct comparison of two sampling methods, the collecting of colonies and of floatoblasts, is given in Figure 2. During summer 1986 a survey of 23 backwaters in the riverine forests of Althenwörth/ Grafenwörth (Danubian region 35 km west of Vienna) revealed seven bryozoan species. When the monitoring of the water bodies was continued in November of that year in search for floatoblasts, the results showed a correspondence between 22% and 100% in the different species (Wöss 1989a, 1991). This leads to an average concordance of 70% regarding the six bryozoans that produce floatile statoblasts (F. sultana, which also occurred in the summer sampling, is excluded from the study as it only produces piptoblasts). A test of different mesh sizes showed no significant differences in the results.

4 CONCLUSIONS
The results show a clustered aggregation of findings in some regions which is artificial, as many regions in Austria have never been searched for freshwater bryozoans. Information from certain types of water bodies, such as the more alkaline water bodies in the very east.
of Austria (e.g. Neusiedlersee and the lakes of the Seewinkel, Burgenland) is missing as well as reports of the bryozoan fauna of Alpine lakes in high regions is lacking - in contrast to the situation in Switzerland (Zschokke 1900). Species of smaller zooid size, such as the only gymnolaemate bryozoan *P. articulata*, show fewer entries in data bases, which could also mean that they have been overlooked. In general, the occurrence of *P. articulata* and *F. sultana* might be underestimated, as they are often found in greater depths (Zschokke 1906, Wäss 1996) and require diving and investigation of the benthic zone. Furthermore, both species do not produce floatable asexual propagation stages which could be traced in plankton samples. Nevertheless the dominant role of species like *P. fungosa* (backwaters and eutrophic ponds), *P. repens* (mainly various stagnant water body types) and *F. sultana* (various stagnant and running water body types) remains unquestioned.

Additional remarks have to be made to the results achieved by investigation of plankton and benthos samples. In the latter case, in contrast to former results where only *P. repens* (Liepold 1967) and colonies of *P. emarginata* and *F. sultana* (Wäss 1989b) had been mentioned for the Danube River, all Austrian freshwater bryozoans with the exception of *P. casmiana* could be verified, at least by statoblasts. However, the occurrence of many of these species will be interpreted as allochthon, e.g. being brought in by floods from the neighbouring backwaters. In the case of the very rare bryozoan *L. crystallinus* this leads to the conclusion that it may possibly be found in a further floodplain area at Stopfenreuth. For *P. articulata*, however, an actual occurrence in the river seems very probable, as the benthos samples contained colony fragments with living zooids. Furthermore, this species is reported for one site in the Hungarian and two sites in the Slovakian stretch of the Danube (Péce & Erdelics 1970).

Comparing species lists obtained by plankton sampling with investigations of aufwuchs on substrates can result in a more extensive bryozoan list, but the reverse could also be true. Additional statoblasts can be brought in by water birds, on the other hand species without floatable resting stages will be represented less often. As a conclusion, if colony sampling is not possible, it is recommended to combine plankton with benthos sampling, as also suggested by Jones et al. (2000). Otherwise, benthos sampling is more reliable as it provides a higher probability to include all types of statoblasts and even fragments of colonies.

ACKNOWLEDGEMENTS

I thank Univ.-Prof. Dr O. Moog and Dr A. Schmidtkloiber (both University of University of Natural Resources and Applied Life Sciences, Vienna), Mag. J. Troyer-Mildner (Museum of the Province of Carinthia), Dr E. Aescht (Biology Centre of the Museum of Upper Austria) and Dr H. Sattmann (Natural History Museum, Vienna) for providing of databases and references.

REFERENCES


A bryozoan fauna from the Carboniferous (Mississippian, Late Viséan) of the Velbert Anticline, Germany

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ABSTRACT: During a recent assessment of the geological and scientific importance of a construction site at Velbert in the Rhenish Massif in Germany, a Lower Carboniferous (Late Viséan) fauna was recovered. Situated in the north-north-east portion of the Velbert Anticline, this section exposes shallow water limestones that indigitate with deeper water shales typical of Culm facies. The limestone displays small karstic features; within one small cavity loose debris lined the floor. On microscopic examination this material was found to comprise a highly diverse and exceptionally preserved silicified microfauna. The fauna contains twelve to fifteen foraminifera genera which include textulariids with preserved foramina. Over six hundred ostracod valves were recovered that belong to as many as twenty genera. Rare juvenile trilobites, gastropods and bivalves are also present, as are sponge spicules and calcareous algae. The bryozoans are diverse and beautifully preserved. Delicate cryptostomes include the taxa *Pseudonematopora* and *Nematopora*, fenestrate genera include the distinctive *Rhombocladia* and *Thammiscus*, numerous fenestellids including *Fenestella s.l.frutex*, and smaller pinnate forms including *Diploporaria, Baculopora* and *Penniretepora*. Cystoporates are rare, as are trepostomes which usually form small adnate or ramose expansions. A number of delicate cryptostomes may represent new genera. This fauna which includes ostracods of a mixed fauna (including some typical of the Thuringian ecotype), shows most similarities with that described from the Glencar Limestone of north-west Ireland which is of similar Viséan age.

1 INTRODUCTION

During a recent assessment of the geological and scientific importance of a construction site at Velbert in the Rhenish Massif in Germany, a Lower Carboniferous (Late Viséan) fauna was recovered by one of the authors (HMW). Situated in the north-north-east portion of the Velbert Anticline, this section exposes shallow water limestones that indigitate with deeper water shales typical of Culm facies. The limestone displays small karstic features; within one small cavity loose debris lines the floor. On microscopic examination this material was found to comprise a highly diverse and exceptionally preserved silicified microfauna (Weber 2002, 2003). The ostracods are of a mixed fauna: some are characteristic of the rare Thuringian ecotype (or ecofacies or biofacies) (Becker in Bändel & Becker 1975), while other genera are more typical of a shallow-water association in which the Hollinacea are rare but the Kirkbyacea are diverse. The Thuringian facies ranges in age from Ordovician to Lower Carboniferous, has been found in parts of Western Europe and Asia, contains exceptionally well preserved silicified faunas and floras, and is considered to be indicative of low-energy environments (Becker & Bless 1990). Carboniferous bryozoans in Germany have not been extensively studied and only a small number of papers has been published (Nekhoroshev 1932, Ernst this volume).

This paper describes the geological setting of the limestones, illustrates and comments on the bryozoans that they contain, and compares the faunal composition with other faunas of a similar age found elsewhere. A full taxonomic account of the bryozoan fauna will appear elsewhere.

2 GEOLOGICAL SETTING

In the northern part of the Rhenish Massif - situated in Nordrhein-Westfalen in west central Germany - especially along the north eastern flank of the Velbert Anticline are found shallow-water Mississippian, Lower Carboniferous limestones (Kohlenkalk-Facies)
that interdigitate with deeper water lithologies (Culm-Facies) (Franke et al. 1975). Massive limestone layers (up to 1.40 m in thickness), are common. Only very few are definitely authochtonous (the supposed ‘cre/ji’s/ri/a-limestone’ in the Culm-facies) and most of the others are detrital limestones which contain large intraclasts, pelmatozoan fragments (columnnals up to 2.5 cm in diameter), few corals and brachiopods (large products). Silicified limestones, layers with cherts, alum and silicified shales with several phosphorite pebble horizons and supposed bentonite layers are also common.

In the industrial area of Velbert-Röbbeck, south of Essen, an exposed section about 20 m in thickness in a construction site (Gauss-Krüger-Coordinates: TK 25 Sheet 4608 Velbert R 2574530 and H 5691370) was found to be highly fossiliferous. Within a 28 cm thick limestone a small cave of about 5 cm high, 8-10cm wide, and 25 cm long was located about 2 m above the base of the section. This cave contains a dark to brownish weathered ‘sand’ or residue which yielded all of the bryozoans described here. Palaeontological evidence (see below) suggests that this limestone is Late Viséan (V3b) in age. The top of the section consists of a reddish-brown, completely weathered silicified limestone, and is upper latest Viséan in age (V3c; Brigantian; Rugose-coral-zone RC 8 after Conil et al. (1990: 26), Poty (1993: 142) indicated by a rugose coral fauna with numerous colonies (Actinocyathus, Aulophyllum, Lithostroton, and ‘Orionastraea’).

A comparison with other outcrops in the adjacent area of the Velbert Anticline is not possible at the moment. Even in the old quarry at Sondern (= Plöger Quarry), which is situated about 400-500 m to the north west, the Upper Viséan horizons were either missing or not well exposed (Paul 1937: 56 ff., 1938: 197 ff., Böger 1962: 143 ff., Conil & Paproth 1968: 61 ff). Weyer (2001: 61) gives some data about a lost Quarry), which is situated about 400-500 m to the south east of Velbert) where a construction site (Gauss-Krüger-Coordinates: TK 25 Sheet 4608 Velbert R 2574530 and H 5691370) was found to be highly fossiliferous. Within a 28 cm thick limestone a small cave of about 5 cm high, 8-10cm wide, and 25 cm long was located about 2 m above the base of the section. This cave contains a dark to brownish weathered ‘sand’ or residue which yielded all of the bryozoans described here. Palaeontological evidence (see below) suggests that this limestone is Late Viséan (V3b) in age. The top of the section consists of a reddish-brown, completely weathered silicified limestone, and is upper latest Viséan in age (V3c; Brigantian; Rugose-coral-zone RC 8 after Conil et al. (1990: 26), Poty (1993: 142) indicated by a rugose coral fauna with numerous colonies (Actinocyathus, Aulophyllum, Lithostroton, and ‘Orionastraea’).

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Comparison with the typical Kulm sediments from Aprath on the southern flank of the Velbert Anticline may prove more possible, as greater detail is known of the geology of this area (Thomas 1992).

3 MATERIAL

During the first examination of the in situ residue that lined the cave floor, a single bryozoan fragment was noticed and the material looked largely unfossiliferous. Nevertheless a small volume of residue was collected and when washed and examined under a binocular microscope, revealed an extraordinarily well-preserved silicified microfossil fauna. While this fauna is very diverse it does not contain any echinoderms. All figured specimens are deposited in the Ruhrlandmuseum Essen in Germany under the accession numbers: RE 551.735.100 A 2053 to RE 551.735.100 A 2079.

4 COMPONENTS OF THE VELBERT-RÖBBECK FAUNA

The residue collected from the cave at Velbert-Röbbeck was generally rich in ostracods, trilobites and foraminifera with juvenile trilobites, gastropods, bivalves, sponges, rare fish teeth and conodonts, some macroplant material and calcareous algae are also present. Bryozoans are common, but until now have been largely ignored, except in the paper by Nekhoroshev (1932) who noted some bryozoans from the Velbert anticline.

4.1 Bryozoans

As many as twenty-one genera contained in four stenolaemate orders are represented in the Velbert-Röbbeck fauna (Table 1). Fenestrates and cryptostomes dominate the fauna, which is highly fragmented. Most colony fragments are tiny, and are beautifully preserved (Figs 1 and 2) and acanthostyles are readily seen particularly in the cryptostomes. Holdfast structures of some fenestrates are also present. In some cases the external zoarial walls of colonies have been lost and details of the internal chambers can be observed (Fig. 2E). Fenestrate genera include the distinctive Rhombocladia (Fig. 1L-M) with its semicircular growth lines on reverse surfaces (Fig. 1M) and Thamniscus (Fig. IK), numerous fenestellids (Fig. 1G-I) including Minilyla, Fenestella s.l. frutex M’Coy 1844, and smaller pinnate forms (Fig. 1A-F) including Diploporaria, Baculopora and Penirettopora. In Diploporaria marginalis (Young & Young, 1875) short lateral spines are associated with autozoocia (Fig. IB) while in some Penirettopora colonies lateral branch growth is not regular along the length of branches. While short lateral branches develop at regular intervals most remain stunted, and only a few develop into secondary branches that resemble the primary branch and carry tertiary branches (Fig. IE). Delicate cryptostomes (Fig. 2A-N) include Pseudonematopora and Nematopora, and the more robust Rhabdomeson, Rhombopora, Hyphasmopora and Clausotrypa. Cystoporates are rare but include some small button-shaped Fistulipora colonies and the rarer Hinacelma. Trepostomes too are infrequent (Fig. 20, R) and
Table 1. Bryozoans from Velbert-Röbbeck.

<table>
<thead>
<tr>
<th>Order Fenesterida</th>
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<tbody>
<tr>
<td>Acanthocladiidae</td>
</tr>
<tr>
<td>Diploporaria marginalis (Young &amp; Young, 1875)</td>
</tr>
<tr>
<td>Diploporaria tenella Wyse Jackson, 1988</td>
</tr>
<tr>
<td>Bacuiopora megastoma (M'Coy, 1844)</td>
</tr>
<tr>
<td>Penniretpora ssp.</td>
</tr>
<tr>
<td>Thamniscus colei Wyse Jackson, 1988</td>
</tr>
<tr>
<td>Fenestellidae</td>
</tr>
<tr>
<td>Fenestella s.l. frutex M'Coy, 1844</td>
</tr>
<tr>
<td>Fenestella s.l. ssp</td>
</tr>
<tr>
<td>Minilya sp.</td>
</tr>
<tr>
<td>Rhombocladia sp.</td>
</tr>
<tr>
<td>Order Cryptostomida</td>
</tr>
<tr>
<td>Arthrostylid indet.</td>
</tr>
<tr>
<td>Plexites sp.</td>
</tr>
<tr>
<td>Nematopora sp.</td>
</tr>
<tr>
<td>Pseudonematopora sp.</td>
</tr>
<tr>
<td>Rhabdomeson sp.</td>
</tr>
<tr>
<td>Rhabdomeson rhombiferum (Phillips, 1836)</td>
</tr>
<tr>
<td>ISaffordo taxis sp.</td>
</tr>
<tr>
<td>Rhombopora sp.</td>
</tr>
<tr>
<td>Hyphasmopora sp.</td>
</tr>
<tr>
<td>Clausotrypa sp.</td>
</tr>
<tr>
<td>Order Cystoporida</td>
</tr>
<tr>
<td>Eridopora sp.</td>
</tr>
<tr>
<td>Fistulipora sp.</td>
</tr>
<tr>
<td>Hinaclema sp.</td>
</tr>
<tr>
<td>Order Trepostomida</td>
</tr>
<tr>
<td>Pleioclema sp.</td>
</tr>
<tr>
<td>Tabulipora howsii (Nicholson, 1881)</td>
</tr>
</tbody>
</table>

include Tabulipora which usually forms small adnate expansions. At least one delicate cryptostome may represent a new genus (Fig. 2A-B). In this case the zoarium is quadrate in cross-section, with autozooidal apertures emerging from distally situated flange-like peristomes. Unusual features such as overgrowths are present - these may be either colony growth over a possible parasitic organism (see Figs 2L and 2N) or produced by encrustation around an algal stipe (Fig. 2R). Ovicell-like expansions in dendroid cryptostomes are also present (Fig. 2J); it is unclear if these are actual brooding structures and they require further study.

4.2 Other groups represented in the cave residue

Foraminifera: Nearly 2,500 biserial, endothyrid, and unilocular foraminifera specimens have been recovered. Some textulariids present with preserved foramina. Genera present: Tetrataxis and Valvulinella and c. 20-25 other genera.

Ostracoda: Common, with over six hundred ostracod valves recovered; about 25-30 genera including different Palaeocopida, especially Kirkbyacea (including Amphissites, Kellettina and Aurikirkbya), and a lot of Podocopida (including Healdia, Rectonaria, Praepilatina, Acratia and Tricornina).

Trilobita: Fragmentary, with rare juveniles including three dimensional hypostomes, cranidia and other portions of the exoskeleton.

Gastropoda: Rare indeterminate specimens.

Bivalvia: Aviculopecten and unidentified juvenile.

Rostracoconchia: Rare with some very small Conocardium valves, and several juveniles.

Brachiopoda: Only very few fragments. From the whole section large products, small rhynchonellids, and few spiriferids are known. None identified.

Porifera: Rare Chaetetes and sponge spicules.

Microproblematica: Three-dimensional and silicified forms of Eotuberitina (formerly considered to be a foraminiferan) and a small conical shell, possibly a tentaculite.

Conodonta: Only one complete specimen of Gnathodus ex gr. bilineatus.

Calcareous algae: Well preserved three-dimensional branches of Koninckopora were isolated.

4.3 Additional faunas from the section at Velbert-Röbbeck

Trilobita: Only Brachymetopus, Belgibole, Cummingella, and Archegonus.

Cephalopoda: Although no cephalopods were recovered from within the cave, approximately two metres below the silicified coral horizon, below the top of the section a small Arnsbergites (D. Korn, pers. comm. 2002) was found. Another two or three metres further below this horizon are two goniatite bands which contained Goniatites cf. hudsoni (D. Korn, pers. comm.). The lower horizon could represent the 'cristiastrea-limestone', which if correct, would be the first example of such a lithology in the Velbert Anticline (see Mestermann 1998). In one of the phosphorite pebble layers few fragments of very small goniatites have been found. One orthoconic cephalopod was recovered from the middle part of the section.

Gastropoda: Platyzona cf. goepperti and non-identified species of the groups Euomphalidae and 'Straparollus' (M. Amler, pers. comm.).

Bivalvia: Euchondria cf. aprathensis and Cypriocardina bistriata.

Corals: Numerous corals (Rugosa, Tabulata, and Heterocorals) have been found at several levels of this section. Silicified colonies of Actinocyathus, Lithostrotion and possibly the first record of 'Orionastrea' at the top of the section date the section to the upper part of the Viséan (V3c following the Belgian subdivisions). Solitary rugose corals such as Palaeosmilia are also
Figure 1. Carboniferous (Late Viséan) bryozoans of the Velbert Anticline, north east Germany. Order Fenestrida. A, Baculopora megastoma (M’Coy, 1844) [A 2053], B, Diploporaria marginalis (Young & Young, 1875) [A 2054], C, Diploporaria tenella Wyse Jackson, 1988 [A 2055]. D-F, Penniretpora sp. [D: A 2056, E: A 2057, F: A 2058]. G, Fenestellid holdfast [A 2059], H, Fenestella s.l. sp. [A 2060]. I, Fenestella s.l. frutex M’Coy, 1844 [A 2061], J, Minilya sp. [A 2062]. K, Thamniscus colei Wyse Jackson, 1988 [A 2063]. L-M, Rhombocladia sp.; L, obverse surface [A 2064]; M, reverse surface [A 2065]. All scale bars 300 p.m. Specimen numbers in square brackets are prefixed with RE 551.735.100.
present, as are many other genera. *Michelinia*, *Syringopora-group*, *Cladocochus* comprise the tabulates, and *Heterophyllia* and *Hexaphyllia* the heterocorals. One silicified and three-dimensional *Hexaphyllia* representing an early ontogenetic stage with two whorls of four spines was recovered from the cave. This is very similar to an example described by Cossey (1997). This section has yielded the largest number and most diverse fauna of Lower Carboniferous corals in Germany; for example in the last 150 years, only 5-7 rugose coral colonies have been found in the whole of the Velbert anticline - 35-40 were collected during this project.

**Vertebrata:** Rare *Orodus* (shark) and *Petalodus*, cladodontids and *Istiodamus* are present in the section.

**Macro-plants:** One horizon in the middle part of the section contained well preserved, large plant fragments up to 40 cm long (possibly *Calamites*) together with coaly wood in which the microstructure was intact.

### 5 COMPARISON WITH OTHER BRYOZOAN FAUNAS

The unusual Thuringian ecotype fauna which spans from the Ordovician (Melnikova 2000) to Lower Carboniferous has been noted from various parts of Europe (including north west Spain (Becker 1977), Montagne Noire, central southern France (Casier et al. 2001, 2002), Germany (Becker 1999), and Poland), northern Africa (Becker 1987), and Asia (Melnikova 2000). To date most work has been focussed on the bryozoan component of this rare fauna and flora. We are grateful to Dr Markus Aretz (University of Cologne) who suggested that the authors collaborate on the bryozoan component of this rare fauna and flora. He also transported the specimens to Dublin for study. Dr Andrej Ernst (Kiel) and Dr Ken McKinney (Boone) commented on aspects of the fauna, while Dr Mags Duncan (TCD) noticed the similarity of this fauna with those from various horizons in the Dinantian of Ireland, as well as kindly providing much information.

**ACKNOWLEDGEMENTS**

We are grateful to Dr Markus Aretz (University of Cologne) who suggested that the authors collaborate on the bryozoan component of this rare fauna and flora.


A bryozoan and foraminifera association from the Miocene of Podbrezice, south Moravia (Czech Republic): an environmental history

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Katarina Holcová
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ABSTRACT: The Miocene locality Podbrezice has yielded a rich fauna of 103 bryozoan species. The precise biostratigraphy allow jointed two separated profiles to one sedimentation sequence. According to a foraminiferal study performed on each distinguishable layer the development of environments have been proposed. The bryozoan marls were deposited during cool period of subtropical climate, on deeper water than bryozoan limestone. The extreme warm and high-energy seawater environment was suggested for deposition of limestone contains almost only Celleporids colonies.

1 INTRODUCTION

Bryozoans are common components of Cenozoic faunas in sediments of south Moravia, but bryozoan-dominated sediments are generally very rare. Bryozoan-dominated sediments are mostly sandstone to micro-conglomerate but only in few localities bryozoans created true limestone buildups. There are at least two different types of bryozoan buildups: the first formed in normal sea conditions usually during Early Miocene, the second type developed in brackish conditions during Late Miocene. The main difference between these two types of buildups is the diversity of bryozoan species. In the first usually more than 50 species of bryozoans can be distinguished, while the brackish bioherms are formed usually of one bryozoan species Cryptosula terebrata (Sinzov, 1892) and by serpulids.

During our research for project FWF P 15600, we focused on Moravian Miocene localities, where bryozoans are very common. We visited 16 localities in south Moravia an attempt to find bryozoan bioherms. Detailed studies aimed to locate sections that showed a dominance of Bryozoa, and where bryozoan associations showed changes in composition during time. The ideal locality seems to be Podbrezice, where we found limestone buildup formed by bryozoans colonies overlay by bryozoan marl and clay.

The study of bryozoan assemblages was accompanied by a detailed quantitative analysis of foraminiferal and calcareous nannoplankton assemblages. These micro- and nannofossils enable precise biostratigraphical correlation of localities. Composition of bryozoan assemblages and a comparison with foraminiferal assemblages could help explain paleoecological requirements of some bryozoan taxa.

2 THE LOCALITY OF PODBREZICE

The locality of Podbrezice is situated around the village with the same name, about 5 km south-east from the village of Rousinov (Brno district). There are two crops with different sediments and faunal content. The first outcrop occurs in bryozoan marls is situated on the eastern margin of the village of Podbrezice (GPS position 49°12;909 N and 016°55;579 E); the second profile is represented by limestone build-ups with bryozoan framework that occurs on a southern slope of a small hill about 2 km south of the village Podbrezice (GPS position 49°12;692 N and 016°55;870 E). Sketch of the localities is given in Figure 1.
a large manuscript was deposited in the archive of Masaryk University Brno (Sváček 1995).

The section at Podbrezice village is situated in an outcrop in the local rubbish dump and is about 3 m high. There is no visible stratification in the profile where three samples (Pv-1, Pv-2 and Pv-3) were collected from bottom to the top of the outcrop (Fig. 2). The samples were washed and studied for occurrence of Foraminifera and Bryozoa. Calcareous nannoplankton was studied from slides.

2.2 Podbrezice build-up

The Podbrezice build-up was first time mentioned by Vlach (1974), who described 15 species of bryozoans. Subsequently, Novák (1975) determined 18 bryozoan species, but described none. Unfortunately both of these papers remain unpublished; one published note about this locality is Hladilová & Zdraziková (1989), who did not determine or described any Bryozoa. From 1992 the build-up is protected paleontological locality.

The bryozoan build-up in Podbrezice is more than 6 m high and can be divided into ten horizons (Fig. 2). Five of them (P-1, P-3, P-5, P-7 and P-8), which make up the bioherm itself, are massive (thickness from 60
were studied. Histograms of size distribution of tests of the video system. About 100 specimens from each sample was collected, from layer P-7a we were unable to take a washable sample (the layer is too thin) and the layers P-1 and P-8 are too thick, so we take two samples P-8a and P-8b. All the samples were for occurrence of calcareous nannoplankton, Foraminifera and Bryozoa. Positions of the samples are given on Figure 2.

3 METHODS

Bryozoans from limestone layers were studied from acetic acid treatment residues as described in Zágorsek & Vávra (2000). Usual time for treatment was 5-6 weeks. The samples from marl layers were only washed and sieved as usual, rarely using so-called “laboratory weathering” (details see Zágorsek & Vávra, 2000). The minimum size of studied specimens was 0.09 mm.

Bryozoans were studied and documented through SEM Jeol type JSM-6400 and prints have been produced in University of Vienna. Foraminiferal assemblages were analyzed from washed residues using sieved fractions 0.063-2 mm. Altogether 103 bryozoan species were determined and documented from the whole profile in Podbrezice Village (Table 1).

Taphonomical analysis of foraminiferal assemblages included analysis of size sorting of tests. The greatest diameter of rounded tests were measured using a VIA microanalyzer. The method of taphonomical analysis was described in detail by Holcová (1996).

BMDP software (Dixon 1993) was used for multivariate statistical analysis of foraminiferal as well as aggrading bryozoan assemblages. Palaeoecological interpretation of foraminiferal assemblages was based on actuocenologic data (Pfleger 1965, Boltovskoy & Wright 1976, Murray 1973, 1991, Reiss & Hottinger 1984), calcareous nannoplankton were studied in a standard way using an optical microscope.

RESULTS

Biostratigraphy

Both sections (Podbrezice village and Podbrezice build-up) can be correlated with Langhian standard biozones M6 Globorotalia peripheroronda (planktonic Foraminifera, Berggren et al. 1995) and NN5 (calcareous nannoplankton. Martini 1971). The interval corresponds to the Lower Badenian in the local Central Paratethys stratigraphy (Rögl 1998) (Fig. 3).

Stratigraphical ranges of the planktonic foraminiferal species described for the Central Paratethys (Cicha et al. 1998) enable precise biostratigraphical correlation of studied profiles. Figure 3 summarized abundances of stratigraphically significant taxa. The section Podbrezice build-up with Globigerinoides bisphericus (Todd, 1954, Praeorbulina glomerosa Blow, 1956) and sporadic occurrence of Orbulina suturalis (Bronnimann, 1951) can be correlated with lower part of the Lower Badenian. Disappearing of G. bisphericus, Todd, Praeorbulina and common occurrence of Orbulina suturalis (Bronnimann) in the section Podbrezice village are characteristic for the upper part of the Lower Badenian. Therefore the studied sections can be summarized into the one profile (Fig. 2), when the lower part is represented by the section Podbrezice build-up (layers P-1 to P-8) and upper part is represented by section Podbrezice village (sample PV-1 to Pv-3).

From benthic foraminifers, the occurrence of the endemic Paratethyan species Uvigerina macrocarinata (Papp & Tumowski, 1953) confirms a Lower Badenian age of the profile (Cicha et al. 1983, 1998).
Figure 3. Biostratigraphical correlation of section at Podbrezice based on planktonic foraminifers.

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Beck determined (Table 1). Other faunal elements are more abundant than in the lower part of the profile and are represented mainly by molluscs and echinoderms, only rare fragments of brachiopods and Balanus (Cirripedia) were found.

The diversity of Bryozoa increases from the layer P-1 up to the layer P-6, where 49 species were determined. Than, the diversity rapidly decrease and again increase on the marls sediment in the samples Pv-1 and Pv-3 (Fig. 4). The composition of the fauna was however different: cyclostomatous Bryozoa with erect growth forms and cheilostomatous with encrusting colonies dominated in the layers P-1 to P-6, erect and large cheilostomatous colonies dominated in samples Pv-1 to Pv-3 and flexible and fenestrate erect growth forms are more abundant in layers P-6 and samples Pv-1 and Pv-3 than in other samples (Fig. 4). On the basis of bryozoan diversity we can separate also the middle part of the profile, which is characterized by large quantity of Celleporid bryozoans with lower diversity of other forms of bryozoans (layers P-7 and P-8).

4.3 Foraminifera! assemblage

Totally, 81 of benthic and 16 of planktonic foraminiferal species were determined. In individual samples, numbers of benthic species vary from 17 to 51, lower numbers are in the lower part of the profile (17-33 species), higher in the upper part of the profile (37-51 species). The abundance of foraminifers are high with exception of samples from the lower part (samples P-la, P-lb) and middle part (sample P-s) of the profile.
Abundance of planktonic taxa (expressed as P/B ratio) is low in limestones (to 10%), higher in pelitic intercalation as well as in upper part of the profile (15-30%).

In assemblages, significantly prevailed *Asterigerinata planorbis* (d’Orbigny, 1846), which represents 16-50% in the lower part of the profile and about 10% in upper part. Pelitic intercalations and the upper part of the profile contain diversified foraminiferal assemblages with high abundance of foraminifers and higher P/B-ratio. Assemblages with high relative abundances of *Asterigerinata planorbis* (d’Orbigny) and *Elphidium* spp. are characterized by low values of P/B-ratio. Those assemblages occur in the limestones.

Taphonomical analysis based on size sorting of foraminiferal tests (Fig. 5) and their preservation enabled us to distinguished three types of assemblages:

1. Assemblages without any mark of postmortem transport (Fig. 5A). The assemblages occur in samples from limestone from lower part of the profile (samples P-1 a to P-5) and in the upper part of the profile (Pv samples) and can be characterized as indigenous assemblages.

2. Assemblages with abraded and corroded tests and with missing small-sized tests (samples P-8a, P-8b and P-7). The assemblages contain both large abraded tests as well as well preserved, size unsorted tests and can be characterized as bedload-transported assemblages (Fig. 5B).

3. Assemblages with small-sized, well size-sorted tests (samples from marls P-6, P-4 and P-2) can be characterized as suspension-transported (Fig. 5C).

4.4 *Calcareous nannoplankton*

Twenty-six calcareous nannoplankton species were determined from the section Podbrezice. *Reticulofenestra minuta* Roth, 1970 (20-80% of assemblages) and *Coccolithus pelagicus* (Wallich, 1871) Schiller, 1930 (5-50% of assemblages) significantly prevailed in assemblages. From the stratigraphically significant taxa, *Sphenolithus heteromorphus* Deflandre, 1953 and *Helicosphaera walbersdorfensis* Muller, 1974 occur, but planktonic foraminifers enable more precise stratigraphical correlation (see above). Reworked Cretaceous, Eocene and Oligocene to lowermost Miocene taxa occur dispersed in the whole section.

4.5 *Multivariate statistical analysis of foraminiferal and bryozoan assemblages*

Foraminiferal and bryozoan assemblages were analysed using standard methods of multivariate statistics: cluster and factor analysis (Dixon, 1993).

For foraminiferal assemblages, only factor analysis gave a satisfactory result and enabled to cluster the assemblages into three groups (Fig. 6): Assemblages...
from limestones represent the first group. The second group is more dispersed and includes samples from pelitic intercalations from the lower part of the section. The third group contains samples from the upper part of the section.

The factor analysis of bryozoan assemblages yielded slightly different results (Fig. 6). The first group includes samples from the lower part of the section with the exception of sample P-1b, which is substantially different. The cluster analysis, however, separated also samples P-2 and P-6 (from pelites), which is paralleled by foraminifers. Samples from the upper part of the section (samples Pv-1 to Pv-3) are clustered to the second group. Sample P-7 lies between groups 1 and 2.

Grouping of bryozoan assemblages slightly differs from foraminiferal ones; however, the combination of factor and cluster analyses provided comparable results.
5 INTERPRETATIONS

5.1 Paleoecology: Foraminifera vs. Bryozoa

A detailed paleoecological analysis of foraminiferal assemblages enables to interpret the paleoenvironment of deposition of the bryozoan sediment. These paleo-bathymetric and paleoclimatic interpretations were compared with changes of bryozoan assemblages. The main goal is to find particular bryozoan association indicating a specific paleoenvironment.

(1) Generally, foraminiferal assemblages from the Podbrezice build-up (lower part of the studied section, layers P-1 to P-8) required stenohaline, well aerated, shallow-water environment (first tens of metres) (Boltovskoy & Wright 1976, Murray 1973, 1991 Reiss & Hottinger 1984, Spezzaferri & Coric, 2001). This agrees with the conclusions of Novák (1975) who proposed the palaeoenvironment for the lower part of the studied profile as shallow water with normal marine conditions.

(2) Cyclical changes in foraminiferal assemblages in the lower part of the section correlated with the alternation of limestones (layers P-1, P-3 and P-5) and pelites (layers P-2, P-4 and P-6). Indigenous assemblages dominated by shallow-water, epiphytic taxa were recorded in the limestones. Pelites are characterized by suspension-transported, open-marine foraminiferal tests mixed with indigenous, shallow-water associations. Cyclical changes may be caused by short-term climatic oscillations: humid intervals with higher input of terrigenous material can result in the deposition of pelites (for example, layers P-4 and P-6). This corresponds with the occurrence of suspension-transported tests, which can be connected with storm events. Limestone layers were formed during dry periods with low terrigenous input (layers P-7 or P-8, respectively).

These short-time climatic oscillations (humid/dry climate) influenced the postmortem transport of foraminiferal assemblages, which substantially changed their composition. The bryozoan colonies are much larger than foraminiferal tests and can be hardly transported in suspension. Therefore, these oscillations were not observed in bryozoan assemblages.

On the other hand, the dominance of cyclostomatous bryozoans in samples P-1a to P-3 and the dominance of erect flexible and celleporid bryozoans in samples P-3 to P-6 cannot be explained by changes in foraminiferal assemblages. According to McKinney & Jackson (1989) this change can be interpreted as an increase in water energy and/or succession of development of the bryozoan assemblages (cyclostomatous Bryozoa represented a rather pioneer association, while erect flexible and celleporid bryozoans developed subsequently).

(3) Changes in the relative abundances of cool- and warm-water indicators among planktonic foraminifers (Spezzaferri 1995) indicate warming during the deposition of the studied sediment (Fig. 7). A major change occurs between layers P-6 and P-7 and subsequent layers P-1 to P-3. Also the relative abundances of large foraminifers increase as other indicators of warm water (Fig. 7). This warming can be correlated with the global one, which was described from the base of the Langhian (Haq 1980). The Central Paratethys Basin was covered by tropical-subtropical waters of Indo-Pacific origin which penetrated here during the reopened Mediterranean - Indo-Pacific seaway in the Badenian (Rögl 1998).

The most diversified bryozoan association occurs in layer P-6, which perhaps represents the longest humid period. It can be assumed that bryozoans generally dominated in a cooler and more humid environment with large input of terrigenous material.

Figure 7. Climatic curve based on ratio of cool- and warm-water indicators among planktonic foraminifers. Sorting of planktonic foraminifers on warm-water and cool-water indicators follows Spezzaferri 1995.
the wave base during the deposition of the upper part of the lower section (layers P-7 and P-8).

The transition from low- to high-energy environments and from cool to warm water in layers P-7 and P-8 is characterized by the dominance of large colonies of *Cellepora* and a decrease in the diversity of smaller bryozoan colonies. This change is proved by a higher proportion of flexible erect forms (like *Cellaria fistulosa*), which flourished in a higher water-energy environment (McKinney & Jackson 1989).

The upper part of the section (samples Pv-1 to Pv-3) was deposited in a deeper-water environment (50-100 m), and was stenohaline and well aerated. Deepening of the depositional area between layers from the build-up of the Podbrezice locality (P-1 to P-8) and Podbrezice village (Pv-1 to Pv-3) is characterized by the dominance of big erect rigid bryozoan colonies at the Podbrezice village. Such colonies are frequent in the deeper part of the Recent Atlantic Ocean (McKinney & Jackson 1989). In shallow environments, they indicate cooling of waters in the sedimentary basin (Zágorsek 1996).

Long-time warming cannot be observed on bryozoan assemblages in samples Pv-1 to Pv-3. Warming, connected with deepening of the environment in the analysed section, was interpreted from planktonic foraminifers, which live in the upper part of the water column. This warming cannot be observed on the benthic bryozoans living on sea bottom, where the temperature was not affected by the input of tropical-subtropical waters and was therefore much lower than on the surface.

5.2 History and development of the bryozoan life in Podbrezice

Bryozoan meadows started to grow on the shallow, warm water near the shore with very low input of terrigenous material to the basin. The bryozoan colonies formed sediment which was during the time more and more calcitic also because the input of terrigenous material became smaller - the land near shore became warmed and dryer (layer P-1). The sedimentation of organodetritic (bryozoans) limestone was interrupted by more humid environment (or temporary increase of water depth) during sedimentation of the layer P-2. The development of bryozoan build-up continuing when conditions turned again in shallow, warm water and deposited the layers P-3 and P-5 with short humid period were layer P-4 was created. Generally the diversity of bryozoans increase, so environment should be stable for a long time (Fig. 8).

Water depth then rapidly increased and near the bottom of the sea the water was much cooler than before. The sedimentation of limestone terminated and more terrigenous material came into the basin. These conditions were very suitable for the growth of Bryozoa, they occupied the most of the area and were very diverse. The layer P-6 was deposited during this period.

Afterwards the dynamics of the environment and water energy slowly increased, water depth became shallower and because less terrigenous material came to the basin. The deposition of bryozoan limestone started again (layer P-7). The shallowing continuing and the minimum depth, maximum water energy and
Figure 9. The commonest species from the lower part of the Podbrezice (Podbrezice build-up): a) *Pleuronea pertusa* Reuss, 1848, sample P-2, b) *Cellepora* sp., sample P-8a (scale bar 1 cm), c) *Ybselosocia typica* (Busk, 1859), sample P-4, d) *Crisia ebumea* (Linnaeus, 1758), sample P-3 (scale bar 100 pm), e) *Disparella goldfusi* (Reuss, 1864), sample P-6, f) *Hippopleurifera sedgwicki* (Milne-Edwards, 1836), sample P-7, g) *Reteporella beaniana* (King, 1846), sample P-4, h) *Puellina venusta* (Canu & Bassler, 1925), sample P-5, i) *Hornera verrucosa* Reuss, 1866, sample P-4, j) *Cellaria fistulosa* Auct, sample P-6. Unless otherwise indicated, all scale bars 1 mm.
Figure 10. The commonest species from the upper part of the section at Podbrezice (Podbrezice village): a) *Metrarabdotos malecki* Cheetham, 1968, sample Pv-2, b) *Steginoporella cucullata* (Reuss, 1848), sample Pv-1, c) *AdeoneUopsis oscinophora*, sample Pv-1 (scale bar 100 pm), d) *Schizoporella geminipora*, sample Pv-1 (scale bar 100 pm), e) *Adeonella polystomella*, sample Pv-1, f) *Turbicellepora* cf. *canaliculata*, sample Pv-1, g) *Smittina cervicomis*, sample Pv-3, h) *Myriapora truncata*, sample Pv-1, i) *Reussirella haidingeri*, sample Pv-1 (scale bar 100 pm). Unless otherwise indicated, all scale bars 1 mm.
higher temperature was approximately during sedimentation of the sample P-sb. This condition was extremely suitable for large celleporid bryozoans, which created build-ups in this area.

The deposition of limestone continuing, but later (P-9) the conditions became unsuitable for bryozoans. The whole sedimentation in this place was topped by algal limestone, where bryozoans formed only very minor part of the community, dominant are algae remains, molluscs and serpulids. It was the end of the life of bryozoan build-up.

Later however the depth of the water again increased and general environment near the bottom of the basin became cooler than during deposition of layer P-8. The claystone to calcareous marl was deposited. In this time again Bryozoa flourished, but were unable to developed built-ups, and grew only as bryozoan meadow (samples Pv-1 to Pv-3). These conditions were very similar to those when layer P-6 was deposited.

6 CONCLUSIONS

The environmental condition in the area around Podbrezice can be characterised as warm, shallow normal marine sea during Miocene. During the sedimentation however the humidity of area and/or the depth of the sea slightly changed. The shallowest conditions was suitable for large bryozoan colonies of *Cellepora*, which formed the framework of the build-up. The largest diversity of bryozoan association so perhaps the best conditions for bryozoans with small erect and encrusting colonies was during relatively deepest and coolest time.

Generally we can suggest, that similarly like in Eocene also in Miocene the diversity of small colonies of bryozoans is highest in the deepest, coolest and low water energy condition within shallow water environment.

The large celleporids colonies however flourished in very shallow, high energy and hot to warm water conditions.

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Taxonomic index

Acamarchis dentata 239
Acamarchis neritina 233
Acanthoceramoporella 36
Acanthocladiad cf. rhombicellata 65
Acanthocladiad cf. sparsifurcata 65
Acanthophragma polaris 175
Acratia 377
Acropora cervicis 44
Acropora palmata 44
Actinocyathus 376, 377
Adelascopora 336, 339
Adelascopora jeqolqa 175
Adelascopora secunda 175
Adeonella 188
Adeonella calveti 264
Adeonella patagonica 188, 189, 190, 191
Adeonella polystomella 386, 394
Adeonelopsis 287
Adeonelopsis coscinophora 386
Adeonelopsis distoma 264, 267
Adeonelopsis oscinophora 394
Adeonelopsis symmetrica 288
Adetognathus 65
Aetea 234, 263
Aetea truncata 219-220
Aethozoon 128
Alariafistulosa 103
Alcyonidium 121-122, 153, 163, 271, 274, 279
Alcyonidium disciforme 153-54, 158-160
Alcyonidium duplex 125, 271
Alcyonidium gelatinosum 156, 157, 272-77, 355, 363
Alcyonidium hirsutum 271
Alcyonidium mamillatum 157
Alcyonidium mytili 157, 279
Alcyonidium polyum 274-279
Alcyonidium reticulum 271
Alcyonidium variegatum 271
Alderina subtilimargo 386
Altemifenestella bifida 65
Altemifenestella crassiseptata 65
Altemifenestella cyclotriangulata 65, 67
Altemifenestella oerh海绵ouren sis 199, 203
Altemifenestella cf. invisiata 65
Altemifenestella spitzbergensis 199
Amastigia 189
Amphibiostrema appendiculatum 386
Amphibiostrema familiaris 175
Amphibiostrema inermis 175
Amphibiostrema lyrumad 263
Amphibiostrema rossii 175
Amphpoirella 148
Amphissites 377
Amplexopora 245, 253, 254
Amplexopora variabile, 249
Andreella megapora 190
Anemia sulcata 363
Anguisia verrucosa 261-63, 265
Anisotrypella 199, 200, 202
Anisotrypella certa 202
Annectocyma major 263
Annectocyma sparsa 386
Annectocyma tubulosa 263
Anotheropora rajnathi 107
Antarcticaetos bubeccata 175
Antarctothea 95
Antedon mediterranea 219
Apertostella crassata 45
Apertostella foramenmajor 45
Apertostella venusta 45
Aplousina bobiesi 18, 19
Apsendesia fasciculate 353
Arachnopusia columnaris 175
Arachnopusia unicarinata 72-74
Araxopora 204
Archegeonis 377
Archimedes 143
Archimedes nesilgeae 45
Archimedes wortheni 45
Arctonula 99, 105
Arctonula kunashirii 104
Arthrophaga rugulosa 386
Asajirella gelatinosa 362
Ascopora 202, 204
Aspericretare crassatina 175
Aspidostoma corona tum 175
Aspidostoma giganteum 187, 189, 195
Asterigerinata planorbis 389
Atactotoechus chazyensis 30-33
Avulophylum 376
Avulopocella 286
Aurelia aurita 363
Auriculkyra 377
Astroflustra vulgaris 175
Avulopocella 377
Bacillaria rapax 322
Bactrella 95
Bactrellaria! choropadiens 107
Bactrellaria lateralis 93
Baculopora 376-378
Baculopora megastoma 377,378
Balantiostoma 94
Balantiostoma crotacea 94
Balanus 100, 102, 385-386
Banastella biseriata 45
Banastella guensis 45
Banastella limitaris 44
Banastella medioforma 45
Banastella regalis 44-46, 46
Bashkiria operculata 65, 66
Batostoma rosula 265
Batostoma 27-30, 33, 245, 253
Batostoma chazyensis 27-30, 41, 46
Batostoma adhaerens 27, 30, 41
Batostoma campensis 27-30
Batostoma lanensis 27-30
Batostoma varium 29
Batostomella 253
Beania erecta 8, 9, 175
Beania fragilis 188-190
Beania magellanica 219, 220
Beania maxilla 187, 189
Beania mirabilis 220
Belgibole 377
Bicelisella 223
Bicellerella ciliata 223
Bicerisina compressa 386
Biflestra 95
Biflestra ramosa 95
Entalophoroecia gracilis 263
Eofletcheria incerta 30
Eopachydictya 38
Eopachydictya gregaria 38
Eopachydictya aff. gregaria 27, 37-38, 41
Eotuberitina 377
Eridopora 377
Eridotrypa 33
Eridotrypa aedilis 27
Eschara actaea 95
Eschara athulia 95
Eschara danael 95
Eschara dorilas 95
Eschara edwardsiana 93
Eschara eurita 95
Eschara gracilis 93
Eschara imbricata 357
Eschara macrocheila 93
Eschara punctata 357
Eschara semitubulosa 352
Escharella 93, 387
Escharella arge 95
Escharella chiragra 387
Escharella grossa 19
Escharella klugei 165
Escharella mamillata 176
Escharella octodentata 17
Escharella peachi 19
Escharella reussiana 19
Escharella tenera 387
Escharella variolosa 387
Escharella ventricosa 165
Escharella watersi 176
Escharella 93
Eschariforma 93
Escharella argus 93
Escharina 339
Escharina bougainvillae 95
Escharina dutertrei 17, 19
Escharina waiparaensis 336
Escharinella 93
Escharinella lorieri 93
Escharipora 93
Escharipora inornata 93
Escharoides 93
Escharoides aliferus 387
Escharoides coccinea 17, 19, 93
Escharoides cocinea 387
Escharoides grotriani 387
Escharoides mamillata 387
Escharoides mega lota 19, 387
Escharoides praestita 176
Escharoides tridens 176
Escharopora 245, 249, 253
Euchondria cf. aprathensis 377
Eucratea loricata 153, 156-158, 163, 168
Euginoma vermiciformis 263, 265-266
Eunicella cavolinii 219
Euritina 95
Euritina eurita 95
Euryestomella foraminigera 72-73
Evactinopora 49-50, 60
Evactinopora incerta 51
Evactinopora irregularis 51
Evactinopora radiata 51
Evactinopora trifolliata 51
Exfenestella exigua 43-44, 46
Exidmonea 264
Exidmonea cf. flexuosa 263, 265
Exidmonea coerulea 263
Exidmonea flexuosa 259
Exidmonea hoernesi 387
Exidmonea trifornis 261, 263, 265
Exochella avicularis 176
Exochella hymanae 176
Fabifenesella 203
Fabifenesella complêta 199
Fabifenesella cf. subvirgosa 65, 67
Fabifenesella tortuosa 65
Favositella minganensis 27
Fenestella 202
Fenestella akselensis 65
Fenestella compressa 45
Fenestella filistrata 45-46
Fenestella frutex 45-46
Fenestella s.l. frutex 375-377
Fenestella hemispherica 45-46
Fenestella inaequalis 45
Fenestella rotundata 45
Fenestella triserialis 45
Fenestralia sanctiludovici 45
Fenestrulina 189, 303, 307, 311, 329
Fenestrulina cervicornis 176, 178
Fenestrulina crystallina 176
Fenestrulina disjuncta 72
Fenestrulina farnsworthi 181-182, 185
Fenestrulina malusii 72-73, 229, 305
Fenestrulina miramara 224
Fenestrulina parvipora 176
Fenestrulina proximo 176
Fenestrulina rugula 8, 10, 176
Fenestruloides 303, 307, 310-311, 336, 339
Fenestruloides morriseae 181-182, 310, 312
Fibularia 287, 288
Figularia discors 176, 178
Figularia fīgīdaris 17, 19
Filaguria spatulata 176
Filiflustra 93
Filiflustra compressa 93
Filiflustrella 93
Filiflustrella lateralis 93
Filiflustrellaria 93
Filiflustrellarial oblique 93
Filiflustrina 83
Filiramoporina kretaphilia 46
Fistulipora 65, 202, 376
Fistulipora incrustons 51, 60
Fistulipora jakovlevi 200
Fistulipora micidolamina 51
Fistulipora taydonensis 51
Fistulipora volongensis 65
Flabellopora 93
Flabellopora elegans 93
Flustra bombycina 93
Flustra dentata 93
Flustra membranaceo-truncata 223
Flustramorpha 336, 339
Flustra 93
Flustrella turonensis 93
Flustrellaria 93
Flustrellaria fragilis 93
Flustrellidra 122
Flustrina 93
Flustrina transversa 93
Foveolaria elliptica 190, 192
Franzenella 128
Fredericella 366
Fredericella indica 374
Fredericella sultana 297, 300, 317, 362, 366, 369-370
Frondipora verrucosa 263
Fucus eva nes cens 103
Fucus serratus 273
Funiculina quadragridaris 257
Fusicellaria 93
Fusicellaria pulchella 93
Gaudryanella 112, 115
Gemellipora eburnea 261, 263, 265-266
Gephyrotes 387
Gephyrotes fortunensis 19
Gilbertopora 228
Gilmoropora heintzi 201-202
Globigerinoides bispherics 385
Globorotalia peripheroronda 385
Gnathodus ex gr. bilineatus 377
Goniattites cf. hudsoni 377
Goniocladia cellulifera 50, 52
Goniocladia steanovi 52
Loxosoma rotundum 137
Loxosomasam 137
Loxosoma sluteri 137
Loxosoma subsessile 137
Loxosoma troglodytes 137
Loxosomella 137
Loxosometta aloxiata 134
Loxosomella antarctica 134
Loxosomella antedonis 134,136
Loxosomella constricta 133, 134
Loxosomella crassicauda 134
Loxosomella discopoda 137
Loxosomella hispida 134
Loxosomella intragemmata 134
Loxosomella lappa 134,136
Loxosomella lecythifem 134
Loxosomella leptoclini 134
Loxosomella monocem 134
Loxosomella murmanica 134
Loxosomella nitchei 134
Loxosomella olei 133,134
Loxosomella phosphosomaia 134
Loxosomella shizugawaemis 133-134
Loxosomella stomatophora 134
Loxosomella varions 137
Lmuilites 88
Lunulites conica 94
Lunulites umbellata 93
Lyrocladia cf. vena 202
Lyrocladia vera 199
Lymporella divergens 45
Madrepora oculara 257, 259
Magellania fangilis 5
Margaretta 94,115
Margaretta cereoides 94, 387
Mecynoecia proboscidea 387
Mecynoecia pulckella 387
Mediapora injaemis 45-46
Meekopora 49-50, 52, 60
Meekopom approximata 52
Megerlia truncata 363
Melicerita 281, 283
Melicerita angustiSoba 287
Membranipom diademata 387
Membranipora membrandacea 72
Membranipom diademata 387
Membranipomom nobilis 387
Membranipomom omata 95
Membranipora tuberulata 72
Mesenteryptom meandrina 387
Mesogondolella 65
Mesotrypa 253
Metalcyonidium 128
Metmmbdotos 357
Metmmbradotos malecki 354, 357-358, 385, 387, 394
Michelinia 380
Micropom brevissima 176
Micmopm notialis 176,179,189
Micropom papymeea 387
Microporfm perfomta 387
Micmopora (Cribriloporella) 331
Micmoporella 118, 121, 189,
303-307, 309, 313, 315,
329-331
Micmoporella aff. arctica 332
Micmoporella agoniistes 334
Micmoporella alaskana 334
Micmoporella arctica 305,
333-334, 341
Micmoporella areolata 305
Micmoporella bifoliata 331, 336
Micmoporella borealis 305, 309
Micmoporella califomica 305,
309
Micmoporella catalinensis 333
Micmoporella cemmia 334
Micmoporella ciliata 17, 19, 122,
223, 264, 304-305, 313,
329-331, 333, 335, 352
Micmoporella comnata 19, 327
Micmoporella cribmsa 304, 331
Micmoporella diademata 309
Micmoporella discors 304, 309
Micmoporella donovani 334
Micmoporella echinata 305
Micmoporella elegans 305,
308-309, 333
Micmoporella formosa 305
Micmoporella germani 305
Micmoporella harmeri 334
Micmoporella hyadesi 313, 331,
333, 335
Micmoporella infundibulipom 331
Micmoporella intermedia 331
Micmoporella lineata 331, 333,
334
Micmoporella hmfem 335
Micmoporella marsupiata 308,
331, 333
Micmoporella monilifera 331
Micmoporella neorcbimbdes 305,
308-309
Micmoporella ordo 331, 333
Micmoporella orientalis 313
Micmoporella papillosa 335
Micmoporella personata 305
Micmoporella pirikaensis 331
Micmoporella pontiflca 334
Micmoporella pulchm 305,
308-309
Micmoporella rogickae 331
Micmoporella serrata 305,
308-309, 334
Micmoporella speciosa 305
Micmoporella speculum 334
Micmoporella spicata 335
Micmoporella stellata 334
Micmoporella stenoporta 176
Micmoporella svalbardensis 166
Micmoporella tractabilis 334
Micmoporella trigonellata 305
Micmoporella umbonata 331, 334
Micmoporella unca 305
Micmoporella vibmculifem 334
Micmoporelloides (Cribriporella)
309, 313
Micmoporelloides
(Micmoporelloides) 303, 304
Micmoporelloides 303-305,
307-309, 311, 313
Micmoporelloides areolata 305
Micmoporelloides catalinensis
307-309, 332
Micmoporelloides galapagensis
307, 309
Micmoporelloides comnula 307,
309
Micmoporelloides cribmsa 181,
182, 184, 304, 305, 307-309
Micmoporelloides flmklini 309,
310, 313
Micmoporelloides planata 307,
309
Micmoporelloides gibbosa 307,
309, 313
Micmoporelloides hawaiensis
181, 183, 307, 309, 312-313
Micmoporelloides infundibulipora
181, 307, 309
Micmoporelloides lepueana 313
Micmoporelloides mazadlanica
306, 307, 309-310, 312, 334
Micmoporelloides peschongi 313
Micmoporelloides planata 181,
183,185, 307, 309
Micmoporelloides pontiflca 307,
309, 313
Micmoporelloides sanmiguelensis
309
Micmoporelloides santabarbamen
sis 309
Micmoporelloides santabarbanen
sis 309
Micmoporelloides setiformis 304,
307-309
Micmoporelloides tractabilis 307,
309
Micmoporelloides umbonata 331
Micmoporelloides umboniformis
307
406
Plumatella repens rugosa 296
Plumatella repens typica 296
Plumatella reticulata 317-321, 324, 362
Plumatella rugosa 317-319
Plumatella cf. velata 297
Polyascosocia coronopus 388
Polypora 197, 202
Polypora cestriensis 45
Polypora confirmata 65
Polypora kossjensis 65
Polypora martis 65
Polypora cf. martis 67
Polypora spininodata 45
Polypora varsoviensis 45
Polyporella optima 202
Polyporella perfecta 203
Porella 189
Porella acutirostris 72-73, 77
Porella laevis 388
Porella minuta 165
Porellina 93
Poricella bugei 19
Poricellaria 93
Poricellaria alata 93
Porina 93
Porina fdiformis 95
Porina gracilis 93
Potidoma clarkiae 134
Praeorbulina glomerosa 385
Praepilatina 377
Prenantia cheilostoma 19, 388
Primorella polita 199, 201
Primorella superba 65, 66
Primorella tundrica 65
Proboscina 163
Proutella discoidea 46
Pseudalcyonidium 128
Pseudofrondipora davidi 388
Pseudolepralia 228
Pseudonematopora 65, 375-379
Pseudonematopora balakini 59
Pseudonematopora planatus 58, 59
Ptiloporella varicosa 45-46
Ptilota plumosa 153, 156
Ptyloporella vodoresovi 45-46
Puellina scripta 388
Puellina 202-204
Puellinella 227-228
Puellina venusta 388, 393
Pyriflustrella 93, 95
Pyripora 93
Pyripora pyriformis 93
Pyripora tuberculum 93
Pyriporoides uniserialis 177
Quadricellaria 93
Quadricellaria elegans 93
Quadriflustrina 93
Ramiopora 202, 204
Ramiopora hochstetteri 199, 202
Ramiopora variolata 65, 66
Rectifenestella compacta 193
Rectifenestella cf. gigiensis 202
Rectifenestella microporata 65, 67
Rectifenestella multispinosa 45-46
Rectifenestella pseudoretiformis 199, 203
Rectifenestella retiformis 202
Rectifenestella robusta 65
Rectifenestella cf. robusta 67
Rectifenestella tenax 45
Rectonaria 377
Reniporella 112, 113
Reniporella gordoni 112, 115
Reptadeonella 94
Reptadeonella violacea 94
Reptedactella 94
Reptedactella violacea 94
Reptedactella 94
Reptedactella violacea 94
Repteschariella 94
Repteschariella subgranulata 94
Repteschariella meudonensis 94
Reptoflustra 83
Reptoflustrina 83
Reptoflustrina arctica 94
Reptoflustrina marginata 94
Reptotegiporida 94
Reptolaterescharella 94
Reptolaterescharella meudonensis 94
Reptolaterescharella ranulifera 94
Reptolaterescharella capensis 94
Reptolaterescharella ranulifera 94
Reptolaterescharella ranulifera 94
Reptolaterescharella capensis 94
Reptolaterescharella ranulifera 94
Reptolaterescharella capensis 94
Reptolaterescharella ranulifera 94
Reteporella couchii 202
Reteporella couchii biaviculata 264
Reteporella elegans 264
Reteporella frigida 177, 178
Reteporella gelida 177
Reteporella hippocrepis 177
Reteporella lepralioides 177
Reteporella longichilla 177
Reteporella protecta 177
Reteporella septentrionalis 388
Reteporella sparteli 261, 264, 266, 267
Reteporidra 197
Reteporidra grandis 202
Reteporidra tuncheimensis 202
Reticulofenestra minuta 389
Reussirella doma 94
Reussirella haedingeri 388, 394
Rhabdomesone 204, 3 76
Rhabdomesone progracile 54, 59-60
Rhabdomesone regulare 54, 59-60
Rhabdomesone regularis 57
Rhabdomesone Irhombiferum 377
Rhamphosmittina bassleri 177
Rhamphostomella bilaminata 166
Rhamphostomella bilaminata var. sibirica 166, 167
Rhamphostomella ovata 166
Rhabasia 95
Rhabasia dorilas 95
Rhinidictya fenestrata 38
Rhombocladia 49, 375-376, 378
Rhombopora 65, 376
Rhombopora bedfordensis 45
Rhombopora exigua 45
Rhombotrypula 245, 249, 251, 253, 254
Rhombotrypella alfredensis 199, 202
Rhombotrypella cf. amdrupensis 65, 66
Rhombotrypella insolita 199
Rhombotrypella invulata 65
Rhombotrypella quadrata 249
Rhynchozoon 347, 388
Rhynchozoon larreyi 72
Rhynchozoon monoceros 17, 19
Rhynchozoon paa 72
Rhynchozoon rostratum 341
Romancheina labiosa 187, 189, 190
Ruzhencevia 204
Saffordotaxis 377
Saffordotaxis angustata 46
Saffordotaxis incrassata 45
Saffordotaxis ohioensis 46
Salmacina dysteri 219
Sargassum furcatum 236, 238
Schizobrachiella sanguinolent 19, 219-220
Schizomavella comuta 219-220
Schizomavella punctiger 72
Schizomavella tenella 388
Schizoparella 95, 142, 363
Schizoparella Crustacea 165
Schizoparella lineata 165
Schizoparella porifera 165
Schizoparella unicornis 72—73, 93, 341
Schizoretepora solanderia 264
Schizostomella dubia 388
Schizotheca fissa 388
Scruparia ambigua 234
Scrupocellaria 164
Semicelleporaria 94
Semieschara 94
Semieschara flabellata 94
Semiescharella 94
Semiescharella flexuosa 94
Semiescharellina 94
Semiescharinella 94
Semiescharinella complanata 94
Semiescharipora 83
Semiescharipora mumia 95
Semiflustra 94
Semiflustrella 83
Semiflustrina 83
Semiporina 94
Semiporina elegans 94
Septopora 203
Septopora synocladiiformis 202
Serpula 386
Sertularia neritina 233
Sertulipora guttata 261, 264, 266, 267
Setosella vulnerata 261, 263, 265, 267
Setosellina capriensis 263
Setosellina roulei 261, 263, 265, 266
Siamodus 380
Sinupetraliella formidabilis 190
Siphonicytara 281, 288
Smittina abditavicularis 177
Smittina ancedota 169,177
Smittina antarctica 177
Smittina bella 165
Smittina cervicornis 263, 385, 388, 394
Smittina cheilopora 352
Smittina crystallina 261, 264, 267
Smittina directa 177
Smittina excertavicularia 177
Smittina incemicula 177
Smittina majuscula 161
Smittina messiniensis 19
Smittina minuscula 161
Smittina monacha 183
Smittina pileata 177
Smittina rugicikea 177
Smittina undulimargo 187, 189, 190
Smittinella rubrilingulata 177, 178
Smittipora platystoma 352
Smittoidea albula 177
Smittoidea conspicua 177
Smittoidea levis 72
Smittoidea malleata 177
Smittoidea maunganuiensis 72
Smittoidea puguncula 177
Sparsiporina 94
Sparsiporina elegans 94
Sphaeropora 286
Sphenolithus heteromorphus 389
Spondylus gussoni 259
Staurosteginopora 95
Staurosteginopora irregularis 95
Stegopora 94
Stegopora omata 94
Stegoporella 17, 21, 77, 112
Stegoporella bhujensis 112, 115
Stegoporella cucullata 17, 19, 388, 394
Stegoporella manzonii 352
Stegoporella rhodanica 112, 115
Stellahexaformis 200, 202
Stenodiscus haddingtonensis 55
Stenodiscus tumida 55
Stenophragmidium 55, 65, 67, 142
Stenophragmidium incrustans 55, 56
Stenophragmidium megistum 55
Stenophragmidium mirandum 55
Stenophragmidium obscurum 55
Stenopora 52
Stenopora adhaerens 30
Stenopora confusioensis 52
Stenopora fibrosa 27
Stenopora grandis 202
Stenopora redesdalensis 52
Stenopora timanensis 199
Stereachmella buski 261, 263, 267
Sterechinus neumayeri 5, 6, 7
Stictopora 38, 253
Stictopora fenestrata 38
Stictopora cf. fenestrata 27, 35, 38, 41
Stictopora cf. lata 249
Stigmatella 253
Stigmatella cf. personata 249
Stigmathechos striatus 107
Stolella indica 319
Stomachetosella cruenta 166
Stomatopora 189
Straparollus 377
Stræbascopora germana 65
Stræbascopora vera 65, 66
Streblotrypa (Streblotrypa) cortacea 57
Streblotrypa (Streblotrypa) pectinata 54, 57
Streblotrypella major 46
Strongylomena droebachiensis 168
Stylopora viride 72
Sulcoretepora 49
Sulcoretepora parallela 45-46
Sulcoretepora?, ramosa 59
Swanomia belgica 177
Swanomia brevimandibulata 177
Swarupella andamanensis 365
Sweetognathus 65
Syringopora 380
Systenopora contracta 177
Tabulipora 199
Tabulipora 65, 141, 147
Tabulipora aberrans 199, 202
Tabulipora arcticensis 199
Tabulipora greenlandensis 202
Tabulipora howsii 377
Talivittaticella frigida 177
Tanganella miilleri 317,319, 321, 324
Tarphophragma 245, 253
Tavazpora 204
Tegella 94, 164, 228
Tegella arctica 8, 9, 10, 94, 157, 164, 168
Tegella arctica 94
Tegella armifera 157, 164, 168
Tegella retraversa 9, 164, 168
Tegella unicornis 224
Tellyella tuberculata 73
Tenthenulina 336–337, 339
Terebratulina retusa 363
Terminoflustra membranaceotruncata 223
Temecellaria 94
Tervia barrieri 261, 263–264, 266
Tervia irregularis 261, 263–265, 388
Tessaradoma boreale 261, 264
Tetracladus bryosalmonae 317
Tetracapsuloides bryosalmonae 317
Tetradium 253
Tetraplaria turgida 107
Tetrataxis 377
Thalamoporella 107, 110–111, 115
Thalamoporella arabiensis 111
Thalamoporella archiacci 110–111
Thalamoporella domifer 110–111
Thalamoporella dorothea 110–111
Thalamoporella kachchhensis 110–111
Thalamoporella kharinadienses 111
Thalamoporella minuta 110–111
Thalamoporella reniformis 110–112, 115
Thalamoporella rhombifera 111
Thalamoporella setosa 111
Thalamoporella tewarii 110–111
Thalamoporella transversa 110–111
Thalamoporella traversa 111
Thalamoporella vinijhanensis 111
Thalamoporella voighti 110–111
Thalamoporella wynnei 110–111
Thalassium clathrus 103
Thamniscus 375–376
Thamniscus coleii 377, 378
Therenia 113
Therenia indica 107, 113, 115, 118
Thrypticocirrus phylactelloides 177
Thrypticocirrus rogickae 177–178
Timanodictya nikiforovae 201, 202
Toretecheilum turbinatum 177
Tremogasterina 224
Tremopora radicifera 354, 357–358
Tretocycloecia dichotoma 388
Tricellaria 94, 164, 228
Tricellaria aculeata 94, 189
Tricellaria témata 157, 168
Tricomina 377
Tridacna maxima 346
Trilaminopora trinervis 177
Trilochites biformatus 177, 178
Trochiliopora insignis 388
Trochopora 94
Tryphyla zoan munitum 224
Trypostega rugulosa 19
Trypostega venusta 72, 341
Tubucella papilosa 388
Tubucellaria 94
Tubulipora 261, 263, 267, 388
Tubulipora concinna 73–74
Tubulipora dimidiata 388
Tubulipora flabellaris 163
Tubulipora notomale 263, 267
Tubulipora pulcherrima 73, 77
Turbicellepora 114
Turbicellepora cf. canaliculata 388, 394
Ulrichotrypa ramulosa 65
Ulva fenestrata 103
Umbonula 93, 95, 99–100
Umbonula arctica 104–105, 165
Umbonula ascarabaeus 358
Umbonula endlicheni 358, 388
Umbonula inarmata 99, 104–105
Umbonula kunashiri 104–105
Umbonula littoralis 99, 104–105
Umbonula macrocheila 93, 358, 388
Umbonula monoceros 388
Umbonula ovicellata 99, 103–105
Umbonula patens 99, 104–105
Umbonula spinosa 354, 358
Umbonula verrucosa 103
Uvigerina macrocarinata 385
Valdenniella lata 177
Valvulinella 377
Vibracella trapezoida 388
Victorella pavia 321
Vinicularia elegans 95
Vinicularia 94
Vinicularia sulcata 94
Watersipora goniostoma 18–19
Watersipora subovoidea 72, 234, 236
Watersipora subtorquata 72–73, 75–76, 77
Wilbertopora 223–227
Wilbertopora mutabilis 224
Wjatkella assueta 202
Ybseloecia typica 385, 388, 393
Yoldia eightsi 5
Author index

Barnes, D.K.A. 1,161
Batson, P.B. 293
Beming, B. 15
Betzler, C. 15
Bolton, T.E. 25
Bone, Y. 281
Brunton, M.A. 293

Cancino, J.M. 207
Chaney, H.W. 303
Cocito, S. 215
Cuffey, R.J. 25,43

Ernst, A. 49, 63

Gerdes, G. 69
Gopikrishna, K. 107
Gordon, D.P. 83
Grave, De, S. 341
Grischenko, A.V 99
Guha, A.K. 107

Hâkansson, E. 141
Holcová, K. 383
d'Hondt, J.-L. 119
Hughes, R.N. 207

Iseto.T. 133
Kaselowsky, J. 69
Key, Jr., M.M. 141
Kuklinski, P. 153,161
Lauer, A. 69
Lore, M.B. 361
López-Fé, C.M. 173
Mawatari, S.F. 69,99, 329
Moissette, P. 15
Moore, M.D. 141
Morris, P. A. 181,303
Moyano G., H.I. 187,207
Muricy, G. 231
Nakrem, H.A. 63,197
Navarrete Z., A. 207
Novosel, M. 215
Olujic, G. 215
Ostrovskey, A.N. 223
Patterson, W.P. 141
Pieroni, G. 317
Porter, J.S. 271
Pozar-Domac, A. 215
Ross, C.A. 245
Ross, J.R.P. 245
Rosso, A. 257
Ryland, J.S. 271

Schmidt, R. 281
Scholz, J. 69
Smith, A.M. 293
Soule, D.F. 181,303
Taticchi, M.I. 317
Taylor, P.D. 83,223,231,329
Tilbrook, K.J. 341

Vieira Ramalho, L. 231
Vávra, N. 351

Weber, H.M. 375
Wood, T.S. 361
Wyse Jackson, P.N. 141,375
Wöss,E.R. 369
Zágorsek, K. 383
Bryozoan Studies 2004 contains papers presented at the 13th International Conference of the International Bryozoology Association held in Concepción, Chile in January 2004 and hosted by the Universidad de Concepción and Universidad Católica de la Santísima Concepción. Bryozoans are fascinating complex colonial invertebrates that inhabit both freshwater and marine environments. They have a long geological range, from the early Ordovician some 480 million years ago until the present day.

The topics presented in this volume reflect the diversity of studies on Bryozoa with authors from 18 countries. They include investigations in seven thematic areas: ecology and life strategies; recent and fossil faunas of Australia and New Zealand; past and present bryozoans from both Antarctic and Arctic seas; geology and palaeontology of bryozoans from Eurasia and North America; freshwater bryozoans around the world; fossil bryozoans of the Mediterranean and Tethyan realms and, evolution and diversity of recent species.

This volume represents the newest synthesis of the current advances made in bryozoological studies during the last three years, and makes a significant contribution to the literature on bryozoans.