

Living benthic foraminifera: biogeographical distributions and the significance of rare morphospecies

JOHN W. MURRAY

National Oceanography Centre Southampton, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, UK

*Corresponding author (e-mail jwm1@noc.soton.ac.uk)

ABSTRACT – Previous studies have investigated regional distribution but this is the first attempt to investigate the global biogeographical distribution of individual morphospecies of living/stained smaller benthic foraminifera. From 8032 samples collected between 1952 and 2011 data have been gathered on the relative abundance of >120 species in five major environments ranging from marsh to deep sea. There is a spectrum of six groups of species with abundance ranging from very high (Group 1) to extremely low (Group 6). In the latter species abundance never reaches 10% of an assemblage and, in many cases, it is only 1–2%. Individual species are shown to occupy a range of environments with very few being confined to a single environment (usually either marsh or deep sea). Some species occur in several oceans while others are confined to just one. There is no correlation between species abundance and being either widely or narrowly distributed. Propagules are the most likely mechanism of dispersal but some narrowly distributed species may not produce them. Generalists may be widely or narrowly distributed but opportunists are likely to be widely distributed. The rare species of Group 6 contribute to high diversity in shelf and deep-sea assemblages. These species may be adapted to minor differences in microhabitats induced by disturbance and patchy food supply. Patterns of biogeography have application to ecology, palaeoecology and taxonomy. *J. Micropalaeontol.* 32(1): 1–58, January 2013.

SUPPLEMENTARY MATERIAL: Taxonomy and details of types; sources of data (N1–N55) additional to that of Murray (2006); and sources of data for Figures 4–95 plus other agglutinated and hyaline taxa are available at www.geolsoc.org.uk/SUP18576

KEYWORDS: *rare, biogeography, disjunct, propagules*

BACKGROUND TO THE STUDY

In the early 2000s the author became interested in the distribution of rare morphospecies of benthic foraminifera. Rare species must have some ecological significance as they are key contributors to high diversity. However, it soon became apparent that the topic could not be pursued without gathering all the data on species occurrences and that took a lot of time and effort. When those data had been gathered it led to the writing of the book on ecology (Murray, 2006) but the focus was on assemblages and common species rather than rare species. Constraints of time and the size of the book agreed with the publishers meant that consideration of rare species had to be saved for a future date.

In 2011 the author decided to go through the post-book literature in order to complete the survey of living occurrences to that date. Initial results from the analysis of abundance and biogeographical distributions of a few species yielded a number of surprises. For example, some species thought to be universally rare have occasional occurrences of higher abundance. Rare, common and abundant are relative terms (without any numerical definition) for describing segments of a continuous series of occurrences. It became obvious that defining rarity could best be achieved by comparing the numerical abundance and biogeography of a spectrum of species from this continuous series. Although it is already known that even an abundant species is rare towards the margins of its distribution this new analysis reveals the extent of that rarity in a way that has not previously been possible.

INTRODUCTION

It is a paradox that rare species are common.

Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range

and is rare? Yet these relations are of the highest importance, for they determine the present welfare and, as I believe, the future success and modification of every inhabitant of this world.

Thus wrote Darwin in 1859 in his Introduction (final paragraph) to the *Origin of Species*. Although much has since been written on this topic very few answers have emerged, as can be seen from the following comments. ‘Understanding the causes and consequences of rarity is a problem of profound significance because most species are uncommon to rare, and rare species are generally at greater risk to extinction’ (Hubbell, 2001, p. 30). Among the key concepts discussed by Hayek & Buzas (2010, p. 2) in their valuable overview of the statistics of surveying natural populations is that ‘All organisms have the potential to reproduce at a geometrical rate, and hence to populate the world’. However, we know from observation that this rate of expansion is never fully realized not even in abundant species. But the reasons for this are largely unknown.

In spite of the fact that the majority of species of all groups of animals and plants are rare many ecologists seem to consider rarity to be anomalous (e.g. Angel, 1995; Kunin, 1997). They seek special explanations for rarity and for how rare species manage to survive. This is partly because some rare species are threatened by the activities of humans so research on rarity is funded for its potential in planning conservation. Indeed, much of the literature on rarity is either conservation-orientated, especially with respect to land plants, certain land animals and marine fish stocks, or is theoretical (Hubbell, 2001). But is rarity an anomaly? Looking at the matter objectively and without preconceptions, if most species are rare then that is the norm and may require no special explanation. The unusual species are those that show local geographical or temporal abundance. Perhaps we should be less concerned with

how or why rare species survive and more concerned with determining why only some species become so abundant.

The differences between rare and common morphospecies may be better understood by analysing a group of organisms that has been widely studied and which is not in the public eye so there are no concerns over loss of species or of conservation. Benthic foraminifera fulfil this role. Their distribution is reasonably well known (Murray, 2006; 2007) based on an analysis of ~2.4 million living (stained) individuals in ~7300 samples of surface sediment. They occur from the intertidal zone to the deepest ocean trench and from pole to pole. There are ~2140 recorded species of which ~33% have abundances >10% and ~67% are of minor importance. Yet, with the exception of being used in calculations of species diversity, rare species are largely ignored in ecological studies of benthic foraminifera. Perhaps we should give them more attention as they may be more ecologically significant than we have hitherto realized. The aim of this paper is to open up the topic for consideration and debate.

A choice had to be made as to whether to use data on live (stained) or dead forms. The author favours the former because dead distributions have always been subject to post-mortem change, some of which may be very significant. On a local scale there may be transport from one environment to another (e.g. from marsh to adjacent lagoon) but this causes only minor anomalies. However, some processes are much more wide-ranging. For example, on continental shelves there are faunas relict from former lower sea-level (e.g. Gulf of Mexico drowned reefs, Ludwick & Walton, 1957; European shelf, Blanc-Vernet, 1969) and there is significant down-slope mass-flow transport of sediment in submarine canyons from shelf and upper slope to continental rise and abyssal plains (leading to the deposition of turbidites) and also mass slides on continental margins (e.g. Storegga slide (Bugge *et al.*, 1987) involving Tertiary to Quaternary sediments). In some areas Neogene and older foraminifera are reworked from erosion of cliffs or submarine outcrops (e.g. Uchio, 1960). In the author's opinion it is better to have reliable data from fewer locations than to include data of such uncertain reliability from dead or relict distributions.

This study is the first attempt to examine the global biogeography and abundance of individual living/stained morphospecies. Previous studies of foraminiferal biogeography have been concerned with the recognition of faunal provinces based on assemblages of morphospecies (including live and dead) mainly through the detailed work of Buzas and Culver (see Culver & Buzas, 1999 and references therein; review in Murray, 2006, pp. 257–260) and the only global analyses of individual morphospecies have been of shallow-water larger foraminifera (Belasky, 1996). The internet World register of Marine Species (WoRMS) lists the distribution (presence/absence) of modern species based on any type of data: live, dead, total without making any distinctions between them and without any information on abundance. Using data on 938 common morphospecies from Murray (1991), Pawlowski & Holzmann (2008) determined that more than 50% show a restricted distribution from 1–10 biogeographical regions. Only 20 of the 25 most widely distributed morphospecies occur in more than 5 regions. Biogeographical studies are also being made on phylotypes (via molecular genetics; e.g. Hayward *et al.* 2004; Pawlowski *et al.*, 2007; Pawlowski & Holzmann, 2008; Schweizer *et al.*, 2011). These are fundamentally altering our concept of some morphospecies and throwing new light on biogeography.

METHODS

Definition of terms

Several of the terms used in ecological and biogeographical studies are relative with no numerical definition. The definitions used in this study are presented here.

- Rare species: one that is infrequently encountered. Most truly rare species have a very low relative abundance of <1% of an assemblage.
- Low abundance: generally any species forming <5% of an assemblage and very low abundance for <1% of an assemblage.
- Biogeographical distributions: two ill-defined terms have been used to define broad extremes: 'cosmopolitan' for widely distributed species and 'endemic' for those species restricted to a limited area. In a critical review of the concept of endemism, Anderson (1994) pointed out that the term means different things to different people (e.g. biogeographers, evolutionists, those studying diseases). There are many factors that control the restriction of a species to an area: the size of the area under consideration, the size of the organisms and their taxonomic status, changes in distribution through time (seasonal, annual, geological), variability or stability of the environment, etc. Because there is no consensus on the precise definition of these terms they are avoided here. Instead the terms 'wide' and 'narrow' are used for the two extremes of distribution. The widest distribution is occurring in all oceans. The narrowest distribution is occurring in part of a single ocean.
- Major environments:
 - *Marsh/mangal* have been separated from other marginal marine environments because they are permanently vegetated with higher land plants and are distinctive.
 - *Marginal marine* includes estuaries and lagoons and their non-vegetated intertidal zones; the Baltic is considered to be marginal marine because it is brackish.
 - *Fjord* relates to glacially deepened valleys that are connected to the sea but invariably having shallow sills that restrict the exchange of deep marine water with the adjacent shelf. Fjords are restricted to higher latitudes.
 - *Shelf* includes environments on the continental shelf including some deeper enclosed basins resulting from glacial erosion. The shelf break dividing the shelf from the continental slope varies in depth according to regional geology but is broadly in the depth range 100–200 m. A depth of 200 m is taken as the deeper limit of the shelf.
 - The *deep sea* (>200 m) includes the continental slope and rise, the abyssal plains and trenches. It also includes the borderland basins of the California margin of the USA.
- Salinity. No unit is given. Measurements from older literature are based on chemical methods (ppt, ‰) and, more recently, by the conductivity ratio (practical salinity unit, psu, or more correctly Practical Salinity Scale, PSS; see Simpson & Sharples, 2012).

Selection of species

The morphospecies chosen for biogeographical analysis include many forms selected because they are easily identified (e.g. *Patellina corrugata*, *Spirillina vivipara*) but also several species of a single genus for comparison (e.g. *Fissurina*, *Pullenia*). They span a range of relative abundance from high to very low, and a range of distribution from wide to narrow. It has not been possible

to check the identification of every species since not all authors provide illustrations and rarer species are commonly not illustrated. The taxa are listed in Supplementary Publication table 1 together with the original name, the type locality, type level and age. No attempt has been made to plot the occurrences of any monothalamous organic or agglutinated taxa.

Samples

Every synthesis depends on the available published data. The author is unaware of any study of benthic foraminifera that has been designed specifically to target rare species. All distributional studies concentrate on the common forms. In those cases where there is only a single survey of the fauna of an area (most studies), it can be regarded as a preliminary study. Only rarely is there repeat sampling of an area over a period of time in order to track temporal changes.

The history of development of sampling methods has been reviewed by Schönfeld (2012). The almost universally utilized staining method for recognizing ‘living’ foraminifera uses rose Bengal to stain protoplasm red (Walton, 1952; see reviews by Bernhard, 2000 and Murray & Bowser, 2000 for discussion of problems and solutions). In the six decades since 1952 hundreds of surveys of the abundance and local distribution patterns of stained (‘living’) foraminifera have been carried out. Most are single surveys taken over a period of days and never repeated. Few studies include replicate sampling. Apart from affecting abundant taxa the time-scale of sampling must also affect rare taxa and this may be particularly significant as regards the recording of short-term, localized blooms of abundance resulting from infrequent reproduction.

There is a range both of sieve size used and number of individuals counted in each sample. Examples of the range of sieve size are given by Schönfeld (2012, table 1). The commonly used size fraction for marsh, marginal marine and shelf samples is >63µm but for fjords and the deep sea many authors use >125 or >150 or even occasionally >250µm. It is not possible to assess the effect of this on the results discussed here except to point out the obvious fact that small tests will be most commonly overlooked when larger size fractions are studied. Some samples are quantitative so the absolute number of individuals per unit area of sea floor and volume of sediment are known; others are qualitative with no information on either area or volume so only relative abundance (%) can be determined. Quantitative samples are more readily taken in intertidal settings. They can also be taken in cohesive (usually muddy) sediments from the shelf or deep sea using multicorers or box corers (see Schönfeld, 2012). Coarse, non-cohesive sediments are not easily sampled using corers. The size of the count (*n*) and the number of species encountered (*S*) are linked to the species diversity of the sample. Another aspect of sample size is whether a given sample is large enough to be representative of the species present. By definition, rare species (i.e. those infrequently sampled) have low absolute and relative abundance (<1%). Hayek & Buzas (2010, pp. 144–145) demonstrate that the confidence limits of very low abundances ‘contribute nothing to the characterization of the flora or fauna’ because of the degree of fit of the Normal approximation. This improves as *p* (estimated abundance) comes closer to 0.5. Furthermore, they conclude (pp. 148–9) ‘if we were to apply statistical theory, we could say that we would never be able to sample anywhere near all the rare species’. In other words, the recorded data are incomplete and there is nothing we can do about it. Although this generalization is true for a single sample a suite of

Table 1. The six categories of abundance based on the proportion of samples having species abundances >10% in an assemblage.

Group	% of samples
1	>40
2	20–40
3	10–20
4	2–10
5	0.1–2
6	0

samples from a restricted area will provide a more representative record of rare species, albeit still incomplete.

Counting/census data

It would be impractical to use only standing crop data in an analysis of rare species as the pool of information would be very limited. Therefore, relative abundance data (%) are the basis for this study but they are supplemented with information on standing crop (normally number of individuals per 10cm³ sediment) where that is available. Nevertheless, where the standing crop of a sample has been determined, the number of individuals of each species can be calculated from the relative abundance. For a standing crop of 1000 per unit area, 1% =10 individuals. As it is relatively uncommon for a standing crop to reach 1000 per 10cm³ sediment, it follows that almost all <1% occurrences invariably represent few individuals.

Sources and treatment of data

Altogether, data on 8032 samples have been compiled (using only those with a count >50 individuals; choosing a higher count would have eliminated a large number of samples). Virtually all the counting/census information in publications from 1952 (introduction of staining method) to June 2005 is available in spreadsheets in Murray (2006, web appendix tables WA-1–WA-219; 7276 samples of living assemblages). There are additional new data from papers published since 2005 (Supplementary Publication table 2, 756 samples). Where authors have used separate size fractions from the same sample these are treated as separate samples because unequal parts of the different fractions were often counted (S. Hess, pers. comm., 2011) so a true average cannot be calculated.

For each species, all the abundance data have been organized by major environment and geographical area. Zero occurrences have been ignored in calculating mean values.

Five major environments are recognized: marsh/mangal, marginal marine, fjord, shelf, deep sea, as defined above.

A species abundance >10% in an assemblage is the criterion for defining the six categories of abundance (Table 1).

Biogeographical template

The scope of data is shown on the world map (Fig. 1). In order to show both biogeography and environment it is much more convenient to plot species distributions on a template (Fig. 2). This allows more detail to be recorded in less space.

RESULTS

Summary of numerical data

The complete dataset comprises 8032 samples. The 7276 samples of living assemblages considered by Murray (2006) are distributed

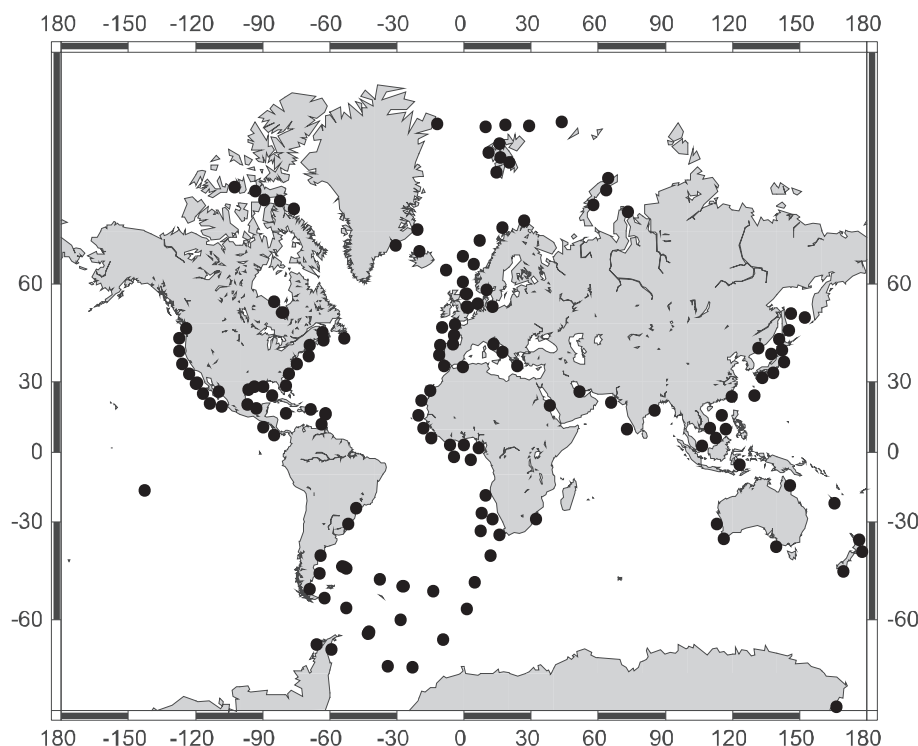


Fig. 1. Map broadly indicating the distribution of data by means of dots.

between environments in the following way: 52% marginal marine, 5% fjords, 31% continental shelf and 12% deep sea. The geographical distribution of species which are dominant or subsidiary (having >10% abundance) is shown in a series of diagrams in the book. Species that never reach 10% abundance are omitted from the diagrams but are nevertheless included in the web appendix tables. There is a strong bias towards the North Atlantic with very little information from the Pacific in relation to its great size (mainly from western USA and Japan) or the Indian Ocean which has hardly been explored. The 756 additional samples from 2005–2011 show the same geographical bias and the distribution by environments is broadly similar to that of the book data: 37% marginal marine, 1% fjords, 43% continental shelf and 18% deep sea.

Summary information on the distribution of abundance in the complete dataset and between environments is given in Table 2. The taxa are listed alphabetically to make it easier to find a species. The data are presented in the following way, taking the example of *Ammoastuta inepta*. This species occurs in 46 samples which make up 0.6% of the 8032 samples. There are 13 samples where the species abundance is >10% and these make up 28.3% of the samples in which this species is present. Therefore, 71.7% of the occurrences have a species abundance of <10%. There are 2 samples with a species abundance of <1% and these make up 4.3% of the occurrences of this species.

All species have some abundances <1% even if they are locally highly abundant. The section of Table 2 labelled ‘% samples in each major environment’ shows the distribution of samples between major environments. Perhaps the most surprising feature of these results is the number of environments over which some species are spread; in many cases it is 3 or 4 out of the 5 divisions. The only species confined to a single environment are *Balticammina pseudomacrescens* (marsh), *Guttulina problema*,

Reussella spinulosa, *Vasiglobulina* (shelf), and 12 deep sea species: *Astrononion echolsi*, *Fursenkoina apertura*, *Gyroidina altiformis*, *G. polia*, *Laticarinina pauperata*, *Nuttallides pusillus*, *N. umboniferus*, *Oridorsalis sidebottomi*, *O. tener*, *Osangularia culter*, *Pullenia salisburyi* and *P. simplex*. None of the taxa studied is confined to either marginal marine or fjord environments.

Statistics have been assembled on 31 agglutinated, 2 porcelainous and 99 hyaline taxa (Table 3). The overall mean abundance is not commonly >10% in the species selected for study. The maximum abundances refer to the single highest value in each environment. Nevertheless, some maximum abundances of >10% are found even in species having a low mean abundance.

Categories of species abundance

A species abundance in an assemblage of >10% is the criterion for defining the six categories in Tables 1 and 4. The proportion of occurrences (%) relates to the number of samples in which the species is present. At the high extreme, Group 1, the listed species have abundances >10% in >40% of the occurrences. In the case of Group 6 no samples have >10% abundance for any of the species listed. Graphical plots of species abundance against number of occurrences show different patterns from group to group (Fig. 3). The curves of rare species in Group 6 are flat along the x-axis whereas the very abundant forms in Group 1 have a significant number of high values.

Biogeography and comments on species ecology

Details of the numerical distributions are given in Tables 2 and 3. In order to improve the flow of the text the notes and biogeographical plots of individual taxa (Figs 4–95) are given in the Appendix. The sources of data used to compile these figures are given in Supplementary Publication tables 3–18.

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marginal marine	Fjords	Shelf	Deep sea
	Arctic Ocean		36	95-98	36, 111	111,212
70-60	N & W Norway			99,100, N19,N20		193,N41
65	Iceland				191	191,192
55-59	S Scandinavia/Baltic	1	37,112,N10,N11	101-106	113	
56	Seas around UK	1-3, N1	38-46	107	40, 114-120,192	
43-45	Biscay	4, 5	47-49		121,122, N25,N26	199,N26,N42-N46
39	Portugal	N5	N5		123,194,N47	123, 194-196,N47-N49
43	W Mediterranean		90		90, N27,N28	204,N50-N51
45	E Mediterranean	6	50,51,N12, 124		124-130,N29	127
20	NW Africa				131,132	131,200
0	Gulf of Guinea				133	133,201
10-30	S Atlantic					202
35-56	S Atlantic					203

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marginal marine	Fjords	Shelf	Deep sea
70	E Greenland			93,94		197,198
73	Arctic Canada				134,135	134,135
50-43	Canada	7-13,N2	52-54		53,136,137	
45-40	E USA	14-16	55-57,59,60		138,139	205,206
40-25	E USA	17-20,62,N3,N4	58,61-66		140-142	N52
30	N Gulf of Mexico	21-23	67-69,91,92,N13		91,92,143-146	207
25-18	S Gulf of Mexico		70-72			
18-12	Caribbean Sea		73-76,78		147-149,N30	
5	French Guiana	24				
24-31	Brazil	25,26	79,80			
38-54	Argentina	25	81		150,151	151
58	Scotia Sea					214
67	Weddell Sea					173,213,215,216

REST OF WORLD

~ lat.	Area	Marsh	Marginal marine	Fjords	Shelf	Deep sea
48	Pacific Canada	27,28				
47-33	Pacific USA	27,29	82-84,152,N14		153	154-160,208,209
28	Baja California	27,30,31	30,31		153	160
12	El Salvador-Nicaragua				162	162,N31
35	Korea & Japan	32,86	85,N15		163-167,181,N33	163-166, N40,210
x	S China Sea		86		N32	211,N53
5	Banda Sea	35				
40	New Zealand	33,34,N6			169	
18	Atolls				170,N34	
	Red Sea/Arabian Gulf		182-183,185		184	
10	Indian Ocean		88		88,171	N54,N55
28	S Africa		89			
15-30	Australia	N7	168			
65	Antarctic				172,217	217-219

Fig. 2. Template for plotting biogeography by environment. The numbers refer to the data spreadsheets (see Supplementary Publication table 2).

DISCUSSION

‘Explaining observed patterns of densities by environmental variables is much more difficult than their recognition’ (Buzas *et al.*, 1977, p. 56).

No synthesis of data collected over six decades can provide an instantaneous ‘snapshot’ of distribution or abundance; at best they give an overview. Nevertheless, some clear patterns are evident:

Although all species show low abundance (are rare) in part of their range, only some species also show high abundance (Fig. 3).

For the first time it is shown that species thought to be typical of one environment are also found quite commonly in other environments (Tables 2, 3).

There is a mix of disjunct (discontinuous) and continuous biogeographical distributions (Figs 4–95).

Patterns of abundance

Six categories of abundance are distinguished (Fig. 3, Tables 1, 4). It is inevitable that the typical representatives of Group 1 are from low diversity assemblages because only where the number of species is low is it likely that high relative abundances can be

reached. What is surprising is that even in species normally considered to be abundant the proportion having a relative abundance of >10% is modest. For example, this value is reached in only 45% of samples containing *Miliammina fusca* and 41% for *Stainforthia fusiformis* (both in Group 1). *Textularia earlandi*, a Group 4 species which is widespread (Fig. 27), has only 5% of its occurrences >10% while 50% of its occurrences have relative abundances of <1%. As discussed in the Introduction, many ecologists regard rarity as an anomaly whereas these results clearly show that for benthic foraminifera it is quite normal.

Environmental spread of species

The divisions between major environments are arbitrary and anthropogenic (e.g. selecting a specific depth as the boundary between shelf and slope) whereas in nature there is a continuum between adjacent environments. Therefore, it is not surprising that individual species do not respect these boundaries. Thus, marginal marine species may extend their distributions on to marshes or inner continental shelf, and shelf and deep-sea species may overlap. However, it is very surprising that so many species occur in four of the major environments (Table 2, e.g. *Ammobaculites agglutinans*, *Ammoscalaria*

Table 2. The number of samples and their proportions in the whole dataset.

Species	Occurrences							% of samples in each major environment					
	Samples with sp.	% all samples	Samples abund >10%	% samples abund >10%	% samples abund <10%	Samples abund <1%	% samples abund <1%	Abundance Group	Marsh	Marginal marine	Fjord	Shelf	Deep sea
Agglutinated													
<i>Ammonoastuta inepta</i>	46	0.57	13	28.26	71.74	2	4.35	2	56.52	41.30	absent	2.17	absent
<i>Ammobaculites agglutinans</i>	228	2.84	10	4.39	95.61	102	44.74	4	absent	4.82	0.88	26.75	67.54
<i>Ammobaculites balkwilli</i>	103	1.28	10	9.71	90.29	45	43.69	4	1.94	93.20	4.85	absent	absent
<i>Ammobaculites dilatatus</i>	92	1.15	5	5.43	94.57	30	32.61	4	38.04	47.83	absent	14.13	absent
<i>Ammobaculites exiguus</i>	89	1.11	17	19.10	80.90	26	29.21	3	68.54	7.87	absent	23.60	absent
<i>Ammobaculites filiformis</i>	75	0.93	2	2.67	97.33	38	50.67	4	absent	absent	absent	1.33	98.67
<i>Ammoscalaria runiana</i>	114	1.42	7	6.14	93.86	45	39.47	4	1.75	83.33	9.60	5.26	absent
<i>Ammotium salsum</i>	620	7.72	267	43.06	56.94	66	10.65	1	51.77	40.32	absent	7.90	absent
<i>Arenoparella mexicana</i>	214	2.66	50	23.36	76.64	37	17.29	2	84.11	15.89	absent	absent	absent
<i>Balticamina pseudomacrescens</i>	337	4.20	265	78.64	21.36	4	1.19	1	100.00	absent	absent	absent	absent
<i>Eggerella advena</i>	517	6.44	103	19.92	80.08	277	53.58	2	1.16	9.28	1.35	62.28	25.92
<i>Eggerella europea</i>	18	0.22	0	0.00	100.00	16	88.89	6	absent	absent	16.67	83.33	absent
<i>Eggerelloides medius</i>	110	1.37	24	21.82	78.18	11	10.00	2	absent	absent	24.55	73.64	1.82
<i>Eggerelloides scaber</i>	846	10.53	141	16.67	83.33	231	27.30	3	absent	14.30	16.78	59.57	9.34
<i>Gaudryina exilis</i>	98	1.22	4	4.08	95.92	36	36.73	4	21.40	61.20	absent	17.30	absent
<i>Gaudryina pauperata</i>	32	0.40	1	3.13	96.88	10	31.25	4	56.30	21.90	absent	18.75	3.13
<i>Glomospira gordialis</i>	155	1.93	1	0.65	99.35	96	61.94	5	0.64	17.95	0.64	35.90	44.23
<i>Haplophragmoides bradyi</i>	314	3.91	15	4.78	95.22	143	45.54	4	absent	absent	8.60	28.66	62.74
<i>Haplophragmoides shallow spp.</i>	402	5	119	29.60	70.40	45	11.19	2	92.79	6.97	absent	0.25	absent
<i>Jadammina macrescens</i>	818	10.18	363	44.38	55.62	118	14.43	1	81.42	17.97	0.12	0.49	absent
<i>Miliammina fusca</i>	1807	22.50	808	44.71	55.29	173	9.57	1	56.89	40.01	1.77	1.33	absent
<i>Reophax moniliformis</i>	256	3.19	17	6.64	93.36	123	48.05	3	11.72	76.56	0.39	11.33	absent
<i>Reophax nana</i>	170	2.12	15	8.82	91.18	84	49.41	4	19.41	71.18	absent	9.41	absent
<i>Siphotrochammina lobata</i>	56	0.70	14	25.00	75.00	4	7.14	2	82.10	17.90	absent	absent	absent
<i>Textularia earlandi</i>	607	7.56	33	5.44	94.56	305	50.25	4	13.51	34.43	6.59	28.83	16.64
<i>Tiphotrecha comprimata</i>	412	5.13	194	47.09	52.91	19	4.61	1	98.30	1.70	absent	absent	absent
<i>Trochammina inflata</i>	1169	14.55	548	46.88	53.12	166	14.20	1	81.42	17.97	0.12	0.49	absent
<i>Trochammina lobata</i>	21	0.26	0	0.00	100.00	7	33.33	6	absent	absent	absent	95.20	4.80
<i>Trochammina pacifica</i>	197	2.45	18	9.14	90.86	84	42.64	4	absent	6.60	absent	44.67	48.73
<i>Uszbekistania charoides</i>	150	1.87	0	0.00	100.00	93	62.00	6	absent	6.67	absent	15.33	78.00
Porcelaneous													
<i>Cornuspira involvens</i>	428	5.33	15	3.50	96.50	253	59.11	4	28.97	13.32	3.97	31.78	21.96
<i>Pyrgo williamsoni</i>	77	0.96	1	1.30	98.70	43	55.84	5	absent	1.30	32.47	31.17	35.06
Hyaline													
<i>Amphicoryna</i>	180	2.24	3	1.67	98.33	114	63.33	5	absent	absent	absent	51.67	48.33
<i>Astacolus</i>	52	0.65	0	0.00	100.00	43	82.69	6	absent	absent	5.77	67.31	26.92
<i>Asterigerina carinata</i>	70	0.87	12	17.14	82.86	17	24.29	3	absent	61.43	absent	38.57	absent
<i>Asterigerinata adriatica</i>	23	0.29	2	8.70	91.30	5	21.74	4	absent	absent	absent	100.00	absent
<i>Asterigerinata mamilla</i>	150	1.87	2	1.33	98.67	93	62.00	5	absent	14.67	absent	84.67	0.67
<i>Astronion echolsi</i>	46	0.57	0	0.00	100.00	15	32.61	6	absent	absent	absent	absent	100.00
<i>Astronion gallowayi</i>	151	1.88	19	12.58	87.42	54	35.76	3	absent	absent	34.44	39.74	25.83
<i>Astronion sidebottomi</i>	64	0.80	1	1.56	98.44	37	57.81	5	absent	absent	absent	100.00	absent
<i>Astronion stelligerum</i>	39	0.49	0	0.00	100.00	26	66.67	6	absent	2.56	absent	79.49	17.95
<i>Astronion all spp.</i>	361	4.49	21	5.82	94.18	161	44.60	4	absent	1.94	14.13	45.71	38.23
<i>Bulminella elegantissima</i>	887	11.04	109	12.29	87.71	373	42.05	3	1.80	56.26	0.23	40.92	0.79
<i>Dentalina spp.</i>	228	2.84	0	0.00	100.00	178	78.07	6	absent	0.44	5.26	38.16	56.14
<i>Ehrenbergina</i>	72	0.90	4	5.56	94.44	29	40.28	4	absent	1.39	absent	33.33	65.28
<i>Fissurina laevigata</i>	132	1.64	1	0.76	99.24	94	71.21	5	0.76	21.21	3.79	71.97	2.27
<i>Fissurina lucida</i>	416	5.18	4	0.96	99.04	251	60.34	5	7.21	59.62	absent	30.05	3.13
<i>Fissurina marginata</i>	108	1.34	2	1.85	98.15	60	55.56	5	absent	12.04	4.63	64.81	18.52
<i>Fissurina orbignyana</i>	70	0.87	0	0.00	100.00	45	64.29	6	absent	1.45	absent	86.96	11.59
<i>Fissurina all spp.</i>	1140	14.19	12	1.05	98.95	868	76.14		3.17	11.37	1.67	52.86	30.93
<i>Fursenkoina apertura</i>	113	1.41	49	43.36	56.64	11	9.73	1	absent	absent	absent	absent	100.00
<i>Fursenkoina bramletti</i>	30	0.37	0	0.00	100.00	19	63.33	6	absent	absent	absent	absent	100.00
<i>Fursenkoina complanata</i>	97	1.21	0	0.00	100.00	53	54.64	6	absent	25.77	absent	59.79	14.43
<i>Fursenkoina earlandi</i>	45	0.56	11	24.44	75.56	13	28.89	2	absent	absent	absent	4.44	95.56
<i>Fursenkoina mexicana</i>	35	0.44	1	2.86	97.14	18	51.43	4	absent	22.86	absent	2.86	74.29
<i>Fursenkoina pontoni</i>	212	2.64	103	48.58	51.42	32	15.09	1	absent	28.30	absent	64.62	7.08
<i>Fursenkoina punctata</i>	158	1.97	18	11.39	88.61	39	24.68	3	absent	31.01	absent	68.99	absent
<i>Fursenkoina sandiegoensis</i>	78	0.97	3	3.85	96.15	34	43.59	4	absent	16.67	absent	2.56	80.77
<i>Fursenkoina schreibersiana</i>	81	1.01	2	2.47	97.53	31	38.27	4	absent	23.46	absent	64.20	12.35
<i>Glandulina</i>	106	1.32	0	0.00	100.00	75	70.75	6	absent	absent	3.77	66.04	30.19
<i>Globulina all spp.</i>	22	0.27	0	0.00	100.00	16	72.73	6	absent	absent	9.09	72.73	18.18
<i>Globocassidulina subglobosa</i>	595	7.41	33	5.55	94.45	284	47.73	4	absent	4.37	absent	45.04	50.59
<i>Guttulina lactea</i>	30	0.37	0	0.00	100.00	20	66.67	6	absent	3.33	3.33	93.33	absent
<i>Guttulina problema</i>	53	0.66	3	5.66	94.34	18	33.96	4	absent	absent	absent	100.00	absent
<i>Guttulina all spp.</i>	154	1.92	7	4.55	95.45	80	51.95	4	absent	4.55	10.39	81.82	3.25

Table 2. (Continued)

Species	Occurrences						% of samples in each major environment						
	Samples with sp.	% all samples	Samples abund >10%	% samples abund >10%	% samples abund <10%	Samples abund <1%	% samples abund <1%	Abundance Group	Marsh	Marginal marine	Fjord	Shelf	Deep sea
<i>Gyroidina altiformis</i>	76	0.95	0	0.00	100.00	58	76.32	6	absent	absent	absent	absent	100.00
<i>Gyroidina lamarckiana</i>	90	1.12	0	0.00	100.00	45	50.00	6	absent	absent	absent	3.33	96.67
<i>Gyroidina neosoldanii</i>	50	0.62	0	0.00	100.00	27	54.00	6	absent	absent	absent	2.00	98.00
<i>Gyroidina orbicularis</i>	121	1.51	3	2.48	97.52	59	48.76	4	absent	absent	absent	0.83	99.17
<i>Gyroidina polia</i>	83	1.03	0	0.00	100.00	51	61.45	6	absent	absent	absent	absent	100.00
<i>Gyroidina umbonata</i>	167	2.08	1	0.60	99.40	118	70.66	5	absent	absent	absent	14.97	85.03
<i>Gyroidina</i> all spp.	739	9.20	5	0.68	99.32	462	62.52		absent	absent	0.27	4.74	94.99
<i>Haynesina germanica</i>	1185	14.75	821	69.28	30.72	78	6.58	1	15.78	81.77	1.10	1.35	absent
<i>Haynesina orbiculare</i>	134	1.67	68	50.75	49.25	12	8.96	1	35.07	50.75	14.18	absent	absent
<i>Helenina anderseni</i>	148	1.84	26	17.57	82.43	54	36.49	3	51.35	31.76	16.89	absent	absent
<i>Hoeglundina elegans</i>	290	3.61	25	8.62	91.38	120	41.38	4	absent	absent	absent	14.48	85.52
<i>Hopkinsina pacifica atlantica</i>	354	4.41	38	10.73	89.27	117	33.05	3	absent	47.46	absent	52.54	absent
<i>Hyalinea balthica</i>	246	3.06	11	4.47	95.53	125	50.81	4	absent	absent	11.79	48.37	39.84
<i>Lagena clavata</i>	46	0.57	0	0.00	100.00	35	76.09	6	absent	13.04	absent	84.78	2.17
<i>Lagena gracillima</i>	54	0.67	0	0.00	100.00	44	81.48	6	absent	absent	11.11	57.41	31.48
<i>Lagena laevis</i>	49	0.61	0	0.00	100.00	38	77.55	6	absent	12.00	6.00	78.00	4.00
<i>Lagena striata</i>	64	0.80	1	1.56	98.44	56	87.50	5	absent	4.69	absent	89.06	6.25
<i>Lagena substriata</i>	38	0.47	0	0.00	100.00	28	73.68	6	absent	7.89	2.63	84.21	5.26
<i>Lagena</i> all spp.	825	10.27	4	0.48	99.52	631	76.48	5	2.91	4.48	2.18	62.06	28.36
<i>Lamarckina haliotideae</i>	61	0.76	0	0.00	100.00	33	54.10	6	absent	9.84	1.64	88.52	absent
<i>Laricarinina pauperata</i>	35	0.44	0	0.00	100.00	24	68.57	6	absent	absent	absent	absent	100.00
<i>Lenticulina peregrina</i>	95	1.18	0	0.00	100.00	78	82.11	6	absent	absent	absent	18.95	81.05
<i>Lenticulina</i> all spp.	635	7.91	2	0.31	99.69	519	81.73	5	absent	0.79	0.94	46.61	51.65
<i>Marginulina</i>	43	0.54	0	0.00	100.00	42	97.67	6	absent	absent	absent	48.84	51.16
<i>Melonis barleeaanum</i>	553	6.88	112	20.25	79.75	138	24.95	2	absent	absent	2.17	22.97	74.86
<i>Melonis pompilioides</i>	124	1.54	2	1.61	98.39	53	42.74	5	absent	4.03	absent	29.84	66.13
<i>Melonis</i> all spp.	679	8.45	12	1.77	98.23	194	28.57	5	absent	0.74	1.77	24.15	73.34
<i>Nodosaria</i>	55	0.68	0	0.00	100.00	48	87.27	6	absent	1.82	1.82	56.36	40.00
<i>Nonion depressulus</i>	548	6.82	77	14.05	85.95	231	42.15	3	0.91	60.40	0.73	37.96	absent
<i>Nonionellina labradorica</i>	205	2.55	70	34.15	65.85	32	15.61	2	absent	absent	58.54	21.46	20.00
<i>Nuttallides pusillus</i>	51	0.63	16	31.37	68.63	19	37.25	2	absent	absent	absent	absent	100.00
<i>Nuttallides umboniferus</i>	150	1.87	18	12.00	88.00	53	35.33	3	absent	absent	absent	absent	100.00
<i>Oolina</i>	133	1.66	0	0.00	100.00	96	72.18	6	3.01	3.76	1.50	36.84	54.89
<i>Oridorsalis sidebottomi</i>	7	0.09	0	0.00	100.00	3	42.86	6	absent	absent	absent	absent	100.00
<i>Oridorsalis tener</i>	31	0.39	0	0.00	100.00	9	29.03	6	absent	absent	absent	absent	100.00
<i>Oridorsalis umbonatus</i>	335	4.17	17	5.07	94.93	141	42.09	4	absent	absent	1.19	2.09	96.72
<i>Osangularia culter</i>	48	0.60	0	0.00	100.00	24	50.00	6	absent	absent	absent	absent	100.00
<i>Patellina corrugata</i>	215	2.68	8	3.72	96.28	97	45.12	4	absent	4.15	3.69	80.18	11.98
<i>Polymorphinid</i>	124	1.54	0	0.00	100.00	94	75.81	6	absent	absent	14.71	73.53	11.76
<i>Pullenia bulloides</i>	389	4.84	20	5.14	94.86	123	31.62	4	absent	absent	2.31	10.28	87.40
<i>Pullenia osloensis</i>	83	1.03	22	26.51	73.49	13	15.66	2	absent	absent	20.48	65.06	14.46
<i>Pullenia quinqueloba</i>	100	1.25	0	0.00	100.00	60	60.00	6	absent	absent	absent	7.00	93.00
<i>Pullenia salisburyi</i>	63	0.78	0	0.00	100.00	48	76.19	6	absent	absent	absent	absent	100.00
<i>Pullenia simplex</i>	105	1.31	4	3.81	96.19	42	40.00	4	absent	absent	absent	absent	100.00
<i>Pullenia subcarinata</i>	266	3.31	4	1.50	98.50	134	50.38	5	absent	absent	2.26	15.79	81.95
<i>Reussella aculeata</i>	42	0.52	1	2.38	97.62	16	38.10	4	absent	2.33	absent	97.67	absent
<i>Reussella atlantica</i>	84	1.05	3	3.57	96.43	30	35.71	4	absent	39.29	absent	60.71	absent
<i>Reussella pacifica</i>	16	0.20	1	6.25	93.75	9	56.25	4	absent	6.25	absent	93.75	absent
<i>Reussella spinulosa</i>	223	2.78	4	1.79	98.21	99	44.39	5	absent	absent	absent	100.00	absent
<i>Reussella</i> all spp.	376	4.68	9	2.39	97.61	179	47.61	4	absent	9.31	absent	90.69	absent
<i>Robertina arctica</i>	81	1.01	3	3.70	96.30	38	46.91	4	absent	1.23	19.75	66.67	12.35
<i>Robertina charlottensis</i>	28	0.35	0	0.00	100.00	10	35.71	6	absent	absent	1.96	29.41	68.63
<i>Robertina</i> all spp.	288	3.59	6	2.08	97.92	87	30.21	4	absent	0.35	6.60	30.90	62.15
<i>Siphonina bradyana</i>	33	0.41	0	0.00	100.00	22	66.67	6	absent	absent	absent	18.18	81.82
<i>Siphonina pulchra</i>	38	0.47	0	0.00	100.00	8	21.05	6	absent	55.26	absent	42.11	2.63
<i>Siphonina reticulata</i>	16	0.20	0	0.00	100.00	7	43.75	6	absent	absent	absent	62.50	37.50
<i>Siphonina tubulosa</i>	23	0.29	0	0.00	100.00	11	47.83	6	absent	4.35	absent	91.30	4.35
<i>Siphonina</i> all spp.	114	1.42	0	0.00	100.00	49	42.98	6	absent	19.30	absent	50.00	30.70
<i>Sphaeroidina bulloides</i>	133	1.66	0	0.00	100.00	81	60.90	6	absent	absent	absent	23.31	76.69
<i>Spirillina vivipara</i>	277	3.45	36	13.00	87.00	109	39.35	3	9.72	12.11	absent	76.47	1.74
<i>Stainforthia fusiformis</i>	647	8.06	263	40.65	59.35	149	23.03	1	absent	23.96	17.31	54.10	4.64
<i>Stainforthia concava</i>	102	1.27	1	0.98	99.02	68	66.67	5	absent	0.98	17.65	64.71	16.67
<i>Stainforthia loeblichii</i>	70	0.87	11	15.71	84.29	22	31.43	3	absent	absent	64.29	30.00	5.71
<i>Trifarina angulosa</i>	621	7.73	77	12.40	87.60	200	32.21	3	absent	3.22	1.77	68.28	26.73
<i>Trifarina fluens</i>	74	0.92	2	2.70	97.30	17	22.97	4	absent	absent	20.27	35.14	44.59
<i>Vasiglobulina</i>	40	0.50	0	0.00	100.00	20	50.00	6	absent	absent	absent	100.00	absent

Column 2 gives the number of samples containing a named species and column 3 its proportion of the whole dataset. Column 4 gives the number of samples where the species abundance is >10%. Columns 5 and 6 give the proportion of samples where the abundance of a species is > 10% or 10% respectively. Column 7 gives the number of samples where the species abundance is <1% and Column 8 the proportion of samples with this abundance. Column 9 gives the abundance group defined in Table 1. Columns 10-14 give the proportion of samples of the named species in each major environment; the maximum values are highlighted in **bold**.

Table 3. Mean and maximum abundance values for each taxon in each major environment.

Species	Overall mean %	Environments – abundance mean %					Environments – abundance maximum %				
		Marsh	Marg. mar.	Fjord	Shelf	Deep sea	Marsh	Marg. mar.	Fjord	Shelf	Deep sea
Agglutinated											
<i>Ammonoastuta inepta</i>	11.33	17.12	3.95	absent	1.00	absent	51.50	12.00	absent	1.00	absent
<i>Ammobaculites agglutinans</i>	2.51	absent	0.89	5.00	1.65	2.94	absent	2.20	6.00	15.40	25.60
<i>Ammobaculites balkwilli</i>	3.75	6.95	3.73	3.00	absent	absent	13.60	44.00	7.50	absent	absent
<i>Ammobaculites dilatatus</i>	3.76	6.09	2.67	absent	1.14	absent	93.00	34.00	absent	3.20	absent
<i>Ammobaculites exiguus</i>	5.76	7.61	1.26	absent	1.85	absent	90.00	2.00	absent	13.80	absent
<i>Ammobaculites filiformis</i>	1.66	absent	absent	absent	0.20	1.68	absent	absent	absent	0.20	14.90
<i>Ammoscalaria runiana</i>	3.06	1.19	3.40	1.75	0.77	absent	1.60	34.65	3.80	1.50	absent
<i>Ammotium salsum</i>	16.39	17.17	17.22	absent	7.07	absent	100.00	100.00	absent	38.00	absent
<i>Arenoparella mexicana</i>	9.13	10.12	3.86	absent	absent	absent	92.00	28.10	absent	absent	absent
<i>Balticammina pseudomacrescens</i>	39.69	absent	absent	absent	absent	absent	39.69	absent	absent	absent	absent
<i>Eggerella advena</i>	7.90	1.13	26.68	2.20	7.68	2.29	2.00	78.80	6.40	68.40	30.80
<i>Eggerella europea</i>	0.50	absent	absent	0.37	0.53	absent	absent	absent	0.40	4.80	absent
<i>Eggerelloides medius</i>	7.02	absent	absent	14.19	4.80	0.10	absent	absent	49.40	24.90	0.10
<i>Eggerelloides scaber</i>	6.39	absent	4.16	16.17	4.87	1.92	absent	67.60	83.20	47.60	10.51
<i>Gaudryina exilis</i>	2.41	5.74	1.79	absent	0.51	absent	27.50	5.70	absent	1.30	absent
<i>Gaudryina pauperata</i>	2.41	2.12	3.76	absent	1.93	1.00	8.00	14.00	absent	3.00	1.00
<i>Glomospira gordialis</i>	1.11	2.20	1.49	2.67	1.32	0.76	2.20	17.02	2.67	7.02	3.20
<i>Haplophragmoides bradyi</i>	2.29	absent	absent	7.23	2.16	1.67	absent	absent	15.38	13.64	26.15
<i>Haplophragmoides shallow spp.</i>	11.71	12.51	1.47	absent	1.00	absent	96.05	9.60	absent	1.00	absent
<i>Jadammina macrescens</i>	16.84	19.84	3.73	0.50	2.95	absent	100.00	76.30	0.50	4.60	absent
<i>Miliammina fusca</i>	19.66	26.75	10.42	9.83	7.64	absent	100.00	100.00	88.00	44.90	absent
<i>Reophax moniliformis</i>	3.20	3.75	3.41	3.80	1.22	absent	34.20	19.60	3.80	10.90	absent
<i>Reophax nana</i>	3.92	4.14	4.11	absent	2.00	absent	17.00	48.00	absent	7.70	absent
<i>Siphotrochammina lobata</i>	7.63	8.62	3.08	absent	absent	absent	33.00	8.30	absent	absent	absent
<i>Textularia earlandi</i>	2.64	2.69	2.79	2.05	2.85	2.16	17.10	58.50	26.80	30.30	25.50
<i>Tiphotrocha comprimata</i>	14.74	14.96	2.17	absent	absent	absent	80.00	2.30	absent	absent	absent
<i>Trochammina inflata</i>	17.37	19.84	3.73	0.50	2.95	absent	100.00	76.30	0.50	4.60	absent
<i>Trochammina lobata</i>	2.71	absent	absent	absent	2.82	0.65	absent	absent	absent	27.50	1.30
<i>Trochammina pacifica</i>	3.27	absent	2.10	absent	5.33	1.53	absent	34.97	absent	38.33	16.00
<i>Uszbekistania charoides</i>	1.06	absent	1.10	absent	0.84	1.15	absent	1.00	absent	5.74	4.62
Porcelaneous											
<i>Cornuspira involvens</i>	2.19	3.03	2.07	4.41	1.85	1.27	53.00	37.30	48.40	47.00	35.00
<i>Pyrgo williamsoni</i>	1.67	absent	0.47	1.27	1.83	0.91	absent	0.47	5.94	19.17	3.00
Hyaline											
<i>Amphicoryna</i>	1.37	absent	absent	absent	1.46	1.29	absent	absent	absent	15.40	11.30
<i>Astacolus</i>	0.67	absent	absent	1.54	0.55	0.79	absent	absent	4.21	1.90	2.40
<i>Asterigerina carinata</i>	5.33	absent	2.77	absent	9.41	absent	absent	5.20	absent	27.64	absent
<i>Asterigerinata adriatica</i>	4.54	absent	absent	absent	4.54	absent	absent	absent	absent	14.00	absent
<i>Asterigerinata mamilla</i>	1.52	absent	2.00	absent	1.45	0.50	absent	5.20	absent	27.64	0.50
<i>Astrononion echolsi</i>	2.29	absent	absent	absent	absent	2.29	absent	absent	absent	absent	8.02
<i>Astrononion gallowayi</i>	4.38	absent	absent	4.87	5.43	2.12	absent	absent	34.97	38.33	16.00
<i>Astrononion sidebottomi</i>	1.19	absent	absent	absent	1.19	absent	absent	absent	absent	11.00	absent
<i>Astrononion stelligerum</i>	1.27	absent	1.40	absent	1.43	0.57	absent	1.40	absent	6.50	2.00
<i>Astrononion all spp.</i>	2.74	absent	1.57	4.96	2.91	1.78	absent	4.00	34.97	38.33	16.00
<i>Buliminella elegantissima</i>	4.75	4.42	4.91	0.10	4.60	2.93	21.00	77.23	0.10	97.00	17.00
<i>Dentalina spp.</i>	0.76	absent	0.60	0.24	0.89	0.72	absent	0.60	1.40	7.70	4.80
<i>Ehrenbergina</i>	3.02	absent	0.51	absent	2.29	3.44	absent	0.51	absent	22.00	18.96
<i>Fissurina laevigata</i>	0.87	0.70	1.75	0.98	0.61	0.63	0.70	10.00	2.22	2.90	0.60
<i>Fissurina lucida</i>	1.34	3.29	1.39	absent	0.79	1.12	10.30	10.00	absent	3.60	3.00
<i>Fissurina marginata</i>	1.31	absent	0.83	0.57	1.36	1.65	absent	2.35	2.22	10.53	12.50
<i>Fissurina orbignyana</i>	0.98	absent	1.80	absent	0.91	0.84	absent	1.80	absent	3.20	0.90
<i>Fissurina all spp.</i>	1.09	2.86	1.41	1.13	0.94	1.06	10.30	10.00	2.22	24.20	12.66
<i>Fursenkoina apertura</i>	12.60	absent	absent	absent	absent	12.60	absent	absent	absent	absent	62.00
<i>Fursenkoina bramletti</i>	1.54	absent	absent	absent	absent	1.54	absent	absent	absent	absent	6.20
<i>Fursenkoina complanata</i>	1.29	absent	1.75	absent	1.07	1.36	absent	8.00	absent	5.10	8.90
<i>Fursenkoina earlandi</i>	8.62	absent	absent	absent	1.00	8.98	absent	absent	absent	22.00	67.00
<i>Fursenkoina mexicana</i>	2.68	absent	0.64	absent	0.80	3.38	absent	1.20	absent	0.80	23.10
<i>Fursenkoina pontoni</i>	16.65	absent	13.61	absent	18.62	10.80	absent	74.70	absent	90.10	25.80
<i>Fursenkoina punctata</i>	4.90	absent	8.78	absent	3.16	absent	absent	56.40	absent	22.20	absent
<i>Fursenkoina sandiegoensis</i>	2.31	absent	4.31	absent	0.40	1.96	absent	13.00	absent	0.60	12.00
<i>Fursenkoina schreibersiana</i>	2.51	absent	2.66	absent	2.70	1.19	absent	9.60	absent	38.60	3.00
<i>Glandulina</i>	0.83	absent	absent	0.66	0.94	0.63	absent	absent	2.00	6.90	2.00
<i>Globulina all spp.</i>	1.01	absent	absent	0.41	1.17	0.67	absent	absent	0.50	1.31	0.68
<i>Globocassidulina subglobosa</i>	2.54	absent	3.62	absent	2.37	2.61	absent	18.18	absent	27.00	28.80
<i>Guttulina lactea</i>	0.82	absent	0.20	1.20	0.83	absent	absent	0.20	1.20	2.92	absent
<i>Guttulina problema</i>	3.47	absent	absent	absent	3.47	absent	absent	absent	absent	15.22	absent
<i>Guttulina all spp.</i>	2.30	absent	11.12	0.45	2.12	0.42	absent	45.44	1.20	15.22	1.30

Species	Overall mean %	Environments – abundance mean %					Environments – abundance maximum %				
		Marsh	Marg. mar.	Fjord	Shelf	Deep sea	Marsh	Marg. mar.	Fjord	Shelf	Deep sea
<i>Gyroidina altiformis</i>	0.91	absent	absent	absent	absent	0.91	absent	absent	absent	absent	9.79
<i>Gyroidina lamarckiana</i>	1.62	absent	absent	absent	0.70	1.65	absent	absent	absent	0.90	9.00
<i>Gyroidina neosoldanii</i>	1.20	absent	absent	absent	0.59	1.21	absent	absent	absent	0.59	4.90
<i>Gyroidina orbicularis</i>	1.91	absent	absent	absent	0.06	1.92	absent	absent	absent	0.06	24.70
<i>Gyroidina polia</i>	1.16	absent	absent	absent	absent	1.16	absent	absent	absent	absent	5.77
<i>Gyroidina umbonata</i>	1.02	absent	absent	absent	1.30	0.97	absent	absent	absent	8.20	11.80
<i>Gyroidina</i> all spp.	1.31	absent	absent	0.55	1.64	1.29	absent	absent	0.80	11.80	24.70
<i>Haynesina germanica</i>	28.22	24.22	29.73	5.93	1.61	absent	100.00	100.00	17.20	4.30	absent
<i>Haynesina orbiculare</i>	20.26	9.06	30.39	11.67	absent	absent	5.32	66.50	9.60	absent	absent
<i>Helenina anderseni</i>	6.62	12.11	0.77	0.92	absent	absent	78.00	3.00	5.00	absent	absent
<i>Hoeglundina elegans</i>	3.59	absent	absent	absent	5.68	3.23	absent	absent	absent	30.30	46.39
<i>Hopkinsina pacifica atlantica</i>	4.75	absent	6.99	absent	2.72	absent	absent	56.36	absent	24.42	absent
<i>Hyalinea balthica</i>	2.60	absent	absent	3.43	2.47	2.51	absent	absent	11.30	29.79	72.73
<i>Lagena clavata</i>	0.66	absent	0.96	absent	0.62	0.40	absent	1.32	absent	2.09	0.40
<i>Lagena gracillima</i>	0.70	absent	absent	1.23	0.67	0.58	absent	absent	3.51	4.10	2.37
<i>Lagena laevis</i>	0.74	absent	1.05	0.57	0.69	1.01	absent	1.92	1.10	2.41	1.14
<i>Lagena striata</i>	0.69	absent	0.60	absent	0.52	3.94	absent	0.80	absent	2.00	10.50
<i>Lagena substriata</i>	0.73	absent	1.20	0.26	0.71	0.55	absent	1.60	0.30	1.70	1.00
<i>Lagena</i> all spp.	0.82	3.38	1.01	0.73	0.76	0.67	14.12	4.00	3.51	10.50	5.05
<i>Lamarckina haliotideae</i>	1.42	absent	1.57	1.67	1.51	absent	absent	1.10	1.67	7.03	absent
<i>Laricarinina pauperata</i>	0.80	absent	absent	absent	absent	0.80	absent	absent	absent	absent	4.02
<i>Lenticulina peregrina</i>	0.73	absent	absent	absent	0.56	0.77	absent	absent	absent	2.02	3.60
<i>Lenticulina</i> all spp.	0.33	absent	0.84	0.62	0.41	0.64	absent	1.30	1.40	10.53	11.69
<i>Marginulina</i>	0.40	absent	absent	absent	0.44	0.37	absent	absent	absent	0.88	1.32
<i>Melonis barleeianum</i>	7.89	absent	absent	6.42	7.49	8.06	absent	absent	16.34	60.22	86.40
<i>Melonis pompilioides</i>	2.04	absent	0.73	absent	3.11	1.63	absent	1.07	absent	11.61	8.99
<i>Melonis</i> all spp.	6.80	absent	0.73	6.42	6.50	6.97	absent	1.10	16.34	60.22	86.40
<i>Nodosaria</i>	0.58	absent	0.16	0.28	0.54	0.68	absent	0.16	0.28	1.52	2.00
<i>Nonion depressulus</i>	7.19	3.84	9.97	3.40	2.90	absent	5.32	66.50	9.60	32.40	absent
<i>Nonionellina labradorica</i>	11.80	absent	absent	11.84	9.63	14.00	absent	absent	58.54	17.56	23.90
<i>Nuttallides pusillus</i>	7.88	absent	absent	absent	absent	7.88	absent	absent	absent	absent	39.71
<i>Nuttallides umboniferus</i>	4.17	absent	absent	absent	absent	4.17	absent	absent	absent	absent	33.66
<i>Oolina</i>	0.86	1.50	1.11	1.00	1.13	0.62	2.00	2.84	1.50	5.88	5.62
<i>Oridorsalis sidebottomi</i>	1.00	absent	absent	absent	absent	1.00	absent	absent	absent	absent	5.80
<i>Oridorsalis tener</i>	1.00	absent	absent	absent	absent	1.00	absent	absent	absent	absent	5.30
<i>Oridorsalis umbonatus</i>	3.39	absent	absent	3.54	0.72	3.44	absent	absent	7.14	1.64	56.00
<i>Osangularia culter</i>	1.41	absent	absent	absent	absent	1.41	absent	absent	absent	absent	7.61
<i>Patellina corrugata</i>	2.12	absent	0.68	3.35	2.30	1.03	absent	1.70	12.90	46.30	2.00
<i>Polymorphinid</i>	0.98	absent	absent	2.21	0.76	0.81	absent	absent	9.22	4.20	4.55
<i>Pullenia bulloides</i>	2.87	absent	absent	6.85	5.38	2.77	absent	absent	5.49	21.12	31.48
<i>Pullenia osloensis</i>	6.69	absent	absent	2.95	8.98	1.68	absent	absent	6.69	29.79	9.09
<i>Pullenia quinqueloba</i>	1.14	absent	absent	absent	1.26	1.13	absent	absent	absent	5.13	9.52
<i>Pullenia salisburyi</i>	0.72	absent	absent	absent	absent	0.72	absent	absent	absent	absent	4.76
<i>Pullenia simplex</i>	2.48	absent	absent	absent	absent	2.48	absent	absent	absent	absent	25.00
<i>Pullenia subcarinata</i>	1.61	absent	absent	4.30	0.86	1.68	absent	absent	13.74	4.88	41.40
<i>Reussella aculeata</i>	2.24	absent	0.40	absent	2.29	absent	absent	0.40	absent	11.23	absent
<i>Reussella atlantica</i>	2.25	absent	2.72	absent	1.94	absent	absent	10.34	absent	10.00	absent
<i>Reussella pacifica</i>	2.15	absent	0.40	absent	2.27	absent	absent	0.40	absent	13.00	absent
<i>Reussella spinulosa</i>	1.71	absent	absent	absent	1.71	absent	absent	absent	absent	23.18	absent
<i>Reussella</i> all spp.	1.88	absent	2.59	absent	1.80	absent	absent	11.23	absent	23.18	absent
<i>Robertina arctica</i>	2.17	absent	0.79	4.12	1.63	2.14	absent	0.79	24.52	11.83	5.00
<i>Robertina charlottensis</i>	1.91	absent	absent	2.44	1.84	1.93	absent	absent	2.44	4.00	29.30
<i>Robertina</i> all spp.	1.55	absent	0.79	3.81	1.46	1.35	absent	0.79	24.52	11.83	29.73
<i>Siphonina bradyana</i>	1.12	absent	absent	absent	1.29	1.08	absent	absent	absent	5.43	7.09
<i>Siphonina pulchra</i>	2.02	absent	2.38	absent	1.62	1.00	absent	9.80	absent	4.40	0.68
<i>Siphonina reticulata</i>	0.88	absent	absent	absent	1.24	3.02	absent	absent	absent	4.50	6.67
<i>Siphonina tubulosa</i>	1.64	absent	3.22	absent	0.94	0.14	absent	3.22	absent	2.00	0.14
<i>Siphonina</i> all spp.	1.63	absent	2.42	absent	1.24	1.38	absent	9.80	absent	5.43	7.09
<i>Sphaeroidina bulloides</i>	1.17	absent	absent	absent	1.53	1.06	absent	absent	absent	5.30	9.92
<i>Spirillina vivipara</i>	4.11	6.86	1.40	absent	4.25	0.90	89.00	5.40	absent	50.00	1.50
<i>Stainforthia fusiformis</i>	18.83	absent	2.25	40.57	20.72	1.26	absent	32.00	98.41	93.10	12.40
<i>Stainforthia concava</i>	1.20	absent	3.17	1.24	1.26	0.77	absent	3.17	5.90	19.20	2.80
<i>Stainforthia loeblichii</i>	5.05	absent	absent	4.14	6.72	6.53	absent	absent	14.90	32.90	20.90
<i>Trifarina angulosa</i>	5.22	absent	1.55	1.65	2.78	12.15	absent	4.71	5.52	41.30	76.00
<i>Trifarina fluens</i>	2.95	absent	absent	1.54	2.53	3.92	absent	absent	34.97	38.33	16.00
<i>Vasiglobulina</i>	1.49	absent	absent	absent	1.49	absent	absent	absent	absent	6.77	absent

Values >10% are highlighted.

Table 4. Categories of species abundance.

Very abundant Group 1 >40% of samples	Group 2 20–40% of samples	Group 3 10–20% of samples	Group 4 2–10% of samples	Group 5 0.1–2% of samples	Very rare Group 6 0% of samples
<i>Ammotium salsum</i>	<i>Ammonoastuta inepta</i>	<i>Ammobaculites exiguus</i>	<i>Ammobaculites agglutinans</i>	<i>Glomospira gordialis</i>	<i>Eggerella europea</i> *
<i>Balticammina pseudomacrescens</i>	<i>Arenoparella mexicana</i>	<i>Eggerelloides scaber</i>	<i>Ammobaculites balkwilli</i> *	<i>Pyrgo williamsoni</i>	<i>Trochammina lobata</i> *
<i>Jadammina macrescens</i>	<i>Eggerella advena</i>	<i>Reophax moniliformis</i> *	<i>Ammobaculites dilatatus</i> *	<i>Amphicoryna</i>	<i>Usbekistania charoides</i>
<i>Miliammina fusca</i>	<i>Eggerelloides medius</i>	<i>Asterigerina carinata</i>	<i>Ammobaculites filiformis</i>	<i>Asterigerinata mamilla</i> *	<i>Astacolus</i>
<i>Tiphotrecha comprimata</i>	<i>Haplophragmoides</i> shallow spp.	<i>Astrononion gallowayi</i>	<i>Ammoscalaria runiana</i> *	<i>Astrononion sidebottomi</i> *	<i>Astrononion echolsi</i>
<i>Trochammina inflata</i>	<i>Siphotrechammina lobata</i>	<i>Buliminella elegantissima</i>	<i>Gaudryina exilis</i>	<i>Fissurina laevigata</i>	<i>Astrononion stelligerum</i>
<i>Fursenkoina apertura</i> *	<i>Fursenkoina earlandi</i>	<i>Fursenkoina punctata</i>	<i>Gaudryina pauperata</i>	<i>Fissurina lucida</i>	<i>Dentalina</i> spp.
<i>Fursenkoina pontoni</i>	<i>Melonis barleeianum</i>	<i>Helenina anderseni</i>	<i>Haplophragmoides</i> <i>bradyi</i>	<i>Fissurina marginata</i>	<i>Fissurina orbignyana</i> *
<i>Haynesina germanica</i>	<i>Nonionellina labradorica</i>	<i>Hopkinsina pacifica</i> <i>atlantica</i>	<i>Reophax nana</i>	<i>Gyroidina umbonata</i>	<i>Fursenkoina bramletti</i> *
<i>Haynesina orbiculare</i>	<i>Nuttallides pusillus</i> *	<i>Nonion depressulus</i>	<i>Textularia earlandi</i>	<i>Lagena striata</i>	<i>Fursenkoina complanata</i>
<i>Stainforthia fusiformis</i>	<i>Pullenia osloensis</i>	<i>Nuttallides umboniferus</i>	<i>Trochammina pacifica</i> *	<i>Melonis pompilioides</i>	<i>Glandulina</i>
		<i>Spirillina vivipara</i>	<i>Cornuspira involvens</i>	<i>Pullenia subcarinata</i>	<i>Globulina</i> spp.
		<i>Stainforthia loeblichii</i>	<i>Asterigerinata adriatica</i> *	<i>Reussella spinulosa</i>	<i>Guttulina lactea</i>
		<i>Trifarina angulosa</i>	<i>Ehrenbergina</i>	<i>Stainforthia concava</i>	<i>Gyroidina altiformis</i>
			<i>Fursenkoina mexicana</i>		<i>Gyroidina lamarckiana</i>
			<i>Fursenkoina sandiegoensis</i>		<i>Gyroidina neosoldanii</i>
			<i>Fursenkoina schreibersiana</i>		<i>Gyroidina polia</i>
			<i>Globocassidulina</i> <i>subglobosa</i>		<i>Lagena clavata</i> *
			<i>Guttulina problema</i>		<i>Lagena gracillima</i> *
			<i>Gyroidina orbicularis</i>		<i>Lagena laevis</i> *
			<i>Hoeglundina elegans</i>		<i>Lagena substriata</i> *
			<i>Hyalinea balthica</i>		<i>Lamarckina haliotideia</i> *
			<i>Oridorsalis umbonatus</i>		<i>Laricarinina pauperata</i>
			<i>Patellina corrugata</i>		<i>Lenticulina peregrina</i>
			<i>Pullenia bulloides</i>		<i>Marginulina</i>
			<i>Pullenia simplex</i>		<i>Nodosaria</i>
			<i>Reussella aculeata</i>		<i>Oolina</i>
			<i>Reussella atlantica</i> *		<i>Oridorsalis sidebottomi</i> *
			<i>Reussella pacifica</i> *		<i>Oridorsalis tener</i> *
			<i>Robertina arctica</i>		<i>Osangularia culter</i>
			<i>Trifarina fluens</i>		<i>Polymorphinid</i>
					<i>Pullenia quinqueloba</i>
					<i>Pullenia salisburyi</i>
					<i>Robertina charlottensis</i>
					<i>Siphonina bradyana</i>
					<i>Siphonina pulchra</i> *
					<i>Siphonina reticulata</i> *
					<i>Siphonina tubulosa</i>
					<i>Sphaeroidina bulloides</i>
					<i>Vasiglobulina</i> *

Species sorted on % of occurrences with >10% abundance.

*Morphospecies showing a narrow distribution

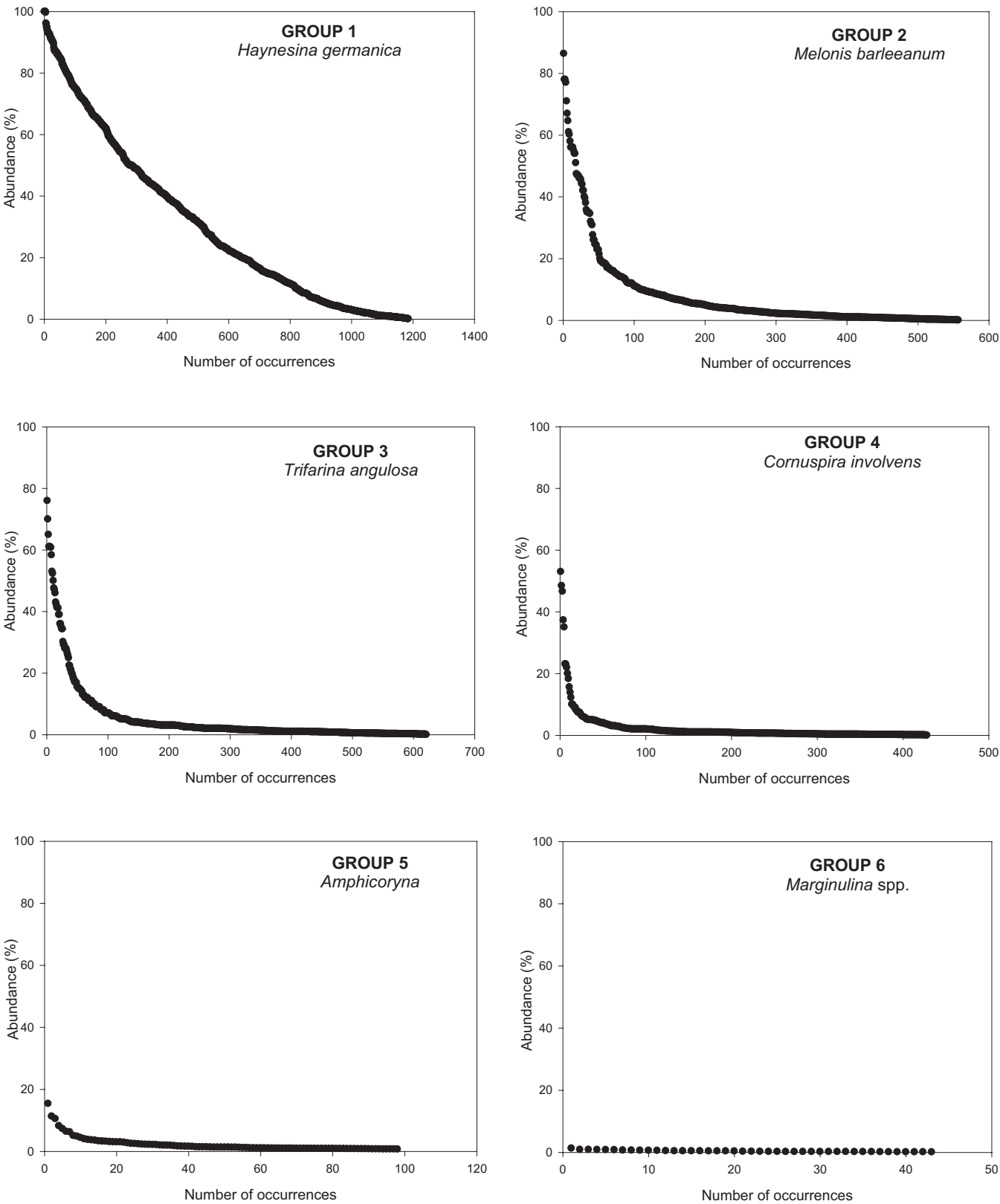


Fig. 3. Examples of abundance/occurrences plots for the six groups shown in Table 4.

Table 5. Distribution of morphospecies in the oceans.

Species	Arctic	Atlantic/Mediterranean	Pacific	Indian	Southern
Agglutinated					
<i>Ammoastuta inepta</i>		X			
<i>Ammobaculites agglutinans</i>		X	X		
<i>Ammobaculites balkwilli</i>		X			
<i>Ammobaculites dilatatus</i>		X			
<i>Ammobaculites exiguus</i>		X			
<i>Ammobaculites filiformis</i>		X	X		X
<i>Ammoscalaria runiana</i>		X			
<i>Ammotium salsum</i>		X	X	X	
<i>Arenoparella mexicana</i>		X	X		
<i>Balticammina pseudomacrescens</i>		X	X		
<i>Eggerella advena</i>	X	X	X		
<i>Eggerella europea</i>		X			
<i>Eggerelloides medius</i>		X			
<i>Eggerelloides scaber</i>		X	X	X	
<i>Gaudryina exilis</i>		X		X	
<i>Gaudryina pauperata</i>		X	X		
<i>Glomospira gordialis</i>	X	X	X		X
<i>Glomospira</i> all spp.	X	X	X	X	X
<i>Haplophragmoides bradyi</i>		X	X	X	X
<i>Haplophragmoides shallow</i> spp.		X	X		
<i>Jadammina macrescens</i>		X	X		
<i>Liebusella goësi</i>		X			
<i>Miliammina fusca</i>		X	X		
<i>Reophax moniliformis</i>		X			
<i>Reophax nana</i>		X	X	X	
<i>Siphotrochammina lobata</i>		X			
<i>Textularia earlandi</i>	X	X	X	X	X
<i>Tiphotrecha comprimata</i>		X			
<i>Trochammina inflata</i>		X	X	X	
<i>Trochammina lobata</i>		X			
<i>Trochammina pacifica</i>			X		
<i>Usbekistania charoides</i>		X	X		X
Porcelaneous					
<i>Cornuspira involvens</i>		X	X		X
<i>Pyrgo williamsoni</i>	X	X			
Hyaline					
<i>Amphicoryna</i>		X	X		
<i>Astacolus</i>		X			X
<i>Asterigerina carinata</i>		X	X		
<i>Asterigerinata adriatica</i>		X			
<i>Asterigerinata mamilla</i>		X			
<i>Astrononion echolsi</i>		X			X
<i>Astrononion gallowayi</i>		X	X		
<i>Astrononion sidebottomi</i>		X			
<i>Astrononion stelligerum</i>		X	X		
<i>Astrononion</i> all spp.	X	X	X		X
<i>Buliminella elegantissima</i>		X	X	X	
<i>Dentalina</i> spp.	X	X	X	X	
<i>Ehrenbergina</i>		X			X
<i>Fissurina laevigata</i>	X	X			
<i>Fissurina lucida</i>		X	X		
<i>Fissurina marginata</i>		X	X		X
<i>Fissurina orbignyana</i>		X			
<i>Fissurina</i> all spp.		X	X	X	X
<i>Fursenkoina apertura</i>			X		
<i>Fursenkoina bramletti</i>			X		
<i>Fursenkoina complanata</i>		X	X		X
<i>Fursenkoina earlandi</i>		X			X
<i>Fursenkoina mexicana</i>		X	X		
<i>Fursenkoina pontoni</i>		X	X		
<i>Fursenkoina punctata</i>		X	X	X	
<i>Fursenkoina sandiegoensis</i>			X		
<i>Fursenkoina schreibersiana</i>	X	X	X		
<i>Glandulina</i>	X	X	X	X	
<i>Globulina</i> all spp.	X	X			
<i>Globocassidulina subglobosa</i>		X			X
<i>Guttulina lactea</i>		X	X		
<i>Guttulina problema</i>		X	X		
<i>Guttulina</i> all spp.	X	X	X		
<i>Gyroidina altiformis</i>		X	X	X	X
<i>Gyroidina lamarckiana</i>		X	X	X	
<i>Gyroidina neosoldanii</i>		X	X		X

Table 5. (Continued)

Species	Arctic	Atlantic/Mediterranean	Pacific	Indian	Southern
<i>Gyroidina orbicularis</i>		X	X		X
<i>Gyroidina polia</i>		X	X		
<i>Gyroidina umbonata</i>		X	X		
<i>Gyroidina</i> all spp.		X	X	X	X
<i>Haynesina germanica</i>		X	X		
<i>Haynesina orbiculare</i>	X	X			
<i>Helenina anderseni</i>		X	X		
<i>Hoeglundina elegans</i>		X	X	X	
<i>Hopkinsina pacifica atlantica</i>		X	X	X	
<i>Hyalinea balthica</i>		X	X	X	
<i>Lagena clavata</i>		X			
<i>Lagena gracillima</i>	X	X			
<i>Lagena laevis</i>	X	X			
<i>Lagena striata</i>		X	X		
<i>Lagena substriata</i>		X			
<i>Lagena</i> all spp.	X	X	X	X	
<i>Lamarckina haliotidea</i>		X			
<i>Laricarinina pauperata</i>		X	X		
<i>Lenticulina peregrina</i>		X	X		
<i>Lenticulina</i> all spp.	X	X	X	X	X
<i>Melonis barleanum</i>	X	X	X		X
<i>Melonis pompilioides</i>		X			X
<i>Melonis</i> all spp.	X	X	X		X
<i>Marginulina</i>		X	X		
<i>Nodosaria</i>		X			X
<i>Nonion depressulus</i>		X	X?		
<i>Nonionellina labradorica</i>	X	X	X		
<i>Nuttallides pusillus</i>		X			
<i>Nuttallides umboniferus</i>		X			X
<i>Oolina</i>	X	X	X		X
<i>Oridorsalis sidebottomi</i>					X
<i>Oridorsalis tener</i>					X
<i>Oridorsalis umbonatus</i>	X	X	X		
<i>Osangularia culter</i>		X	X		
<i>Patellina corrugata</i>	X	X	X	X	X
Polymorphinid					
<i>Pullenia bulloides</i>	X	X	X		
<i>Pullenia osloensis</i>	X	X			X
<i>Pullenia quinqueloba</i>		X	X	X	X
<i>Pullenia salisburyi</i>		X	X		
<i>Pullenia simplex</i>		X			X
<i>Pullenia subcarinata</i>		X	X		X
<i>Reussella aculeata</i>		X		X	
<i>Reussella atlantica</i>		X			
<i>Reussella pacifica</i>			X		
<i>Reussella spinulosa</i>		X	X		
<i>Reussella</i> all spp.		X	X	X	
<i>Robertina arctica</i>	X	X			
<i>Robertina charlottensis</i>		X	X		
<i>Robertina</i> all spp.	X	X	X		X
<i>Siphonina bradyana</i>		X	X		
<i>Siphonina pulchra</i>		X			
<i>Siphonina reticulata</i>		X			
<i>Siphonina tubulosa</i>		X	X		
<i>Siphonina</i> all spp.		X	X		
<i>Sphaeroidina bulloides</i>		X	X		X
<i>Spirillina vivipara</i>		X	X	X	
<i>Stainforthia fusiformis</i>		X	X	X	X
<i>Stainforthia concava</i>	X	X	X		
<i>Stainforthia loeblichii</i>	X	X			
<i>Trifarina angulosa</i>	X	X	X		X
<i>Trifarina fluens</i>	X	X			
<i>Vasiglobulina</i>		X			
Summary					
Total	31	125	85	27	38
Agglutinated	4	31	19	8	6
Porcelaneous	1	2	1	0	1
Hyaline	26	92	65	19	31
Narrow distributions					
Agglutinated	0	12	1	0	0
Porcelaneous	0	0	0	0	0
Hyaline	0	14	4	0	2

Those confined to one ocean are marked with **x** in bold.

runiana, *Eggerelloides scaber*, *Patellina corrugata*, *Spirillina vivipara*) and some span all five (*Eggerella advena*, *Glomospira gordialis*, *Textularia earlandi*, *Fissurina laevigata*). In some cases misidentification of species may be responsible. For instance, before *Ammobaculites balkwilli* was described some authors identified it as *A. agglutinans*. Juvenile *Liebusella goesi* are easily misidentified as *Eggerelloides scaber* (Alve & Goldstein, 2010) and the latter species has not always been separated from *E. medius*. Very few of the taxa analysed are restricted to a single major environment: *Balticammina pseudomacrescens* high marsh and *Vasiglobulina* shelf. All the others are from the deep sea: *Astrononion echolsi*, *Fursenkoina apertura*, *F. bramletti*, *Gyroidina altiformis*, *G. polia*, *Laticarinina pauperata*, *Nuttallides pusillus*, *N. umboniferus*, *Oridorsalis sidebotomi*, *O. tener*, *Pullenia salisburyi*, *P. simplex*.

Biogeographical distributions

Most biogeographical analyses aim to determine patterns of distribution of faunas based on evolutionary (e.g. cladistics, molecular genetics), geological (e.g. plate tectonics) or ecological criteria. This paper is not concerned with either evolutionary or geological aspects but it is noted that the majority of the types are from the Recent although some come from the Tertiary and one from the Cretaceous (Supplementary Publication table 1). Nor is it concerned with the recognition of faunal provinces because only a selection of species has been studied rather than complete faunas. This study deals with individual morphospecies, with the main emphasis on those that are relatively rare.

Ideally global coverage of data is a prerequisite for studying biogeography but this target is rarely met. The data for benthic foraminifera are not yet global in coverage and they are not a snapshot at one time as they represent 60 years of observation. The North Atlantic has the best record of living/stained distributions; therefore, the absence of a species from any part may be real rather than the limitation of sampling. Patterns can be established within the limitations of present knowledge. Some distributions are geographically more or less continuous but others are discontinuous (disjunct). Two extreme disjunct distributions are those of *Pullenia osloensis* (Fig. 82) and *P. simplex* which are essentially bipolar: the former in the Arctic Ocean, high latitude North Atlantic and Southern Ocean; the latter in the mid-latitude North Atlantic and South Atlantic–Southern Ocean. Such distribution patterns have implications for taxonomy. Are these disjunct species genetically the same? In other cases a single occurrence remote from the main area of occurrence may be a consequence of misidentification (e.g. *Gaudryina pauperata* in the Scotia Sea; *Usbekistania charoides* in a Gulf of Mexico lagoon; *Nonion depressulus* in an Australian mangal). From molecular genetic evidence of similarity in the disjunct occurrence of shallow-water phylotypes, such as *Ammonia* T6, it has been suggested that this is through transport of water as ballast in ships (Pawlowski & Holzmann, 2008; Schweizer *et al.*, 2011).

In Table 5 the Mediterranean and Gulf of Mexico–Caribbean Sea are treated as parts of the broader Atlantic Ocean. Most of the selected taxa are moderately widely distributed (94) rather than restricted to a part of one ocean (30); a higher proportion of agglutinated than hyaline forms are narrowly distributed.

Narrowly distributed species

Narrow distributions are of ecological interest. There are several reasons why a species may have a very restricted distribution:

(a) it may have recently evolved and not yet developed its full range (*Asterigerinata adriatica*?); (b) its ecological requirements may be such that its range is limited (*Eggerella europea*, *Eggerelloides medius*); (c) it is newly described and, therefore, other occurrences have yet to be recorded (no examples have been studied here); (d) it may be unable to cross a barrier to distribution (see example below).

Thirty-three morphospecies show narrow distributions (Table 5). Among the agglutinated forms most are predominantly marsh–marginal marine inhabitants but *Eggerella europea*, *Eggerelloides medius* and *Trochammina lobata* are predominantly shelf inhabitants, whereas *T. pacifica* is a shelf–deep-sea form. Among the hyaline taxa a predominantly marginal marine inhabitant is *Nonion depressulus*; marginal marine–shelf *Fursenkoina sandiegoensis*, *Siphonina pulchra*; shelf *Asterigerinata adriatica*, *A. mamilla*, *Astrononion sidebotomi*, *Fissurina orbignyana*, *Lagena clavata*, *L. gracillima*, *L. laevis*, *L. substriata*, *Reussella atlantica*, *R. pacifica*, *Siphonina reticulata* and *Vasiglobulina*; deep sea *Fursenkoina apertura*, *F. bramletti*, *Lamarckina haliotidea*, *Nuttallides pusillus*, *Oridorsalis sidebotomi* and *O. tener*.

There is no correlation between species abundance and narrow distribution as there are examples in all groups (Table 4). This shows that being narrowly distributed is not an ecological disadvantage. The converse must be that being widely distributed does not always lead to high abundance.

In the North Atlantic narrowly distributed *Ammobaculites dilatatus* and *A. exiguus* are confined to mainly marsh–marginal marine environments along the US margin (Figs 6, 7) and absent from similar environments along the European seaboard. Similarly, *Ammobaculites balkwilli* (Fig. 5), *Ammoscalaria runiana* (Fig. 9), and *Reophax moniliformis* (Fig. 24), are confined to the European seaboard. Ellison & Murray (1987) suggested that a possible explanation for *Ammobaculites* and *Ammotium* is that brackish conditions are more continuous along the coastal areas of North America, thus facilitating dispersal, whereas off Europe brackish conditions are confined to discontinuous settings, such as estuaries and lagoons. It was also postulated that the species might be evolving in North America and may have been introduced only recently into European waters. However, the presence of species restricted to either the east or the west side of the ocean may require a different explanation.

In 1936 Myers suggested that the distribution of benthic foraminifera in shallow waters depends on ‘a brief pelagic phase assumed by juvenile or adult individuals’ (Myers, 1936, p. 143). These are now termed propagules (tiny juveniles) and their existence has been proven by experiments (see Alve & Goldstein, 2010 and references therein). This mechanism must be a common way of extending the range of species into suitable habitats and possibly across oceans. It readily explains the disjunct distributions of marsh and marginal marine faunas. It may be a more widespread mechanism than transport of sediment/foraminifera on the feet of birds from one area to another. But do all species have propagules? Are these agglutinated narrowly distributed species examples of taxa that do not produce propagules?

Widely distributed species

It might be expected that widely distributed morphospecies would be abundant over at least part of their range and that they would also be common. Although this is true of many of the species, it

is not universally so. From Table 4 it can be seen that Groups 5 and 6 have few or no samples with >10% abundance for the named species. Furthermore, most of the species in Group 6 are present in <1% of all the samples analysed. The exceptions are *Fursenkoina complanata*, *Gyroidina lamarckiana*, *G. polia*, *Lenticulina peregrina*, *Pullenia quinqueloba*, *Sphaeroidina bulloides* and *Usbekistania charoides* present in <2% of all the samples and *Dentalina* (2.8%). For Group 5, most species occur in <3% of the samples with the exception of *Fissurina lucida* (5.2%) and *Pullenia subcarinata* (3.3%).

Species that are widespread in occurrence but low in abundance are generally considered to be ecologically vulnerable (Hubbell, 2001). The nodosariids (Nodosariida of Haynes, 1981; Nodosariacea of Loeblich & Tappan, 1987) evolved in the Permian, reached their culmination in the Jurassic and since then have declined in importance. Haynes pointed out that prior to the Cretaceous nodosariids occupied shallower-water environments whereas modern examples are generally from deeper water and are therefore not good analogues for interpreting Mesozoic environments. Modern representatives discussed here include *Astacolus*, *Amphicoryna*, *Dentalina*, *Fissurina*, *Glandulina*, *Globulina*, *Guttulina*, *Lagena*, *Lenticulina*, *Marginulina*, *Nodosaria*, *Oolina* and *Vasiglobulina*. With the exception of some species of *Fissurina* and *Lagena* and the genus *Vasiglobulina*, all are widely distributed (Table 5). In terms of abundance >10% (Table 4) there are no examples in Groups 1–3, *Guttulina* is present in 4, and the rest are in 5 or 6 so they are generally of very low abundance. The main environments are shelf and deep sea but some species extend into fjord, marginal marine and marsh (in low abundance in the latter) (Table 2).

Opportunists and generalists

The terms 'opportunist' and 'generalist' are sometimes applied to species. These terms are subjective adjectives not based on precise measurement. It is simple to recognize extreme examples but it is not easy to classify the majority of species that fall in the middle of the range.

An opportunist is able to spread into a new habitat or rapidly increase its numbers in response to an environmental change. A clear example is *Stainforthia fusiformis* which rapidly responds to an increase in food beneath a hydrodynamic front and also to the early recovery of a previously anoxic environment (Alve, 2003). *Textularia earlandi* is also said to be an opportunist (Alve & Goldstein, 2010). The species listed in Group 1 in Table 4 may be opportunists.

A generalist species tolerates a wide range of environmental conditions and is less responsive to rapid environmental changes; this probably applies to the majority of species. Generalists may be widely or narrowly distributed but opportunists are likely to be widely distributed.

One of the keys to being opportunistic or a generalist is reproduction. Some species reproduce throughout the year (e.g. *Haynesina germanica*; Murray & Alve, 2000a) while others do so annually (*Elphidium crispum*; Lister, 1895). Some other very rare species may reproduce only when conditions are favourable (e.g. sufficient food). This leads to a short-lived 'bloom' in abundance and may be on a time-scale longer than one year. This may be the case for Group 5 abundance (Table 4; Fig. 3) because the majority of abundances are very low. The forms in Group 6 either

never produce many offspring when they do reproduce or else they reproduce so rarely that it has yet to be recorded. If the availability of food is the main control on the onset of reproduction then to a certain extent even rare species may be considered opportunistic, albeit on a modest scale.

Summary of the ecological controls noted for the species discussed

All species distributions are characterized by many zero occurrences and these have been ignored in compiling the data. It is evident that there is great variability in abundance in some taxa, as can be seen from the mean and maximum values of abundance (Table 3). The presence or absence of a species is likely to be controlled by many interdependent factors but the extent of that interdependence has not yet been determined for any species. Therefore, authors discuss each factor separately. Nevertheless, it must always be borne in mind that different factors may be more important at different times or in different areas.

The ecological controls include biotic (quantity and type of food, competition, predation, availability of phytal or other substrates elevated above the sea floor), abiotic (salinity, temperature, oxygen levels in the bottom water and sediment, tides/currents, substrate) and biotic/abiotic disturbance brought about by organisms affecting the substrate (bioturbation, trails). The ecological notes accompanying the species distributions bring together comments from various authors and list the citations.

In recent years the role of food as an ecological control has received much attention. Although many different types of feeding have been postulated, most discussion concerns the availability of plant food (see Murray, 2006). It must be assumed that there is always a 'hidden' bacterial element in all food resources (Lee, 1980). Higher plant detritus is essential for marsh dwellers. Intertidal and shallow-water forms feed primarily on benthic food (diatoms and other algae) whereas in deep water, where such food resources cannot grow, phytoplankton (phytodetritus) is the major source (Gooday, 2002). Some species seem to prefer fresh material (*Eggerelloides medius*, *Textularia earlandi*, *Fursenkoina apertura*, *Pullenia osloensis*, *Stainforthia fusiformis*), others degraded material (*Eggerella europea*, *Haplophragmoides bradyi*) and others are less specific (*Melonis barleeanum*). At present there is no information on whether specific phytoplankton species are preferred. The range and optimum supply of organic carbon is given for some of the species discussed (Altenbach *et al.*, 1999).

Salinity is clearly a control on many species; for stenohaline taxa the salinity must be ~35 and for euryhaline taxa each species has its preferred range. For example, *Haynesina germanica* tolerates an extreme range (0–35) yet its absence from areas of permanently very low salinity may be because it needs salinity to exceed a certain minimum in order to reproduce. Salinity is a significant control between some major environments (marsh, marginal marine, fjords and shelf, deep sea). Temperature is a significant factor for many shallow-water taxa; cold water forms include *Astrononion gallowayi* and *Nonionellina labradorica*; and there are temperature thresholds that affect reproduction (e.g. as shown experimentally for *Patellina corrugata*). Temperature controls the latitudinal distribution of marsh to shelf taxa. Bottom waters and subsurface sediments low in oxygen exclude many taxa but there are some that are adapted to tolerate such

conditions (e.g. *Fursenkoina pontoni*, *Reussella spinulosa*, *Stainforthia fusiformis*). There are major differences in the faunas of different sediment types. *Trifarina angulosa* is especially abundant in coarse sands/gravels along shelf edges subject to currents. *Stainforthia fusiformis* is a mud dweller.

Ecological significance of rare species

As already noted, even species that are abundant through part of their range (Groups 1–5, Table 4) will be rare towards the limits of their distribution but here we are concerned with species that are always rare (Group 6). Rare species and high diversity are interlinked. In any given assemblage some of the rare species will be from the marginal distributions of Groups 1–5 and some from Group 6. Since higher diversities are a feature of shelf seas and deep sea it follows that the majority of Group 6 rare species feature in these environments.

We can pose various questions: why are they always rare? How do they manage to continue to be present while being rare? How do they maintain genetic exchange with such dispersed and discontinuous distributions? Rarity cannot be an adaptive strategy nor can it arise through natural selection (Rabinowitz, 1981). Gaston (1997, p. 39) considers ‘The extent to which rare species remain rare in space and time is arguably a pivotal question in community biology’.

From a practical point of view the opportunity to reproduce is fundamental to survival. Benthic foraminifera reproduce both sexually and asexually. In the former the need for individuals to meet, the size of the standing crop and of 3D space may place limitations on the chances of meeting. What is the size of spacing beyond which individuals of a given species are unlikely to meet to reproduce? What are the controls on timing of sexual reproduction for individuals of the same species? There are no such restrictions for asexual reproduction. The latter could be synchronous or random – it would make no difference except that synchronous reproduction would give a greater chance of a species having a period of high abundance. Kunin (1997) noted that in land plants all rare species show disproportionately high levels of asexuality. In benthic foraminifera asexual reproduction is often more frequent than sexual. Asexual reproduction is certainly potentially advantageous when individuals are widely dispersed from one another. However, it is not known whether rare foraminiferal species preferentially reproduce asexually.

One attribute of widely distributed rare species is that they must be broadly tolerant of small-scale environmental variability yet species with small populations are more sensitive to disturbance and more likely to local extinction according to Gilpin & Soulé (1986). The role of disturbance in promoting opportunity was first proposed by Grassle & Sanders (1973) and is now recognized to be very significant. The biodiversity of soft-bottomed communities is much influenced by ‘ecosystem engineers’ that alter the sea floor and create microhabitats for meiofauna, e.g. bioturbators providing not only burrows but also bio-irrigation of sediment, or taxa building elevated structures, such as reefs or macroalgae, which provide substrates for colonization (Heip *et al.*, 2003). Such activity is of potential significance to benthic foraminifera. They also stress the role of microorganisms in the remineralization of organic matter. One has only to examine fresh muddy sediment under a microscope to see how mucus

secreted as a lubricant by molluscs and other benthos holds together fine sedimentary particles which are not otherwise already incorporated in faecal pellets, yet its importance is rarely mentioned. Even at the scale of foraminifera, infaunal taxa create tiny burrows and move detrital particles. This may not be of consequence to larger organisms but it could affect microbial activity. These processes were summarized by Schönfeld *et al.* (2011, p. 199) ‘patchy food input and physical disturbance creates a patchiness to maintain the sea floor as a series of small-scale successional mosaics, which as a whole promote a comparatively high diversity’. Minor differences in the patches may provide a range of microhabitats that individually suit particular rare species. That we cannot specify the precise ecological requirements of rare species is not surprising since the same applies to common species.

There is a view that only a few species are needed for an ecosystem to function and, therefore, most species are redundant. This concept is important for understanding the significance of rare species. If they are redundant, lost species could be replaced without having much impact on the ecosystem. An alternative view is the rivet hypothesis that proposes that interspecific connections mean that every species has some effect on the functioning of an ecosystem. The third alternative is the idiosyncratic response hypothesis which suggests that addition or loss of species will lead to unpredictable changes in the function of an ecosystem (see review by Graf, 2003).

In a review of the diversity–stability concept, McCann (2000) concluded that, on average, diversity gives rise to ecosystem stability; but diversity is not the driver; instead ecosystem stability depends on species that are capable of differential response. There is still great uncertainty about the consequences either of the loss of a species by local extinction or how gain of a species by invasion will affect an ecosystem. As pointed out by Heip *et al.* (2003, p. 294) ‘The overall question is how many species and functional groups are needed to sustain a stable ecosystem’. None of this discussion is specially targeted at rare species. Nevertheless, one must consider what level of reduction in a rare species distribution will ultimately lead to its local or global extinction. In general most attention is paid to changes in abundance of dominant species in monitoring pollution using foraminifera (see examples in Murray & Alve, 2002) but it is often the rare species that die out with increasing stress. It has been argued that rare species are important in community studies and critical for bioassessment (Cao *et al.*, 1998).

Differences between macroorganisms and microorganisms

The distribution of organisms reflects their evolution, ecology, means of or ability to disperse and the consequences of plate tectonic rearrangements through time. A recent conference on the biogeography of microscopic organisms addressed these problems (Fontaneto, 2011). It discussed the theoretical background and examined the distribution of mainly soft-bodied terrestrial groups but also shelled diatoms and testate amoebae. Among the topics discussed was the controversial proposal by Finlay (2002) that there is a size threshold of 2 mm above which there are macroorganisms which show distinct biogeographical patterns and below which there are microorganisms which occur everywhere (‘ubiquity hypothesis’ or everything is everywhere, EiE, hypothesis) but

only where the environment is suitable ('the environment selects'). This latter assertion is based on the idea that all microorganisms have resting stages that can colonize an environment if it changes to become favourable for any given species. A second problem concerns the use of morphospecies as the basic taxonomic unit. Most of the microorganisms studied lack hard parts and morphospecies are, therefore, less clearly defined than is the case for foraminifera which are primarily meiofaunal but mainly <2mm in size. Molecular genetic studies are used to determine genetically-based phylotypes which may also be recognized morphospecies, cryptic species within a morphospecies or totally new species as yet undescribed. In monothalamous forms with organic or agglutinated tests from the Arctic and Antarctic, Pawlowski & Holzmann (2008) found 12 unnamed phylotypes with restricted geographical distributions. However, three deep-sea morphospecies (*Cibicidoides wuellerstorfi*, *Epistominella exigua*, *Oridorsalis umbonatus*) show high genetic similarity (Pawlowski *et al.*, 2007). Such results have consequences for evolutionary and ecological applications of biogeography. The overall conclusions of the conference were that

Given the complexity of the spatial patterns in microorganisms, it seems that their biogeography is more likely to depend on a complex set of interacting phenomena, in which size is of course important, but it is not the only driver. The differences between micro- and macroorganisms can thus be included in a gradient, disregarding the hypothesised abrupt threshold assumed by the EiE hypothesis. (Fontaneto, 2011, p. 9).

The results from this study clearly demonstrate that benthic foraminifera are not present everywhere; even widely distributed species are restricted to parts of oceans and to specific environments. Unlike most biogeographical studies, which are concerned with groups of morphospecies, the focus of this study has been to establish the pattern for individual species. Some abiotic parameters may exert an obvious control, such as temperature differences favouring cool- or warm-water species. Even then there are subtle differences in the response to temperature; some species are more cold-tolerant than others (e.g. *Eggerelloides medius* compared with *Eggerelloides scaber*). Since each species has its own distinct niche controlled by a plexus of factors it is to be expected that each distribution will be different and that appears to be the case in the results presented here. Further studies of biogeography and ecology will be mutually beneficial and there will be significant input from molecular genetic studies as more phylotypes are recognized.

Applications

This review brings together ecological data on a wide range of morphospecies and their distributions which throw new light on ecology and will be of value in palaeoecological interpretations. It also has consequences for taxonomy: recognizing possible misidentifications for isolated records of species outside their normal range and also for questioning whether bipolar distributions are truly of single morphospecies or of two separate morphospecies or even cryptic species. Only genetic studies can resolve that problem.

CONCLUSIONS

This is the first attempt to gather virtually all the available data on live/stained benthic foraminifera to: (a) establish the pattern of relative abundance with respect to number of occurrences, and (b) establish the full environmental range and relative abundance of >120 taxa in each major environment. It is the most detailed investigation of global biogeographical distributions of individual benthic foraminiferal morphospecies. There are a number of main conclusions.

- All species have some very low abundance but only a subset has some high abundance.
- There is a continuum of six groups of species with relative abundance/number of occurrences from the extremes of very high abundance (>40% of samples with >10% abundance) to very low (no samples with >10% abundance).
- Although most species may be predominant in one major environment they also extend into other environments. In an extreme case they span from marsh to deep sea (e.g. *Eggerella advena*, *Cornuspira involvens*).
- Few species are restricted to a single major environment (usually either marsh, e.g. *Balticammina pseudomacrescens*, or deep sea, e.g. *Gyroidina altiformis*, *Laticarinina pauperata*).
- There are widely distributed species (present in several oceans, e.g. *Jadammina macrescens*) and narrowly distributed species (confined to part of a single ocean, e.g. *Trochammina pacifica*).
- There is no correlation between species abundance and narrow distribution; there are narrowly distributed species in all six abundance groups.
- Not all widely distributed taxa have some areas of high abundance, e.g. *Astacolus*.
- Some widely distributed taxa are both rare in abundance and found in only a tiny proportion of the samples analysed (often <1%), e.g. *Ehrenbergina*.
- Disjunct patterns of distribution have implications for taxonomy: are they truly single species (e.g. bipolar distribution of *Pullenia osloensis*)?
- Some disjunct patterns may be due to misidentification (where there is a single record from an area distant from all other occurrences). These require further investigation.
- Propagules are the most likely mechanism of dispersal of species along the margins and across an ocean as well as between oceans.
- The restriction of some species to a segment of an ocean may be because they lack the ability to produce propagules and, therefore, are not easily dispersed.
- Generalists may be widely or narrowly distributed but opportunists are likely to be widely distributed.
- It is the presence of rare species that contributes to high species diversity.
- Group 6 rare species are found mainly in shelf seas and the deep sea.
- Widely distributed rare species must be broadly tolerant of small-scale environmental variability.
- Minor differences in microhabitats may suit individual rare species.
- These results have implications for ecology, palaeoecological interpretations and taxonomy.

APPENDIX

Biogeography and comments on species ecology

The biogeographical plots are given in a series of figures (Figs 4–95). In these figures the areas with no data are light grey (blue online), present with a mean >1% is dark grey (red online), Max indicates the area with the highest relative abundance, * denotes mean <1%, and absence is unshaded. Where a species is missing from an entire section of the figure (e.g. East or West Atlantic or Rest of World) then that section is omitted to save space. In a few cases there is an additional graph showing the distribution of abundance with respect to environment (Figs 58, 93, 94). Comments on species ecology are from the literature and are provided to help explain the distributions. The sources of data are given in Supplementary Publication tables 3–7 (agglutinated), 8 (porcelaneous) and 9–18 (hyaline). For those species with low abundance in the deep sea information is given on the deepest occurrences.

Agglutinated taxa

Ammoastuta inepta. The range of this species is primarily in the Gulf of Mexico where it occurs on marshes in Mississippi and Texas, USA, in a lagoon in Mexico, and rarely on the Mississippi shelf. It has also been recorded as rare infaunal (2–4 cm) in North Carolina marshes, USA (Culver & Horton, 2005).

Ammobaculites agglutinans. The main environment is deep sea and shelf (Fig. 4). In the Weddell Sea it is infaunal to 3.5 cm (Mackensen & Douglas, 1989). The occurrences in fjord and marginal marine may be incorrect identifications. It occurs where the mean sea floor organic C flux is $7 \text{ g m}^{-2} \text{ a}^{-1}$ (Altenbach *et al.*, 1999).

Ammobaculites balkwilli. Two distinctive features of this species are the circular cross-section of the uniserial part and its habit of incorporating dark sedimentary particles into its wall. Although it was first described from a marsh and has since been recorded in another marsh (Arcachon, France, Le Campion, 1970, as *A. agglutinans*) the main occurrences are in marginal marine settings from shallow subtidal to low intertidal (Alve & Murray, 1994). It is restricted to the NE Atlantic (Fig. 5). The range of salinity tolerated in marginal marine southern Scandinavia is 15–29 (Alve & Murray, 1999).

Ammobaculites dilatatus. Most occurrences are marginal marine or marsh, mainly in the West Atlantic but it is also present in the Pacific (Fig. 6). There are minor occurrences on the shelf off North Carolina and Texas, USA. It occurs infaunally to 8 cm off North Carolina (Lueck & Snyder, 1997).

Ammobaculites exiguous. Most occurrences are marsh but it is also present on the shelf off North Carolina and Texas, USA, and there are a few records from marginal marine settings (Fig. 7). It is absent from the East Atlantic and the Indian Ocean. It is infaunal down to 8 cm on the shelf (Murosky & Snyder, 1994) and to 10 cm in a marsh (Steineck & Bergstein, 1979).

Ammobaculites filiformis. With the exception of a single record from the shelf off Cape Hatteras this is known exclusively from the deep sea of the Atlantic and Pacific oceans (Fig. 8).

Ammoscalaria runiana. This species has a very restricted distribution with the majority of occurrences in marginal marine, some

Ammobaculites agglutinans

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK		x			
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean		x			
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					Max
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

	areas not sampled
	species present
Max	maximum abundance
	no occurrences
x	mean <1%

Fig. 4. *Ammobaculites agglutinans*. Key to symbols: areas with no data are light grey (blue online), present with a mean >1% is dark grey (red online), Max indicates the area with the highest relative abundance, * indicates mean <1%, and absence is unshaded.

Ammobaculites balkwilli

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic		Max			
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

Fig. 5. *Ammobaculites balkwilli*.

fjord, with rare records in marsh and shelf. In southern Scandinavian marginal marine environments it is common only on sediments with <20% mud, a median diameter of medium to fine sand, and low total organic carbon (TOC, 0.2–0.7%) (Alve & Murray, 1999). It is confined to the NE Atlantic and Baltic Sea (Fig. 9).

<i>Ammobaculites dilatatus</i>						
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana	Max				
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 6. *Ammobaculites dilatatus*.

<i>Ammobaculites exiguus</i>						
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico	x				
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 7. *Ammobaculites exiguus*.

Ammotium salsum. This species occurs in the Atlantic, Mediterranean and Pacific oceans (Fig. 10). It is abundant in marsh and marginal marine environments with a few occurrences on the shelf. In some instances it forms monospecific assemblages (brackish to hypersaline marsh, Texas, USA, S 2-42 (Phleger, 1966) and very brackish lagoon, S 0-10, in Mexico (Phleger & Lankford, 1978)). The range of salinity tolerated in marginal marine southern Scandinavia is 15-27 (Alve & Murray, 1999). It has been shown to be infaunal (0-10 cm) in North Carolina marshes, USA (Culver & Horton, 2005). In the NE Atlantic and Mediterranean it is much less widespread in marginal marine

<i>Ammobaculites filiformis</i>						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					x
10-30	S Atlantic					
35-56	S Atlantic					Max

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA				x	
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 8. *Ammobaculites filiformis*.

<i>Ammoscalaria runiana</i>						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway			x		
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic		Max			
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

Fig. 9. *Ammoscalaria runiana*.

environments than it is in the West Atlantic and Gulf of Mexico. In the Adriatic it shows a high correlation with the density of sea grass and also with specific diatoms as a food resource but rejects blue-green algae (Hohenegger *et al.*, 1989). In the Gulf of Mexico it extends on to the shelf adjacent to the Mississippi delta. It is a detritivore feeding on bacteria (Matera & Lee, 1972).

Arenoparrella mexicana. A dominantly marsh species it is also found in marginal marine lagoons especially on the western side of the North Atlantic. Occurrences in the NE Atlantic are restricted to France; it is infrequent in South America and the

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico	Max				
25-18	S Gulf of Mexico		Max			
18-12	Caribbean Sea		x			
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 10. *Ammotium salsum*.

Pacific (Fig. 11). Infaunal down to 2cm in New England marshes (Saffert & Thomas, 1998), and in Georgia, USA, it is patchy in surface sediments of the low marsh but infaunal down to 30cm in moist high marsh sediments (Goldstein & Harben, 1993). It is found infaunal down to 50cm in an Australian mangal (Berkeley *et al.*, 2008).

***Balticammina pseudomacrescens*.** There has been some taxonomic confusion surrounding this species. It is recorded as *Trochammina macrescens* f. *macrescens* by Scott and as *T. macrescens* type A by De Rijk & Troelstra (1999) (see Alve & Murray, 1999). This is one of the few species found exclusively in a single environment, highest marsh: in the NE Atlantic from southern Scandinavia to southern England, West Atlantic from Canada (where it reaches its greatest abundance) to the northern Gulf of Mexico, then a gap past Brazil to Argentina. In the Pacific Ocean it is known from California, USA, and Japan (Fig. 12). It is epifaunal and associated with damp, rotting leaf litter (Alve & Murray, 1999) and is an extremely low-salinity euryhaline species.

***Eggerella* Cushman, 1935 and *Eggerelloides* Haynes, 1973.** The Mesozoic genus *Verneuilina* d'Orbigny, 1839, was used by nineteenth- and early twentieth-century workers for triserial forms that have now been assigned to other genera, such as *Eggerella* and *Eggerelloides*. Loeblich & Tappan (1987) place *Verneuilina* in the

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay		x			
43	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada	Max				
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 11. *Arenoparrella mexicana*.

Superfamily Verneuilinacea and *Eggerella* and *Eggerelloides* in the Textulariaceae. In both superfamilies the wall is said to be canaliculate yet this is not true for all species assigned to *Eggerella* or for *Eggerelloides*. However, when Cushman erected the genus *Eggerella* he described the wall as having calcareous cement but made no mention of canaliculae.

The type species of *Eggerella* is *Verneuilina bradyi* Cushman, 1911. This is a deep-sea form with a canaliculate wall and calcareous cement. This is not the case for *Eggerella advena* so the reason for placing the species *advena* in this genus is not clear but perhaps Cushman did not consider the nature of the cement to be a significant taxonomic feature. *Eggerelloides* was erected by Haynes (1973) with the type species *Bulimina scabra* Williamson, 1858. Like *Eggerella advena* it has an agglutinated wall with organic cement. The aperture of the former is a low arch at the base of the apertural face, whereas that of *Eggerelloides* is a high loop-shaped slit extending up the apertural face.

***Eggerella advena*.** Cushman (1922, p. 57) gave as his description: 'Variety differing from the typical in the smaller size and more slender form'. From comments on p. 56 it is clear that 'the typical' is what is now called *Eggerelloides scaber*. Of the 215 occurrences along the eastern seaboard of North America, 57% are from marginal marine settings (mainly Long Island Sound, Buzas, 1965), 37% are on the shelf and the remainder are from marsh

Balticammina pseudomacrescens

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada	Max				
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 12. *Balticammina pseudomacrescens*.*Eggerella advena*

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea				x	
55-59	S Scandinavia/Baltic					
56	Seas around UK				?	
43-45	Biscay					
39	Portugal					
43	W Mediterranean				x	
45	E Mediterranean				?	
20	NW Africa					
0	Gulf of Guinea				?	
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA		Max			
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA				x	
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 13. *Eggerella advena*.

and fjord. These are all from cool waters derived from the north. The salinity in Long Island Sound is 25–29 and on the open shelf it is 32–35. Buzas (1965) considered that the abundance of *E. advena* is probably related to food supply. There are only 5 occurrences in the Caribbean (Jamaica, Puerto Rico) and the identification of these may not be correct.

Along the Arctic, Atlantic and Mediterranean coasts of Europe *E. advena* has been reported mainly from the shelf (97% of 168 occurrences) (Fig. 13). It is likely that some of the identifications are suspect. Scott *et al.* (2003) recorded it in the Celtic Sea (30 samples). However, the author has never seen it there although *Eggerelloides scaber* is present. Daniels (1970) separated *E. advena* from *E. scaber* in the Adriatic Sea on the basis that the former was mainly half the size of the latter. Since both species were recorded in 115 samples it may be that they are really one and that is likely to be *E. scaber* with the juveniles being reported as *advena*. Together these two instances account for 86% of the 168 occurrences. The records from the Arctic may be authentic.

On the Pacific seaboard of North America there are 186 occurrences, 67% of which are from borderland basins (which extend down to >1000m), 25% from shelf and the remainder from marsh and marginal marine. Most of the basin occurrences are those of Uchio (1960), who erected the species *E. scrippsii* on the basis that the wall is composed of finer particles and is smoother than

that of *E. advena*. Nevertheless, he had difficulty separating the two species. Here they are both considered as *E. advena*.

There are 66 records from Japan. Of these, 26 are from heavily polluted Osaka Bay which has restricted connections with the open sea (Tsujimoto *et al.*, 2006). Over the past 50 years there has been a major faunal change which the authors attribute to the increase in pollution leading to hypoxia and anoxia. However, this species is abundant in Ishikari Bay which is open to the sea and was not reported as polluted or hypoxic at the time of sampling (Ikeya, 1970).

This appears to be a detritivore (Murray, 1991) and to tolerate hypoxic conditions in areas subject to pollution. It is highly mobile (Schafer & Young, 1977) and was a pioneer species in recolonizing sediment dumped from dredging in Canada (Schafer, 1982). It is infaunal down to 10cm off North Carolina (Murosky & Snyder, 1994).

Eggerella europeae. This distinctive small, elongate species was first recorded by Höglund (1947) in Gullmar fjord, Sweden as *Verneulina advena* Cushman. It has an organic-cemented wall so does not truly fit in *Eggerella*. Rare living occurrences are confined to Hardangerfjord, Norway, the Skagerrak and the shelf west of Scotland. In a two-year experiment, where the fauna was deprived of fresh phytodetritus, it increased in abundance, indicating that it feeds on degraded food (Alve, 2010).

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
65	Iceland-Norwegian Sea					x
55-59	S Scandinavia/Baltic			Max		
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

Fig. 14. *Eggerelloides medius*.

Eggerelloides medius. First described from Gullmar Fjord, Sweden, this species was originally confused with *E. scaber*. Where the two species co-occur care has to be taken to separate them; *medius* generally has a coarse finish to the wall and is slightly less pointed at the initial end than *scaber*. *Eggerelloides medius* lives primarily on the shelf (74%) and in fjords in Scandinavia (24%) with rare occurrences in deeper water (Fig. 14). The shelf occurrences extend from the northern North Sea and Skagerrak to southern England and to the west of Scotland where core records show it down to 3 cm (the limit of sampling) (Murray, 2003). There are rare records from the deep sea from west Norway down to 856 m (Mackensen, 1985). *Eggerelloides medius* is a cool temperate species. It is confined to water depths >90 m where some mud is present in the sediment (Murray & Alve, 2000b). In a fjord (Alve & Nagy, 1986), in the North Sea (Klitgaard-Kristensen & Sejrup, 1996) and on the shelf off Scotland (Murray, 2003) it shows a correlation with % TOC and fine sediment fraction. In a two-year experiment, where the fauna was deprived of fresh phytodetritus, it decreased in abundance, indicating a need for fresh food (Alve, 2010).

Eggerelloides scaber. Particularly common in the NE Atlantic but absent from the West Atlantic (Fig. 15). It occurs in marginal marine, fjord, shelf and deep sea but is most abundant on the shelf, although the single highest abundance is from Oslo fjord. The range of salinity tolerated in marginal marine southern Scandinavia is 19–28 (Alve & Murray, 1999). It requires a salinity of at least 24 for most of the year in order to flourish and the optimum is 29–35 (Lutze *et al.*, 1983). It may have been more common in the western Baltic in the past but is now found only in higher salinity areas, such as deeper Kiel Bight (Polovodova *et al.*, 2009). It tolerates a broad range of temperature but the optimum may be 15–20°C (Murray, 1968). Although it tolerates oxygen levels of <0.5 ml l⁻¹ it took more than one year for it to colonize sediments recovering from a prolonged period of anoxia (Alve, 1995a). In the Adriatic Sea it occurs in shallow water where there is periodic oxygen deficiency (Donnici & Serandrei Barbero, 2002). In Drammensfjord, Norway, it is most abundant in the upper part of transitional water masses due to a combination of salinity conditions, increased organic flux and depleted oxygen (Alve, 1990). However, Schönfeld (2001) considers it to be an oxic species based on measurements of pore water oxygen. In the Celtic Sea it correlates with high sand content (Scott *et al.*, 2003). It is tolerant of heavy metal pollution (Frontalini & Coccioni, 2008). In the deep sea it extends down to a maximum of 1500 m in the

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic			Max	x	
56	Seas around UK					
43-45	Biscay		x			
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 15. *Eggerelloides scaber*.

Gulf of Guinea and, in submarine canyons, down to 920 m in the Gulf of Lions and 3097 m in Nazare canyon off Portugal. Some of the deep-sea occurrences might be misidentified juveniles of *Liebusella goesi* (Alve & Goldstein, 2010). It is also reported from Japan and the Indian Ocean where it is named *E. scaber australis*. It is generally infaunal: in the North Sea down to 25 cm with peak values at 0–7 cm (Moodley, 1990) and in the Adriatic down to 7 cm but it occurs predominantly in the top cm where it may reproduce (Barmawidjaja *et al.*, 1992). It is also epiphytic on seagrass (Debenay, 2000; Semeniuk, 2001). It sometimes has green protoplasm (suggesting herbivory) but Alve & Goldstein (2010) conclude that it is an omnivore.

Gaudryina exilis. This is primarily a marginal marine form but it also occurs on marsh (where it reaches its highest abundance) and shelf. It is absent from the East Atlantic and Pacific. It is present in the warmer parts of the West Atlantic and the Indian Ocean (Fig. 16).

Gaudryina pauperata. On the Pacific margin of North America it occurs on marshes and in marginal marine environments, while off Japan it is found on the shelf. The only record from the Atlantic is from the shelf in the Caribbean (Fig. 17). The single record from the deep sea at 537 m in the Scotia Sea is almost certainly a misidentification.

Glomospira gordialis. The records span all environments from marsh to deep sea but this is essentially a shelf and deep-sea form (Fig. 18). It is present on shelves in the Arctic, on both sides of the North Atlantic, off California, USA, and Japan. The deep sea records are from the Atlantic Ocean, Scotia Sea and Southern Ocean, Japan and South China Sea. Most abundances are very low and the only location where it exceeds 10% is a single sample from a lagoon in Brazil (Duleba & Debenay, 2003). It occurs where the mean sea floor organic C flux is 7–9 g m⁻² a⁻¹ (Altenbach *et al.*, 1999).

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil	Max				
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 16. *Gaudryina exilis*.

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California		Max			
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 17. *Gaudryina pauperata*.

Haplophragmoides bradyi. Although often considered to be a deep-sea form, *H. bradyi* also occurs commonly on the shelf and more rarely in Norwegian fjords (where it has its highest mean value). Most occurrences are in the East Atlantic (Fig. 19) but it also occurs in the Pacific, Indian and Southern oceans. In a two-year experiment, where the fauna was deprived of fresh phytodetritus, it increased in abundance, indicating that it feeds on degraded food (Alve, 2010).

Haplophragmoides shallow-water species. The common shallow-water species are *Haplophragmoides bonplandi*, *H. manilaensis*,

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic				x	
56	Seas around UK					
43-45	Biscay					x
39	Portugal					x
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea				x	
10-30	S Atlantic					x
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA				x	
40-25	E USA				x	
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea		x		x	
5	French Guiana					
24-31	Brazil		Max			
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					x
35	Korea & Japan					x
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 18. *Glomospira gordialis*.

H. subinvolutum and *H. wilberti*. All these forms are morphologically variable so it is uncertain whether there are truly as many species as have been named. Alve & Murray (1999) noted that their *H. wilberti* included forms regarded as *H. manilaensis* by D.B. Scott (pers. comm.). These four *Haplophragmoides* species are typical marsh forms (93% of occurrences) although there are sparse records in marginal marine and shelf settings (Fig. 20). They occur in East and West Atlantic and Pacific oceans. *Haplophragmoides wilberti* is recorded widely present elsewhere; *H. bonplandi* is found in Canada and North Carolina, USA; *H. manilaensis* in Portugal, eastern USA, Gulf of Mexico, Brazil and Japan; *H. subinvolutum* Texas, USA, and Pacific USA. *Haplophragmoides manilaensis* is found down to 2cm in New England marshes (Saffert & Thomas, 1998). The range of salinity tolerated by *H. wilberti* in marginal marine southern Scandinavia is 10–27 (Alve & Murray, 1999).

Jadammina macrescens. Although a typical marsh species, *J. macrescens* also occurs in adjacent intertidal marginal marine environments. In the NE Atlantic marshes it extends from southern Scandinavia to Portugal and also into the Eastern Mediterranean (Greece, Italy: Scott *et al.*, 1979). In the West Atlantic it occurs from Canada to the northern Gulf of Mexico; there is a gap until it reoccurs in Brazil and Argentina. Pacific occurrences are from Canada to Baja California, also the Banda

Haplophragmoides bradyi

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					x
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					x
35-56	S Atlantic					x

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					x
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					Max
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 19. *Haplophragmoides bradyi*.

Sea and New Zealand (Fig. 21). The marginal marine occurrences parallel those of the marshes but in lower abundance and there is an additional record from the South China Sea. The only shelf occurrence is off the Mississippi delta in the Gulf of Mexico. It is considered to be a generalist with a mode of life ranging from epiphytic on decaying phanerogam leaf debris (Matera & Lee, 1972; Alve & Murray, 1999) to infaunal down to 30cm (Ozarko *et al.*, 1997). It probably feeds on bacteria and decay products from the leaves. The range of salinity tolerated in marginal marine southern Scandinavia is 10–28 (Alve & Murray, 1999).

Liebusella goesi. It is known from fjords, where it occurs in marine waters below the halocline (Alve & Nagy, 1986) and especially on the continental shelf and shelf deeps (Skagerrak, Alve & Murray, 1997) but its highest abundance is at 405m on the slope near Dakar off NW Africa (Lutze, 1980) (Fig. 22).

Miliammia fusca. Extremely euryhaline tolerating salinities of <1–35 but there is no correlation between its abundance and salinity (De Rijk, 1995) although Debenay *et al.* (2002; 2004) found it more abundant in low salinity areas in French Guiana. It is epifaunal to slightly infaunal (Ozarko *et al.*, 1997; Saffert & Thomas, 1998) but Tobin *et al.* (2005) found it down to 20cm in a Canadian marsh and to 30cm in North Carolina, USA. It is epiphytic on filamentous algae on a marsh in southern England (Alve

Haplophragmoides shallow sp.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK		x			
39	Biscay					
43	Portugal	Max				
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico		x			
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil		x			
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 20. *Haplophragmoides* shallow-water spp..

& Murray, 1999) and in the Baltic it makes up to 50% of epiphytic assemblages on algae (Wefer, 1976). In an Australian mangal it is infaunal to 40cm (Berkeley *et al.*, 2008). This widespread species is found abundantly in marsh and marginal marine and occasionally in fjord and shelf environments in the Atlantic and Pacific oceans (Fig. 23). The upper salinity limit is 25 (Alve, 1995) although the range in marginal marine southern Scandinavia is 10–29 and the maximum water depth is 2m (Alve & Murray, 1999). Under experimental conditions using material from Georgia, USA, with varying temperature (12 and 22°C) and salinity (12, 22, 36) it grew at all salinities but was most abundant at salinity 12 and it did least well at 12°C (Goldstein & Alve, 2011). However, in Canada this is considered a cool tolerant species (Scott & Medioli, 1980) so Goldstein & Alve (2011) suggest that it may be a morphospecies complex of cryptic species with different environmental requirements. The US and Canadian representatives also show genetic differences.

Reophax moniliformis. This species is confined to the NE Atlantic with a rare occurrence in the Mediterranean (Fig. 24). It is mainly present in marginal marine environments but also occurs on marsh, fjord and shelf. It probably feeds on debris from higher plants and green algae (Alve & Murray, 1999) and the green pigment may indicate either symbiosis with diatoms or their chloroplasts (Knight & Mantoura, 1985). The optimum temperature may

Jadammina macrescens

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic			x		
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada		x			
45-40	E USA		x			
40-25	E USA		x			
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan	x				
x	S China Sea					
5	Banda Sea					
40	New Zealand	Max				
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 21. *Jadammina macrescens*.*Miliammina fusca*

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada		Max			
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil		Max			
38-54	Argentina		x			
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA	Max				
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 23. *Miliammina fusca*.*Liebusella goesi*

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					Max
10-30	Gulf of Guinea					
35-56	S Atlantic					

Fig. 22. *Liebusella goesi*.

be 15–20°C (Murray, 1968). The range of salinity tolerated in marginal marine southern Scandinavia is 15–28 (Alve & Murray, 1999).

***Reophax nana*.** The type specimens come from the mouth of the Para River, Brazil. It has inflated chambers so the periphery is lobulate rather than smooth as in *R. moniliformis*.

By contrast with the latter, *R. nana* is common in the West Atlantic (sometimes on marsh/mangal but typically marginal marine) from Canada to Brazil (Fig. 25) and likewise along the Pacific seaboard of North America and with 4 records from South Africa in the Indian Ocean. On the eastern side of the Atlantic it

is rare in marshes in northern Spain and present on the shelf in Biscay and off the Ebro in the Mediterranean. In the Adriatic it is restricted to the top 4 cm (Barmawidjaja *et al.*, 1992).

***Siphonotrochammina lobata*.** This primarily marsh/mangal species is found from North Carolina, USA, to French Guiana with marginal marine occurrences in Tobago and Brazil (Fig. 26). It is epiphytic on mangrove tree roots in Brazil (Eichler *et al.*, 1995; Debenay *et al.*, 1996) yet rare in French Guiana (Debenay *et al.*, 2002).

***Textularia earlandi*.** Sometimes recorded as *T. tenuissima*, this species is widespread (Arctic, Atlantic, Pacific, Indian, Southern oceans) and occurs in marsh/mangal, marginal marine, fjord, shelf and deep-sea environments (Fig. 27). In a two-year experiment, where the fauna was deprived of fresh phytodetritus, it increased in abundance, perhaps indicating a need for fresh food (Alve, 2010). In experiments using sediment collected from 320 m water depth in the Skagerrak aliquots were stored for 2 years in a cold room at the original ambient temperature of 5°C and then exposed to shallow-water conditions for 11 months; this was the only species that continued to flourish. The authors attributed this to its opportunistic lifestyle (Alve & Goldstein, 2010).

***Tiphrotrocha comprimata*.** A marsh species found only in the Atlantic from southern Scandinavia to Portugal and from Canada

Reophax moniliformis

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic		Max			
43-45	Seas around UK					
39	Biscay					
43	Portugal					
43	W Mediterranean					
45	E Mediterranean				x	
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

Fig. 24. *Reophax moniliformis*.

Reophax nana

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay		x			
43	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA		Max			
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 25. *Reophax nana*.

Siphotrochammina lobata

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA	Max				
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 26. *Siphotrochammina lobata*.

Textularia earlandi

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea				x	x
56	S Scandinavia/Baltic			x		
43-45	Seas around UK		x			
39	Biscay	x				x
43	Portugal	x				
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea				x	
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					x
50-43	Canada					
45-40	E USA		x			
40-25	E USA				x	
30	N Gulf of Mexico				x	
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California				x	
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean		Max		x	
28	S Africa					
15-30	Australia	x				
65	Antarctic					

Fig. 27. *Textularia earlandi*.

to Brazil, with a few occurrences in marginal marine environments (Fig. 28). It is epifaunal, free or clinging to algae or infaunal down to 20 cm (Saffert & Thomas, 1998) and a herbivore or detritivore. The range of salinity tolerated in marginal marine southern Scandinavia is 20–28 (Alve & Murray, 1999).

Trochammina inflata. This is the typical marsh species widely distributed throughout the Atlantic and Pacific oceans but it also occurs in marginal marine settings including in the Indian Ocean. There are single records on the shelf off Japan and the Mississippi delta and 8 occurrences in the Adriatic Sea (Fig. 29). Although found in small numbers in epiphytic communities (Matera & Lee, 1972), it is most commonly found living infaunally (e.g. Steineck & Bergstein, 1979; Langer *et al.*, 1989; Goldstein & Harben, 1993; Ozarko *et al.*, 1997; Saffert & Thomas, 1998; Berkeley *et al.*, 2008). It is a herbivore or detritivore feeding on bacteria (Matera & Lee, 1972). The range of salinity tolerated in marginal marine southern Scandinavia is 10–28 (Alve & Murray, 1999). Some records of dead *T. inflata* from the deep sea may be misidentifications of *T. subtorbinatus* (see Murray & Alve, 2011).

Trochammina lobata. There are only 21 records of this species, from the Scotian shelf, Canada, to North Carolina, USA, with a single occurrence on the slope at 850 m off the latter.

Tiphotrocha comprimata

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada	Max				
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea		x			
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 28. *Tiphotrocha comprimata*.*Trochammina inflata*

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico				x	
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand	Max				
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 29. *Trochammina inflata*.*Trochammina pacifica*

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
48	Pacific Canada					
47-33	Pacific USA				x	
28	Baja California				Max	
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 30. *Trochammina pacifica**Usbekistania charoides*

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					x
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean				x	
0	NW Africa					
10-30	Gulf of Guinea				Max	
35-56	S Atlantic					x

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico		x			
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					x
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					x
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					x

Fig. 31. *Usbekistania charoides*.

Trochammina pacifica. As the name suggests this is a Pacific species with occurrences in marginal marine, shelf and deep sea along the margin of North America and off Japan (Fig. 30).

Usbekistania charoides. With the exception of records from a lagoon in the Gulf of Mexico (which may be a misidentification), all occurrences are from shelf or deep sea, in the Atlantic and Pacific oceans and the South China Sea. The maximum abundance is on the shelf in the Gulf of Guinea (Fig. 31). In the Gulf of Cadiz the lower and upper limits in the sediment correspond with low and high oxygen so this species is not an indicator of low oxygen conditions (Schönfeld, 2001).

Porcelaneous taxa

***Cornuspira involvens/planorbis*.** Only a few species of *Cornuspira* have been described and the two most commonly recorded in modern sediments are *C. involvens*, based on material from the Tertiary of the Vienna basin, Austria (although d'Orbigny, 1839 also mentioned records from recent sediments off Cuba and Martinique) and *C. planorbis*, from Recent mud off Mozambique. The holotype of *C. involvens* is 1–2 mm in diameter while the type form illustrated for *C. planorbis* is a juvenile. The former seems to be microspheric and the latter megalospheric. There is taxonomic confusion surrounding these species because different workers have different views on morphological variability. Phleger & Parker (1951) noted that because of this, recorded distributions may be inaccurate. However, in view of the features of the types, it seems highly probable that *C. involvens* and *C. planorbis* are one species (discussion with Elisabeth Alve, 2011) and are treated so here.

Cornuspira involvens/planorbis is widely distributed throughout the world's oceans, from marshes to bathyal (Fig. 32), in normal marine salinities but highly variable temperatures. Typically it ranges from zero to low abundance (rarely above 6–7%). However, there are occasional high abundances (up to 55%) which are almost certainly reproductive blooms coincident with the time of sampling. Such blooms are known from marginal

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					x
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK		x			
39	Biscay					
43	Portugal					
43	W Mediterranean					x
45	E Mediterranean				x	
20	NW Africa					
0	Gulf of Guinea					x
10-30	S Atlantic					x
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					x
73	Arctic Canada					
50-43	Canada					
45-40	E USA		x			
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					x

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua				x	
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand	Max				
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 32. *Cornuspira involvens*.

Pyrgo williamsoni

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean		x		x	
65	N & W Norway			x		
55-59	Iceland-Norwegian Sea					x
56	S Scandinavia/Baltic			x		
43-45	Seas around UK				Max	
39	Biscay					
43	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

Fig. 33. *Pyrgo williamsoni*.

Amphicoryna spp.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay				x	
43	Portugal					
43	W Mediterranean				Max	
45	E Mediterranean				x	
20	NW Africa					
0	Gulf of Guinea					x
10-30	S Atlantic					
35-56	S Atlantic					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 34. *Amphicoryna* spp..

marine (northern Spain, summer; Barbuda, autumn), fjord (Svalbard and southern Norway, summer), continental shelf (Scotland, summer) and deep sea. It is epiphytic off Western Australia (Semeniuk, 2001).

***Pyrgo williamsoni*.** Confined to the Arctic Ocean and the NW European seaboard in fjords, shelf and deep sea (Fig. 33) with maximum abundance on the shelf. In the Arctic Ocean it occurs in seasonally ice-free areas and also beneath permanent ice cover (Wollenburg & Mackensen, 1998).

Hyaline taxa

***Amphicoryna*.** This genus is present (mainly as *A. scalaris*) in low abundance in shelf and deep-sea settings in the eastern North and tropical Atlantic Ocean and in the Mediterranean (Fig. 34). It appears to be absent from the South Atlantic. There are a few records from the deep sea in the South China Sea. It occurs where the mean sea floor organic C flux is $\sim 40 \text{ gm}^2 \text{ a}^{-1}$ (Altenbach *et al.*, 1999). The range tolerated in the Gulf of Guinea is $7.4\text{--}124.2 \text{ gm}^2 \text{ a}^{-1}$ (Altenbach *et al.*, 2003).

***Astacolus*.** Three species have living representatives (*A. crepidulus*, *A. hyalaculus*, *A. insolitus*) and other references are recorded

EAST ATLANTIC

Astacolus spp.

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean			x		
70-60	N & W Norway			x		
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean				x	
45	E Mediterranean				x	
20	NW Africa					x
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 35. *Astacolus* spp..

as sp.. The genus occurs only in the Atlantic Ocean in fjords, shelf seas and deep sea but only in the latter two does the mean exceed 1% and the maximum abundance is 4.2% in a Norwegian fjord. It occurs down to 4495 m in the Scotia Sea (Fig. 35).

Asterigerina carinata. This low latitude, warm-water species is confined to marginal marine in the Caribbean Sea and shelf in southern USA and Nicaragua (Fig. 36).

Asterigerinata mamilla. Most records are from the NE Atlantic and Mediterranean in marginal marine and shelf environments but the author also recorded it on the shelf off the USA (Fig. 37) and at 1002 m off the UK. It is epifaunal clinging to larger detrital fragments (Sturrock & Murray, 1981) or on submarine vegetation (Murray, 2006, p. 131).

Astronionion. Several species are known and four (*echolsi*, *gallowayi*, *sidebottomi* and *stelligerum*) are discussed below. These four species have a laterally compressed test, 8–10 chambers in the final whorl, and supplementary chamberlets arranged around the umbilici, distinct in all but *A. echolsi*. The types are from Recent sediments with *A. echolsi* and *A. gallowayi* from high latitudes and *A. sidebottomi* and *A. stelligera* from mid latitudes. Records for named species and including those left in open nomenclature show a distribution from marginal marine to deep sea in the Atlantic and Pacific oceans (Fig. 38) but the genus is typically present in shelf and deep sea.

Astronionion echolsi. The distinctive features are the compressed test with short, somewhat indistinct supplementary chambers with forward slanting apertures. It was described from the Ross Sea, Antarctica. There are no records of stained material from there but it occurs in the Scotia and Weddell seas as well as in the South Atlantic (Fig. 39).

Astronionion gallowayi. This is the most widely distributed species in fjords from Arctic Russia and Scandinavia, shelf seas from the

Asterigerina carinata

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA				Max	
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 36. *Asterigerina carinata*.*Asterigerinata mamilla*

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK		x		Max	x
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 37. *Asterigerinata mamilla*.

Astrononion all spp.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean				Max	
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan		x			
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 38. *Astrononion* spp..

Astrononion echolsi

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					Max

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 39. *Astrononion echolsi*.

Astrononion gallowayi

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean				Max	
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic				x	
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan		x			
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 40. *Astrononion gallowayi*.

Arctic Ocean to the North Sea and English Channel off Europe and to the Grand Banks off Canada, and deep sea from the Arctic Ocean to the Iceland–Faroe ridge. It is also recorded on the shelf and slope off Japan (Fig. 40). Of the 151 records, 87% are of abundances <10% and the mean value for the whole dataset is 4%. The highest abundances are in fjords and shelf seas. This species favours cold to temperate conditions (the types are from Alaska).

Astrononion sidebottomi. Confined to shallow shelf seas of the Adriatic where it has a low mean abundance (1%) with a single high value (11%) which may represent a reproductive bloom.

Astrononion stelligerum. There are 31 occurrences from shelf (Gulf of Guinea and Argentina), one from marginal marine (Tobago; probably a misidentification) and 7 from deep sea (Gulf of Guinea and South China Sea).

Buliminella elegantissima. This readily identified widely distributed species occurs from marsh to deep sea (Fig. 41) with most occurrences in marginal marine and shelf (Table 2) and it occurs in all the oceans. High abundances are found in very shallow water along the Pacific seaboard of North America from Washington, USA, to Baja California. In the North Sea it is infaunal down to 25 cm with peak abundance in the 0–4 cm interval (Moodley, 1990). In the Norwegian Sea it extends down to 896 m.

Buliminella elegantissima						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					x
55-59	S Scandinavia/Baltic			x	x	
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA				x	
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California				Max	
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean				x	
28	S Africa					
15-30	Australia					
65	Antarctic					x

Fig. 41. *Buliminella elegantissima*.

Dentalina/Laevidentalina. *Laevidentalina* lacks the longitudinal costae of *Dentalina* (Loeblich & Tappan, 1987). Although numerous species of these genera have been recorded, all are generally rare with the maximum abundance (7.7%) occurring in the West Mediterranean in the shelf off Algeria (Milker *et al.*, 2009). There are a few occurrences in marginal marine and fjord but mainly it is present in shelf and especially in deep-sea environments, in the Arctic, Atlantic, Pacific, Indian and Southern oceans (Fig. 42).

Ehrenbergina. Several species have been recorded but they are all so rare that it is appropriate to consider them collectively. Apart from a single occurrence in a lagoon on Tobago, it is otherwise known from shelf (Argentina, Ross Sea), borderland basins off California, USA, and deep sea (Portugal, West Africa, Nicaragua, Scotia Sea, Weddell Sea, and Ross Sea (Fig. 43). All abundances >10% are from around Antarctica.

Fissurina. Thirty-six species of *Fissurina* have been recorded living (in one or more of 708 samples) together with *Fissurina* sp. in some of the same samples as well as in others, giving a total record of 1071 samples (nearly 15% of the primary dataset). Several of the minor *Fissurina* species occur in only one geographical area or in a single environment. However, the genus is widely distributed both geographically and environmentally (Tables 2, 3). It is, therefore, remarkable that abundances >10%

Dentalina spp.						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean			x		
70-60	N & W Norway					
65	Iceland-Norwegian Sea					x
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay				x	
39	Portugal				x	
43	W Mediterranean				Max	
45	E Mediterranean				x	x
20	NW Africa					
0	Gulf of Guinea				x	x
10-30	S Atlantic					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada				x	
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					x
67	Weddell Sea					x
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan		x			
x	S China Sea				x	x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					x
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 42. *Dentalina/Laevidentalina* spp..

are present in <1% of the samples and the mean abundance is merely 1.09%.

Fissurina marginata was interpreted to be an ectoparasite on *Discorbis* (Le Calvez, 1947) based on observations on live individuals but he did not conduct experiments to prove his interpretation. Other authors have noted a similar positional relationship between *Fissurina* and a presumed host: *F. marginata* on *Cibicides lobatulus* (Walker & Jacob), on *Chlamys* shells (Haward & Haynes, 1976); *F. submarginata* (Boomgart) on *Rosalina* (Collen & Newell, 1999). Haward & Haynes illustrated two *F. marginata* on an ‘arenaceous cover’ (i.e. feeding cyst) on *Cibicides lobatulus*. The protoplasm of the two seemed to be in contact but it is possible that rather than being ectoparasitic the *Fissurinas* were merely taking food from the feeding cyst (Haynes, pers. comm., 2011). If there is any regular association between these species then they should show some related distributions and abundances. Whereas *C. lobatulus* is very common in current-swept areas, *F. marginata* is not. The two species behave differently hydrodynamically (one much larger than the other) so this may be part of the explanation for the disparate occurrence of dead tests but it should not affect the living forms. Williamson (1848) recorded *F. marginata* (as *Entosolenia*), *Rosalina globularis* and ‘*Polystomella crispa*’ all adhering epifaunally on branching bryozoa but without any obvious association between species.

Ehrenbergina spp.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea		x			
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					x
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic				Max	

Fig. 43 *Ehrenbergina* spp..

The supposed ectoparasitic mode of life of *F. marginata* has yet to be demonstrated for other species of *Fissurina* even though Haynes (1981, p. 54) stated that both *Fissurina* and *Lagena* are parasitic on other foraminifera. Haynes (pers. comm., 2011) noted that the case of *Lagena* 'was suggestive but not conclusive'.

Fissurina laevigata occurs in Arctic fjords and a range of environments in the North Atlantic and Mediterranean but with a single record on a marsh and only three records in the deep sea (Fig. 44) down to 3736 m in the Gulf of Guinea.

***Fissurina lucida*.** This is by far the most frequently occurring *Fissurina* species (401 samples) but is geographically restricted, being absent from the Arctic and Southern oceans and the Gulf of Mexico–Caribbean Sea (Fig. 45). It occurs on marshes in northern Spain (27 samples), California (32) and New Zealand (1). The majority of occurrences are in marginal marine environments (236) and shelf seas (122) and it is uncommon in the deep sea (13) where it is recorded down to 1224m in the Norwegian Sea. It has not yet been recorded in fjords. This may reflect a preference for somewhat less cool conditions. In a 27-month time-series study of pairs of replicates from two stations in the Hamble estuary, England, it occurred 44 times in the lower intertidal station (sta. 1, close to neap low water) and only 7 times in the mid intertidal station (sta. 2, Murray & Alve, 2000a). There was great

Fissurina laevigata

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway			x		
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean				x	
0	NW Africa					
10-30	Gulf of Guinea					x
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA		Max			
40-25	E USA	x	x		x	
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 44. *Fissurina laevigata*.

Fissurina lucida

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay	Max				
43	Portugal					
45	W Mediterranean					
20	E Mediterranean				x	
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA				x	
30	N Gulf of Mexico		x			
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California				x	
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf				x	
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 45. *Fissurina lucida*.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway			x		
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK		x			
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 46. *Fissurina marginata*.

variability in standing crop, biomass and species diversity and no clear correlations with any of the measured environmental parameters, although biomass and diversity seemed to be the best guides to seasonality. Nevertheless, there must be undetected subtle differences between the two stations that make sta. 2 less attractive to *F. lucida*. Examination under the microscope of live individuals of the associated common species showed no physical association between any of them and *F. lucida*.

***Fissurina marginata*.** Occurs mainly in the North Atlantic with few occurrences in the Arctic, Pacific and Southern oceans (in the latter as subsp. *fissa*). It ranges from marginal marine to deep sea (Fig. 46).

***Fissurina orbignyana*.** Occurs in the North Atlantic and Mediterranean (in the latter mainly as subsp. *caribaea*) primarily on the shelf with a single marginal marine record (Barbuda) and a few in the deep sea (Fig. 47).

***Fursenkoina* and *Stainforthia*.** Loeblich & Tappan (1987) place *Stainforthia* in the Superfamily Turrilinaea and *Fursenkoina* in the Superfamily Fursenkoinae, whereas Haynes (1981) placed them both in the Buliminida. *Stainforthia* is initially triserial then biserial with an optically radial wall, while *Fursenkoina* is biserial with an optically granular wall. The majority of species in both genera were originally attributed to *Virgulina*. The species of

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea				x	x
56	S Scandinavia/Baltic					
43-45	Seas around UK				x	
39	Biscay				x	
43	Portugal					
45	W Mediterranean				Max	
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					x
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 47. *Fissurina orbignyana*.

Fursenkoina can be divided into those with elongate tests (*bramletti*, *complanata*, *earlandi*, *punctata*, *sandiegoensis*, *schreibersiana*, *spinosa*) and those with short tests (*apertura*, *mexicana*). *Fursenkoina pontoni* is intermediate.

***Fursenkoina apertura*.** This differs from other species in its very large aperture. The types are from the San Diego Trough in southern California, USA, and all other occurrences are from the Pacific Ocean (San Pedro Basin, California, USA, Japan and Sea of Okhotsk). This is a deep-water species with just a few occurrences shallower than 200m (San Diego Trough, Uchio, 1960). In San Pedro Basin the species is most common at 2–3 cm sediment depth in the 63–150 µm fraction in April and October. It is deep infaunal (ALD 3.6 cm) in the Okhotsk Sea (Bubenshchikova *et al.*, 2008).

The seasonal deposition of phytodetritus in Sagami Bay, Japan, is related to the spring bloom in phytoplankton (late February to May). In a time-series study in 1997–1998, *S. apertura* migrated into the phytodetritus layer in May and their protoplasm was green showing that they were feeding on fresh phytodetritus containing chlorophyll-*a*. There was a high concentration of juvenile individuals in the fluffy detritus layer and fewer in the sediment (Kitazato *et al.*, 2000).

***Fursenkoina bramletti*.** This is rare with only 30 occurrences all in California borderland basins, USA.

***Fursenkoina complanata*.** This has a very elongate test with 4–5 chambers in each row. There are scattered records from the Atlantic, Pacific and Southern oceans from marginal marine to deep sea. The greatest abundance is in the deep sea off Japan (Fig. 48).

***Fursenkoina earlandi*.** It looks like a bolivinid rather than *Fursenkoina*. It occurs in the deep sea in the Gulf of Guinea, South Atlantic, Weddell Sea, Scotia Sea (where it reaches a maximum abundance of 67%) and Ross Sea.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
43	W Mediterranean					x
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico				x	x
25-18	S Gulf of Mexico					
18-12	Caribbean Sea		x			
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					x
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					Max
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 48. *Fursenkoina complanata*.

Fursenkoina mexicana. It looks like a polymorphinid. There are few occurrences in the marginal marine (Indian River, USA, and NW African shelf), with most from the deep sea from North Africa to the South Atlantic and maximum off Japan.

Fursenkoina pontoni. This was described from the Miocene of Florida, USA. It is confined to the east and west coasts of the USA, the Caribbean and Baja California (Fig. 49). It is the most abundant species of *Fursenkoina* with nearly half the occurrences >10%. It occurs primarily in lagoon and shelf environments but it is also recorded from the continental slope in the Gulf of Mexico. Although most records are from sediment samples it is also found to be epiphytal in low abundance on various calcareous algae on Nevis (Wilson, 2007; Wilson & Ramscook, 2007).

The areas of high abundance are: San Francisco Bay, California, USA (Lesen, 2005), NW Gulf of Mexico (Phleger, 1951; 1956) and Puerto Rico (Seiglie, 1974). San Francisco Bay is an estuary with turbid water which is of normal salinity in the summer but diluted by runoff during the winter and spring (annual range of salinity 15–32). There are pronounced spring phytoplankton blooms. The standing crop of *F. pontoni* collected monthly over two years ranged from 0 to 304 per 10 cm³ sediment and was positively correlated with sediment TOC, nitrogen, amino acids and chlorophyll-*a* but not with sediment bacteria. Lesen (2005) suggests that measurement of as many potential food resources as

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA		x			
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea				Max	
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 49. *Fursenkoina pontoni*.

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea		Max			
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 50. *Fursenkoina punctata*.

possible is necessary to fully evaluate the food supply. The shelf and upper slope in the NW Gulf of Mexico have salinities of 35.5–36, temperatures of ~10–20°C but no records were made of potential food supply. Abundances reach >10% in 56% of the shelf samples and 44% of those from the slope (down to 227 m). The standing crop is 0–111 per 10 cm³.

The shelf off Puerto Rico has high abundances 0–91%, mean 41%. The standing crop ranges from 0–321 per 10 cm³. The inner shelf has salinities of 33.3–36.8, temperatures of 24–29°C and silty clay substrate. The area is subject to pollution from

Fursenkoina schreibersiana						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean				Max	
70-60	N & W Norway					
65	Iceland-Norwegian Sea					x
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay				x	
39	Portugal				x	
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea				x	
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf				Max	
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 51. *Fursenkoina schreibersiana*.

industry (fish-canning, animal feed, fertilizer factories) as well as from the human population. Near-bottom dissolved oxygen values range from 4.4–6.8 ppm. There had been a change in the microfauna prior to sampling and *F. pontoni* became the dominant species. As no other environmental factor had undergone any major change, the increase was attributed to pollution (although no measurements of pollutants were reported) so this cannot be confirmed.

In summary, *F. pontoni* is a warm-temperate stenohaline species able to tolerate low oxygen conditions and possibly elevated levels of organic pollutants. It is restricted to southern North America and the Caribbean.

***Fursenkoina punctata*.** Occurs in marginal marine environments in the Caribbean (where it reaches its highest abundance) and on the shelf in the Atlantic and Pacific oceans (Fig. 50).

***Fursenkoina sandiegoensis*.** It is found in marginal marine and borderland basins off California, USA, and in the deep sea off El Salvador.

***Fursenkoina schreibersiana*.** This has a few occurrences in marginal marine environments and in the deep sea but is mainly a shelf form with maximum abundance in the Arctic. Most records are from the East Atlantic with a few from the Caribbean and Pacific USA (Fig. 51).

Glandulina spp.						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway			x		
65	Iceland-Norwegian Sea					x
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					x
39	Portugal					x
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea				x	
10-30	S Atlantic					
35-56	S Atlantic					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea				x	
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf				Max	
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 52. *Glandulina* spp..

***Glandulina*.** Most records are of *Glandulina laevigata*. This genus is restricted to the Arctic, Atlantic and Indian oceans with records from fjord, shelf and deep sea (Fig. 52). The highest abundance is in the slightly hypersaline Arabian Gulf shelf.

***Globocassidulina subglobosa*.** Although there are a few records from marginal marine environments this is essentially a shelf and deep-sea species occurring widely throughout the Atlantic, Pacific and Southern oceans (Fig. 53). It occurs where the mean sea floor organic C flux is ~15 gm²a⁻¹ (Altenbach *et al.*, 1999). The range tolerated in the Gulf of Guinea is 0.8–80 gm²a⁻¹ (Altenbach *et al.*, 2003). Schönfeld (2001) found it to be an oxic species based on measurements of pore water.

***Globulina*, *Vasiglobulina* and polymorphinids *sensu lato*.** Many authors treat polymorphinids as a group. They occur in fjords, shelf and deep sea in the Arctic, Atlantic, Mediterranean and Pacific (Fig. 54). Although *Globulina* and *Vasiglobulina* span the same range of environments they are primarily shelf forms confined to the Arctic and Atlantic (Fig. 55). Originally the subspecies *myristiformis* was placed in *Globulina gibba* but subsequently it was not only raised to species status but transferred to *Vasiglobulina*. Most records of *Globulina* are of *G. gibba* and all are from fjord, shelf or deep sea in the eastern North Atlantic. *Vasiglobulina myristiformis* is likewise a shelf form known from the NE Atlantic and Mediterranean (Adriatic). *Vasiglobulina* sp. is recorded from the shelf of eastern USA (listed as a new but unnamed species by Poag *et al.*, 1980). It is permanently anchored to large detrital grains and in this respect differs from *Globulina*. However, there is no evidence that *V. myristiformis* has an attached mode of life.

***Guttulina*.** The species most widely distributed is *Guttulina lactea* which occurs in marginal marine, fjord and shelf environments in the North Atlantic with a single occurrence on the shelf off Japan. *Guttulina problema*, described from the Tertiary of Italy, occurs

Globocassidulina subglobosa						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay				x	x
43	Portugal					
45	W Mediterranean					x
20	E Mediterranean				x	
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					Max
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					x
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					x
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 53. *Globocassidulina subglobosa*.

in shelf sediments in the Adriatic Sea and east USA. The other species, *G. australis*, *G. austriaca*, *G. communis*, *G. harrisi*, *G. quinqueloba*, *G. rectiornata* and *G. yamazii* have very restricted distributions. An unidentified species is very abundant in the Ob estuary, Russia, with a maximum abundance of 45.4% and a mean of 15.5% (5 samples). Considering all *Guttulina* species together, they occupy marginal marine (in the Arctic), fjord, shelf and deep-sea environments but mostly shelf seas (125 of 151 samples) in the Atlantic and Pacific oceans (Fig. 56).

Gyroidina/Gyroidinoides. There has long been confusion in the assignment of species between *Gyroidina* and *Gyroidinopsis*. Loeblich & Tappan (1987) consider that most species correctly belong in *Gyroidinoides* or *Hansenisca*. Fourteen species have stained (living) records and six of these are known only from the deep sea in the Pacific Ocean (*broekhiana*, *gemma*, *multilocula*, *nitidula*, *quinqueloba* and *rotundimargo*), Atlantic (*perlucida*) and Southern oceans (*subplanata*). Three species occur in shelf seas as well as the deep sea (*neosoldani*, *orbicularis*, *umbonata*). *Gyroidina orbicularis* occurs at variable sediment depths down to 8 cm in Sea of Okhotsk ALD₈ 1.9 cm (Bubenshchikova *et al.*, 2008). It occurs where the mean sea floor organic C flux is $\sim 3.5 \text{ gm}^2 \text{ a}^{-1}$ (Altenbach *et al.*, 1999). Taking all species together the distribution is shelf and deep sea in the East Atlantic and deep

Polymorphinids						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					Max
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic				x	
43-45	Seas around UK					
39	Biscay					x
43	Portugal					
45	W Mediterranean					x
20	E Mediterranean				x	
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California				x	
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea				x	
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 54. Polymorphinids.

Globulina spp. including Vasiglobulina						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway			x		
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean				Max	
0	NW Africa					
10-30	Gulf of Guinea					x
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 55. *Globulina* and *Vasiglobulina*.

Guttulina all spp.						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean		Max	x	x	
70-60	N & W Norway					
65	Iceland-Norwegian Sea					x
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay		x		x	
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada				x	
45-40	E USA					
40-25	E USA				x	
30	N Gulf of Mexico					
25-18	S Gulf of Mexico		x			
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					x
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 56. *Guttulina* spp..

sea only in the West Atlantic, Pacific and Southern oceans (Fig. 57). In only one out of 573 occurrences is the abundance >10% and the mean percentages of all species ranges from 1.03 to 1.74% (Table 2). In the South Atlantic *Gyroidinoides* is associated with North Atlantic Deep Water (NADW) (Mackensen *et al.*, 1995).

***Haynesina germanica*.** This has been recorded under various species names, including *Protelphidium anglicum* and *Nonion tisburyensis*. It is one of the characteristic shallow infaunal species of marginal marine environments (Murray, 2006). It occurs in 15% of the samples and has a mean abundance of 28% (Table 2) and maximum abundances of 100%. There have been several time-series studies of this form (Murray, 1968; Cearreta, 1988; 1989; Murray & Alve, 2000a) so it is known to be abundant throughout the year rather than just occurring at one season. It is strongly euryhaline, shallow infaunal, and feeds on diatoms and cyanobacteria (Murray, 2006). Molecular genetics shows it to be a single species (Langer, 2000). It is most commonly present in intertidal to shallow subtidal brackish marginal marine environments but it is also present on marshes and there are a few occurrences in fjord and shelf environments (Fig. 58 lower). The North Atlantic and Gulf of Mexico are the main areas of occurrence. In the NE Atlantic the northern limit appears to be southern Scandinavia (Oslofjord, Norway). Its absence from the Baltic cannot be due to a salinity control as the species is euryhaline.

Gyroidina - Gyroidinoides all spp.						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway			x		
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK				x	
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean				x	
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					Max
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					x
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 57. *Gyroidina*/*Gyroidinoides*.

Perhaps the water temperature never reaches a level suitable for reproduction. In the Adriatic it avoids substrates with seagrass and higher amounts of blue-green algae and shows a good correlation with the diatom *Nitzschia* as a food source (Hohenegger *et al.*, 1989). In the NW Atlantic its northern limits vary: it does not occur in marshes north of Georgia or in marginal marine environments north of Cape Cod. The only record in the Pacific Ocean is from marsh in New Zealand.

Under experimental conditions sediment collected from 140 and 195 m from Oslofjord was kept in small sealed jars (to simulate shallow-water conditions) for 34 weeks at the end of which small *Haynesina germanica* were present in some of the containers although they were not present in the samples when collected (Alve & Goldstein, 2003). Under experimental conditions with varying temperature (12 and 22°C) and salinity (12, 22, 36) it grew abundantly at all salinities and the highest numbers were reached at 12°C (Goldstein & Alve, 2011). When buried in sediment under experimental conditions it did not climb up to the sediment surface (Lee *et al.*, 1969).

***Haynesina orbiculare*.** This is perhaps the cooler-water equivalent of *H. germanica* although it may require warm summer temperatures for reproduction (Scott *et al.*, 1977). It occurs predominantly in marginal marine environments (maximum abundance in Canada) and to a lesser extent in marshes and fjords. It features in

Haynesina germanica

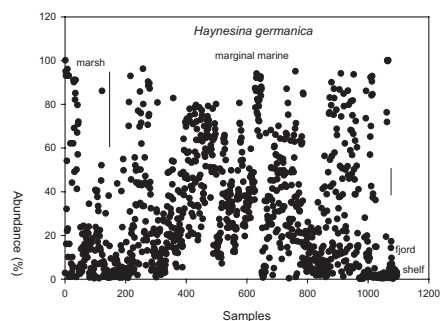
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK	Max				
39	Biscay					
39	Portugal		x			
43	W Mediterranean		Max			
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico		x			
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 58. *Haynesina germanica*.

the Arctic Ocean and the most southerly occurrence in the NW Atlantic is in Long Island Sound, USA (Fig. 59). The record in Arcachon lagoon, Biscay, is almost certainly a misidentification. In an experiment it was found to be a highly mobile species (Schafer & Young, 1977).

***Helenina anderseni*.** Apart from occurrences in the Mediterranean this species is absent from the East Atlantic. It occurs on marshes/mangals and in marginal marine environments in the Atlantic seaboard of North America and Caribbean and in the Pacific (Fig. 60). It is found down to 45–50 cm sediment depth in an Australian mangal (Berkeley *et al.*, 2008).

Haynesina orbiculare

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay		??			
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada		Max			
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 59. *Haynesina orbiculare*.

Helenina anderseni

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada	Max				
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 60. *Helenina anderseni*.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					Max

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					
15-30	S Africa					
65	Australia					
	Antarctic					

Fig. 61. *Hoeglundina elegans*.

Hoeglundina elegans. This epifaunal aragonitic species from the Atlantic, Pacific and Indian oceans typically occurs on the continental slope but is also known from shelf seas (Fig. 61). High abundance is known from Biscay and the South Atlantic, although the mean abundance is modest. It occurs where the mean sea floor organic C flux is 10–15 gm² a⁻¹ (Altenbach *et al.*, 1999). In Biscay it occurs in eutrophic to oligotrophic conditions and is shallow infaunal (Fontanier *et al.*, 2002; 2006; Mojtahid *et al.*, 2010). The range tolerated in the Gulf of Guinea is 0.8–62.3 g m² a⁻¹ (Altenbach *et al.*, 2003). Schönfeld (2001) found it to be an oxic species based on measurements of pore water. In the South Atlantic it is associated with NADW (Mackensen *et al.*, 1995).

Hopkinsina pacifica atlantica. The occurrences in the Atlantic, Mediterranean, Pacific and Indian oceans are confined to marginal marine and shelf environments (47 and 53% respectively, Table 2) mainly in temperate settings (Fig. 62). The highest abundance is in marginal marine Tomales Bay, California, USA, in muddy sediments and it is especially abundant in winter (maximum 56%; 28 out of 38 samples >10%). The annual salinity range is 20.3–33.5 and temperature 7–12°C so the species was regarded by the authors as estuarine but it is also correlated with fine-grained sediment (McCormick *et al.*, 1994). On the Adriatic shelf a single station at 32 m was sampled several times

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA		Max			
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					
15-30	S Africa					
65	Australia					
	Antarctic					

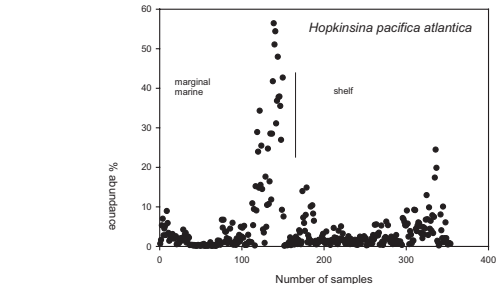


Fig. 62. *Hopkinsina pacifica atlantica*.

throughout the year. This species occurs predominantly in the top centimetre of the muddy sediment but at different times of the year it also extends down to the maximum depth sampled (7 cm) so has been described as ‘potential infauna’ (Barmawidjaja *et al.*, 1992).

Hyalinea balthica. The types are from the Baltic where it was recorded adherent on seaweed. Although there are rare occurrences in the Pacific and Indian oceans, this is essentially a NE Atlantic and Mediterranean species occurring in fjord, shelf and deep sea (Fig. 63). It has peak abundance in the top cm of sediment in Biscay (Hess & Jorissen, 2009).

Lagena. Morphospecies of the unilocular genus *Lagena* can be differentiated only on a few criteria, namely the shape of the chamber,

Hyalinea balthica						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
	Arctic Ocean				x	
70-60	N & W Norway					
65	Iceland-Norwegian Sea					x
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					Max
45	E Mediterranean				x	
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea				x	x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf				x	
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 63. *Hyalinea balthica*.

the presence or absence of any wall surface texture ('ornament') and the nature of the aperture. Notwithstanding this basically simple morphology, numerous genera have been erected primarily on the shape of the chamber. Here species that have been selected as types of other genera are also considered under *Lagena* as there seems no benefit in increasing taxonomic confusion by adding these new genera: *acuticosta*, type of *Obliquina* Seguenza, 1862; *gracilis*, type of *Procerolagena* Puri, 1954; *hispidula*, type of *Pygmaeoseistrion* Patterson & Richardson, 1987. It has been claimed that *Lagena* is parasitic on other foraminifera (Haynes, 1981, p. 54) but no evidence in support of this has been published. MacGillivray observed *L. laevis* adherent on seaweeds and on the byssus of a modiolid bivalve (cited in Williamson, 1848).

Although more than 30 species of *Lagena* are recorded in living (stained) assemblages in 10.3% of the dataset, in only 4 samples out of a total of 825 do they have an abundance >10% and their mean abundance is merely 0.82% so they are undoubtedly rare. Collectively they are distributed in marginal marine to deep sea of all the oceans with just a single record from a mangal. However, individual species show restricted distributions. The highest abundance of *Lagena* is an unidentified species in an Indonesian mangal (14%). The other high abundances are all 10% and from off Japan: *L. apiopleura* and *L. sulcata spicata* at 150 m and *L. striata* at 300 m.

***Lagena clavata*.** This occurs primarily on shelf seas in the North Atlantic and Adriatic (mean 0.66%) with a few occurrences in marginal marine and deep-sea settings in the North Atlantic (Fig. 64).

***Lagena gracillima*.** With a mean abundance of 0.70% it has a similar geographical distribution to *L. clavata* but also with occurrences in Arctic Ocean fjords and shelf. In the North Atlantic it occurs primarily in shelf and deep-sea settings.

***Lagena laevis*.** With a mean abundance of 0.74% it occurs mainly in shelf seas in the North Atlantic but with a single occurrence in

Lagena clavata						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK				Max	x
43-45	Biscay				x	
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA				x	
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 64. *Lagena clavata*.

Lagena laevis						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway			x		
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean				x	
20	NW Africa					
0	Gulf of Guinea				x	x
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea				Max	
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					

Fig. 65. *Lagena laevis*.

the South Atlantic (Fig. 65). It is also present in the Arctic Ocean down to 374 m and in a marginal marine lagoon in the Caribbean.

***Lagena striata*.** With a mean abundance of 0.69% it is most commonly present on the Adriatic Shelf but is also sporadically present in the North and South Atlantic as well as the Pacific (Fig. 66). Its maximum abundance is in the deep sea off Japan (300 m) and it occurs down to 494 m in the Gulf of Cadiz and 3891 m in the Gulf of Guinea.

***Lagena substriata*.** With a mean abundance of 0.73% it is sporadically present from marginal marine to deep sea in the

Lagena striata						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK				x	
39	Biscay		x			
43	Portugal					x
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea				x	x
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA		x			
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California				x	
12	El Salvador-Nicaragua					
35	Korea & Japan					Max
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 66. *Lagena striata*.

North Atlantic and shelf in the Mediterranean (Fig. 67). In the Norwegian Sea it extends down to 693 m.

***Lamarckina haliotidea*.** This species is generally rare (mean 1.42%) and the maximum abundance is 7% on the shelf off northern Spain (Diz *et al.*, 2004). In this area it is also recorded down to a depth of 9 cm in the sediment. It occurs sporadically in estuaries in southern England, a *Thalassia* habitat in Jamaica, and a fjord (Loch Etive, Scotland) but is generally found in shelf environments off NW Europe and eastern USA (Fig. 68). Of the 61 occurrences only 3 are from the USA and Jamaica with a maximum abundance of 0.30% and a mean of 0.26%.

***Laticarinina pauperata*.** There are surprisingly few records of this species (35) and all are from the deep sea in the Atlantic Ocean, South China and Weddell seas (Fig. 69). Notwithstanding this rarity, 22 live individuals collected from 775 m off New England, USA, were used in experiments. They were placed on the sediment surface (using sediment from the sampling location) and photographed at regular intervals over a period of days. They moved over and in the sediment and climbed the walls of the containers. Surface tracks were made by individuals moving in a flat position and also by others moving with the test held vertically. Subsurface movement led to cracks in the sediment surface. Feeding traces were arc-shaped and made by the pseudopodia

Lagena substriata						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway			x		
55-59	Iceland-Norwegian Sea					x
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean				x	
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA		x			
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 67. *Lagena substriata*.

Lamarckina haliotidea						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK				Max	
39	Biscay		x			
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA				x	
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea		x			
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 68. *Lamarckina haliotidea*.

moving over the sediment surface. Average daily movements were 16.43 and 11.54 mm individual⁻¹ for two consecutive months (Weinberg, 1991). The only record of the genus occurring in shelf seas is that of *Laticarinina* sp. living down to 9 cm (limit of sampling) in coarse sediments subject to disturbance off northern Spain (Diz *et al.*, 2004).

***Lenticulina*.** Many records are left in open nomenclature but 18 species are also recorded and one of these (*peregrina*) is sometimes assigned to *Neolenticulina*. This is primarily a deep-sea species but it also occurs in small numbers on the shelf. With the exception of rare occurrences in the South China Sea this species

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					x
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					x
10-30	Gulf of Guinea					x
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					Max

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					x
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 69. *Laticarinina pauperata*.

is confined to the eastern Atlantic. It is tolerant of dysoxic and suboxic pore water but its maximum abundance is in high oxigenic waters close to the sediment surface, therefore, it is not a reliable indicator of low oxygen conditions (Schönfeld, 2001). With a mean abundance of 0.39% it occurs very infrequently in marginal marine and fjord and mainly in shelf and deep-sea environments, in the Arctic, Atlantic, Mediterranean, Pacific, Indian and Southern oceans (Fig. 70). The only abundance >10% is from the shelf off Japan. *Lenticulina gibba* (mean 0.48%, maximum 1.72%) is found in shelf and deep sea in the North Atlantic, Mediterranean and South China Sea.

Marginulina/Marginulopsis. These genera have been recorded in only 26 samples with an overall mean of 0.41%. Each species is very restricted: *bachei* (1 record), *bradyi* (2), *glabra* (15), *obesa* (8). All records are from the North Atlantic, Mediterranean and South China Sea shelf and deep sea (maximum 1.32% off Greenland) (Fig. 71). *Marginulina glabra* occurs where the mean sea floor organic C flux is ~20 g m⁻² a⁻¹ (Altenbach *et al.*, 1999).

Melonis. Basically there are two morphotypes of *Melonis*: compressed or inflated. The compressed forms are generally identified as *M. barleeaanum* but sometimes as *M. affinis*, *M. parkerae* or *M. zandamae*. Some authors have found it impossible to separate

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					Max
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic			x		
43-45	Seas around UK				x	
39	Biscay				x	
43	Portugal				x	
45	W Mediterranean					
20	E Mediterranean					x
0	NW Africa					x
10-30	Gulf of Guinea					x
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					x
73	Arctic Canada					
50-43	Canada					
45-40	E USA		x			
40-25	E USA				x	
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					x

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua				x	x
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 70. *Lenticulina* spp..

barleeaanum and *zandamae* (Schmiedl *et al.*, 1997). The inflated forms are *M. pompilioides* otherwise sometimes called *M. sphaeroides*

Melonis barleeaanum. This is occasionally present in fjords but it is primarily a shelf and deep-sea form occurring widely in the Arctic, Atlantic, Pacific and Southern oceans (Fig. 72). In the Arctic Ocean it occurs in seasonally ice-free areas (Wollenburg & Mackensen, 1998). The mean values are 6.4% fjord, 7.5% shelf and 8% deep sea and maximum values reach 86% off Portugal. It is the dominant species in the top 2 cm of sediment on the continental slope and in canyons off Portugal (Nardelli *et al.*, 2010). In the South Atlantic it is present beneath surface waters showing seasonally varying productivity (Mackensen *et al.*, 1995). It occurs where the mean sea floor organic C flux is 8 g m⁻² a⁻¹ although it tolerates a much greater range (Altenbach *et al.*, 1999). Off NE Greenland the peak abundance is at 1–3 cm down core (Ahrens *et al.*, 1997) but in Biscay it is deep infaunal (Fontanier *et al.*, 2003). It shows vertical migration according to changing environmental conditions and availability of food (Linke & Lutze, 1993). Off Iberia there is tolerance of dysoxic and sub-oxic pore water but its maximum abundance is in high oxigenic waters close to the sediment surface so it is not a reliable indicator of low oxygen conditions (Schönfeld, 2001). But elsewhere, it seems to favour dysoxic sediments linked to a redox front (Licari

Marginulina spp.

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					x
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					x
43	Portugal					
45	W Mediterranean					
20	E Mediterranean				x	
0	NW Africa					x
10-30	Gulf of Guinea				x	
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					Max
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea				x	x
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					
15-30	S Africa					
65	Australia					
	Antarctic					

Fig. 71. *Marginulina*/Marginulopsis.

et al., 2003; Fontanier *et al.*, 2005). It seems to be adapted to live in organic-rich sediments in submarine canyons (Schmiedl *et al.*, 2000). In Biscay it occurs in eutrophic to mesotrophic conditions (Mojtahid *et al.*, 2010). There appears to be a 2–3 month delay between the maximum arrival of food and reproduction because bioturbation is superficial and slows the rate of food transfer into the sediment (Fontanier *et al.*, 2003). In a two-year experiment, where the fauna was deprived of fresh phytodetritus, it increased in abundance indicating that it feeds on degraded food (Alve, 2010) but others have considered that it is independent of the vertical flux of food (Fontanier *et al.*, 2005).

***Melonis pompilioides*.** This is generally less abundant than *M. barleeianum* (Table 2). There are a few somewhat doubtful records from lagoons in the Caribbean but most occurrences are on the shelf and deep sea in the Atlantic Ocean (Fig. 73). In Biscay it occurs in oligotrophic conditions (Mojtahid *et al.*, 2010). In the South Atlantic it is present beneath surface waters showing seasonally varying productivity (Mackensen *et al.*, 1995).

***Nodosaria*.** With the exception of two records from marginal marine and fjord environments, this genus is otherwise confined to shelf and deep sea (Fig. 74). The mean abundance is 0.60% and the maximum 2.0%. Half the records are as sp. (26 out of 52)

Melonis barleeianum

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					Max
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					
15-30	S Africa					
65	Australia					
	Antarctic					

Fig. 72. *Melonis barleeianum*.*Melonis pompilioides*

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					Max
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					x
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 73. *Melonis pompilioides*.

Nodosaria spp.

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean			x		
65	N & W Norway					Max
55-59	Iceland-Norwegian Sea				x	
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					x
43	Portugal					x
45	W Mediterranean					x
20	E Mediterranean				x	
0	NW Africa					
10-30	Gulf of Guinea				x	x
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA		x			
40-25	E USA				x	
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					x

Fig. 74. *Nodosaria* spp..

Nonion depressulus

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK		Max			
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					
15-30	S Africa					
65	Australia					
65	Antarctic					

Fig. 75. *Nonion depressulus*.

Nonionellina labradorica

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic				x	
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada				Max	
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					
15-30	S Africa					
65	Australia					
65	Antarctic					

Fig. 76. *Nonionellina labradorica*.

and individual species have few occurrences: *albatrossi* (1), *calomorpho* (12), *catesbyi* (2), *perversa* (7), *subsoluta* (2).

***Nonion depressulus*.** With the exception of occurrences in an Australian mangal (as *Haynesina* which may be a misidentification for *H. germanica*), this form is confined to the Atlantic Ocean on marsh (rare), marginal marine, fjord and shelf (Fig. 75). In Christchurch Harbour, England, the optimum temperature appeared to be 5–10°C (Murray, 1968). This species is abundant in the intertidal zone of the Exe estuary, England, because the salinities are only slightly brackish (Murray, 1980; 1983) and it reproduces every 3–4 months throughout the year. The range of salinity tolerated in marginal marine southern Scandinavia is 24–28 (Alve & Murray, 1999) but the upper limit is higher (35), as seen from the shelf occurrences. In the Adriatic it shows a high correlation with the density of seagrass and to food resources of blue-green algae and diatoms (Hohenegger *et al.*, 1989).

***Nonionellina labradorica*.** More than half the occurrences are in fjords and the rest evenly divided between shelf and deep sea. This is a cold-water species confined to the Arctic, and high-latitude North Atlantic and Pacific oceans (Fig. 76). In the Arctic Ocean it

occurs in seasonally ice-free areas (Wollenburg & Mackensen, 1998). Korsun & Hald (1998; 2000) found it to be associated with nutrient-rich glacially-distal areas of fjords where it reproduces in spring in response to the phytoplankton diatom bloom. The maximum abundance of 87.7% is on the Grand Banks, Canada. The only record from the Pacific seaboard of North America is from cold methane seeps at 500–525m off northern California, USA, where it occurs in very low numbers down to 3 cm in the sediment (Rathburn *et al.*, 2000). This is similar to the subsurface depths in the Sea of Okhotsk (Bubenshchikova *et al.*, 2008) and off NE Greenland (Ahrens *et al.*, 1997) although it extends down to 10 cm in the Barents Sea (Ivanova *et al.*, 2008). It migrated vertically by ~1 cm in response to experimentally altered oxygen conditions (Alve & Bernhard, 1995).

Nuttallides pusillus. A deep-sea species found only in the East Atlantic in Biscay, Gulf of Guinea and the South Atlantic, although the types were from off Tasmania, Australia.

Nuttallides umboniferus. Like *N. pusillus* this is confined to the deep sea in Biscay, Portugal, Gulf of Guinea to the Scotia Sea and Weddell Sea with rare occurrences in the West Mediterranean and off the USA (Fig. 77). In Biscay it occurs in oligotrophic conditions (Mojtahid *et al.*, 2010) in the surface layers of sediment (Fontanier *et al.*, 2002).

Oolina. Although numerous species are recorded they are all rare. There are isolated occurrences in marsh, marginal marine, and fjord but most are from the shelf and deep sea (Fig. 78). The mean is low (0.86%) and the maxima 5.88% and 5.62% from the shelf and deep sea, respectively.

Oridorsalis. Of the three species discussed two (*O. sidebottomi* Scotia and Weddell seas and *O. tener* Scotia Sea) are confined to the deep sea, while *O. umbonatus* also rarely extends on to the shelf (Fig. 79). The mean for *O. umbonatus* is low (3.39%) but high abundances (56%) are attained to the north and west of Norway. It occurs where the mean sea floor organic C flux is $2 \text{ g m}^{-2} \text{ a}^{-1}$ while that for *tener* is $3 \text{ g m}^{-2} \text{ a}^{-1}$ (Altenbach *et al.*, 1999). The molecular genetics of bipolar examples of *O. umbonatus* show high similarity (Pawlowski *et al.*, 2007).

Osangularia culter. This deep-sea form is known only from the Gulf of Guinea and SE Atlantic and from the South China Sea.

Patellina corrugata. This is a very distinctive species with little possibility of it being misidentified, as pointed out by Williamson when he named it in 1858. Although Williamson gave no reason for choosing the generic name *Patellina* it must surely be based on the morphological similarity with the limpet (*Patella*). With its planoconvex form it has the morphology of an attached or clinging species and this has been confirmed by observation. Myers (1935a, b) studied material from tide pools of California, USA, and noted that the tests are attached to various firm substrates ‘that support a sparse population of diatoms and other unicellular organisms which may serve as food’. However, the tests were not permanently anchored because when he washed coralline algae from the pool, individuals of *P. corrugata* crawled up the sides of the dish. Unfortunately Myers gave no information about the abundance of the species in the tide pools beyond stating that they

Nuttallides umboniferus						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					x
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					x
35-56	S Atlantic					Max
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					x
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 77. *Nuttallides umboniferus*.

Oolina spp.						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					x
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					x
43	Portugal					x
45	W Mediterranean					x
20	E Mediterranean				x	
0	NW Africa					x
10-30	Gulf of Guinea					x
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					x
73	Arctic Canada				x	x
50-43	Canada					
45-40	E USA					x
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan				Max	
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 78. *Oolina* spp..

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					Max
65	N & W Norway					Max
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea				x	x
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					x
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					x
35	Korea & Japan					
x	S China Sea				x	x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 79. *Oridorsalis umbonatus*.

were the source of 'the most plentiful supplies'. However, Cooper (1961) recorded abundances of <3% of this species in his study of Californian tide pools.

The life cycle was worked out by Myers (1935a) and Berthold (1976) and the cultures used by the latter were 'derived from a single agamont'. Myers was the first to demonstrate the whole dimorphic life cycle in a foraminiferan. Under experimental conditions maximum gamontogamous (requiring two or more individuals to come together) reproduction occurred at 21°C with an (obligatory) alternation of generations occurring on average every 41 days (Myers, 1935b; Goldstein, 1999).

Apart from the localities from around the British Isles listed by Williamson, he recorded *P. corrugata* from Hunde Island off the west coast of Greenland in Davis Strait (material collected by Dr Sutherland, Williamson, 1858, p. xix). Thus, from the start, this species was clearly shown to be widespread.

As *P. corrugata* is a small species (often <150µm in diameter), it can live clinging to larger sedimentary particles, such as shell fragments and larger sand grains, as well as algae in shallow water. In assessing its geographical distribution, note must be taken of this mode of life. If suitable substrates have not been sampled then it will be absent. The majority of occurrences are from the shelf (80%) followed by deep sea (12%) with few from marginal marine or fjord. It is present in all the oceans (Fig. 80).

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway			x		
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK		x			
43-45	Biscay		x			
39	Portugal					
43	W Mediterranean					
45	E Mediterranean				x	
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA		x			
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea				x	
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California				x	
12	El Salvador-Nicaragua				x	
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic				Max	

Fig. 80. *Patellina corrugata*.

The majority of records are from surface sediments but off Vigo, northern Spain, it has been recorded down to 9cm in coarse sediment (Diz *et al.*, 2004). In most surface samples its abundance ranges from zero to a few % but a few blooms are recorded from a Svalbard fjord, the continental shelf off northern Spain, Cape Cod, USA, Argentina and the Antarctic Peninsula. It is especially abundant in protected tide pools off Tierra del Fuego, Argentina, where the surface water temperature is ~6°C (Thompson, 1978). Off Antarctic Peninsula the greatest abundance is at 12 and 30 m water depth in rocky cliff microhabitats with seaweeds which provide a substrate for the foraminifera (Lipps & DeLaca, 1980). The water temperature there ranges from -1.5°C in winter to 1.8°C in summer.

The type area for *P. corrugata*, probably the inner continental shelf off Scotland (Arran or Skye), has a bottom water temperature of ~10°C in summer (Lee & Ramster, 1981). From its widespread distribution this species clearly lives well outside the 21°C optimum for reproduction determined experimentally.

Pullenia. The species can be divided into two main groups based on test shape: globular (*bulloides*, *osloensis*, *subsphaerica*); flattened (*elegans*, *quinteloba*, *salisburyi*, *simplex*, *subcarinata*). With the exception of *P. osloensis* all are typically deep sea with limited occurrences on the shelf.

Pullenia bulloides						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					Max
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					x
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					x
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					
REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					x
12	El Salvador-Nicaragua					x
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 81. Pullenia bulloides.

Pullenia bulloides. The mean values are generally low, especially in the Pacific Ocean and the maximum is in the Barents Sea (Fig. 81). In the Arctic Ocean it occurs in seasonally ice-free areas (Wollenburg & Mackensen, 1998). Most records are from the deep sea but it has also been recorded in fjords and shelf. It occurs where the mean sea floor organic C flux is $\sim 5 \text{ g m}^{-2} \text{ a}^{-1}$ (Altenbach *et al.*, 1999). *Pullenia subsphaerica* described from Antarctica looks very similar and may be a synonym.

Pullenia elegans. This is like *quineloba* but with 7 chambers in the final whorl. It is known only from the shelf off California, USA (Lankford & Phleger, 1973).

Pullenia osloensis. This is quite distinct being much smaller than *bulloides* and less spherical. It was described from the Quaternary of southern Norway. Most records are from fjords and shelf adjacent to Norway and the Barents Sea with just a few individuals recorded from the Weddell Sea so the distribution is disjunct (Fig. 82) but no molecular genetic studies have yet been carried out so it is not known whether it is a single or two species. In the Arctic Ocean it occurs in seasonally ice-free areas (Wollenburg & Mackensen, 1998). In a two-year experiment, where the fauna was deprived of fresh phytodetritus, it decreased in abundance perhaps showing its need for fresh food (Alve, 2010).

Pullenia osloensis						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic				Max	
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Bathyal
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 82. Pullenia osloensis.

Pullenia quineloba. Most records are from the Atlantic Ocean but it is also present in the Pacific and rarely in the Indian Ocean (Fig. 83). It occurs where the mean sea floor organic C flux is $\sim 5 \text{ g m}^{-2} \text{ a}^{-1}$ (Altenbach *et al.*, 1999).

Pullenia salisburyi. This has 6 chambers in the final whorl and is said to be more compressed than *quineloba*. It is exclusively deep sea with rare occurrences in the South Atlantic, Pacific USA (where it is more common) and South China Sea.

Pullenia simplex. Not widely distributed (Portugal, South Atlantic, Scotia and Weddell seas) with maximum abundances of 25% Portugal and 24% Weddell Sea. It is said to differ from *quineloba* by its more rounded test but the two may be conspecific.

Pullenia subcarinata. The type looks more like *Melonis* than *Pullenia*. It is primarily a deep-sea form (82%) with some shelf and fjord records. It occurs in the Atlantic and Pacific oceans (Fig. 84). In the South Atlantic it is present beneath surface waters showing seasonally varying productivity (Mackensen *et al.*, 1995). It is infaunal with ALD₈ 2.6 cm in Sea of Okhotsk (Bubenshchikova *et al.*, 2008).

Reussella. Only two species are commonly recorded: *atlantica* and *spinulosa* with 84 and 223 occurrences, respectively. The former was originally described as a variety of the latter, differing in being smaller, more slender, thinner walled and with a tendency for the adult chambers to decrease in diameter. Rarer forms include *aculeata* and *pacifica* (Tables 2, 3) but often the forms are left in open nomenclature so the biogeographical plot is given for all species (Fig. 85). The genus is known primarily from the shelf, with *atlantica* also being common in marginal marine environments especially in the Caribbean and it is confined to the Atlantic and Gulf of Mexico. The most commonly reported form is *R. spinulosa*: from shelf seas in the Adriatic, east USA, Puerto Rico, Japan and Scilly atoll (Pacific). The three abundances $>10\%$

Pullenia quinqueloba						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					Max
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					x
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea				x	x
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					x
15-30	S Africa					
65	Australia					
	Antarctic					

Fig. 83. *Pullenia quinqueloba*.

are from the Adriatic and Scilly atoll. It may be epiphytic with slight tolerance of increased salinities and to oxygen deficiency (Van der Zwaan, 1982). It is also considered to be epiphytic in the Adriatic (Donnici & Serandrei Barbero, 2002). The main occurrence of *R. aculeata* is on the Mediterranean shelf off Spain (with a single record from a lagoon), Japan and the Red Sea. The few records of *R. pacifica* are from Baja California, Gulf of California and Japan. *Reussella* appears to favour temperate to warm fully marine environments.

Robertina/Robertinoides. Höglund (1947) separated *Robertinoides* from *Robertina* on the basis of subtle differences in the apertures and the internal partitions. Only two species are commonly recorded (*arctica* and *charlottensis*) and many records are left in open nomenclature. *Robertina/Robertinoides* occur mainly in the deep sea and shelf with few records from fjords and marginal marine environments (Fig. 86). They span the Arctic, Atlantic, Mediterranean, Pacific and Southern oceans. Overall they appear to favour cooler waters.

Robertina arctica. This is the most common form occurring in marginal marine, fjord, shelf and deep-sea environments of the North Atlantic, Mediterranean and Arctic oceans (Fig. 87).

Pullenia subcarinata						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					x
55-59	Iceland-Norwegian Sea					x
56	S Scandinavia/Baltic				x	
43-45	Seas around UK					
39	Biscay					
43	Portugal					
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina				x	x
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					Max
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					
15-30	S Africa					
65	Australia					
	Antarctic					

Fig. 84. *Pullenia subcarinata*.

Robertinoides charlottensis. This is confined to shelf and deep sea off Greenland, Grand Banks and eastern and western USA and Japan (Fig. 88).

Siphonina. Five species have been recorded in 76 samples and each occurs infrequently so the entire group is very rare. None occurs in marsh or fjord environments but all occur in shelf seas. *Siphonina pulchra* and *S. tubulosa* also occur in marginal marine environments (only in the Caribbean). *Siphonina bradyana* occurs mainly in the deep sea and *S. pulchra* has a single deep-sea occurrence at 253 m in the Gulf of Guinea. All occurrences are in the Atlantic Ocean, Mediterranean or Caribbean except for three deep-sea occurrences in the South China Sea (Fig. 89).

Sphaeroidina bulloides. This deep-sea species occurs in the East Atlantic and the Scotia Sea, in the Mediterranean and in the South China Sea (Fig. 90). It occurs where the mean sea floor organic C flux is $7 \text{ g m}^{-2} \text{ a}^{-1}$ (Altenbach *et al.*, 1999). The range tolerated in the Gulf of Guinea is $0.9\text{--}22 \text{ g m}^{-2} \text{ a}^{-1}$ (Altenbach *et al.*, 2003).

Spirillina vivipara. This is an easily identified species with little scope for error. It has a wide distribution from marsh to deep sea but the majority of records are from the shelf (76%). It occurs in

Reussella spp.

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
43	W Mediterranean		x		Max	
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California		x			
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea				x	
5	Banda Sea					
40	New Zealand					
18	Atolls				Max	
	Red Sea/Arabian Gulf				x	
10	Indian Ocean				x	
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 85. *Reussella* spp..

the Atlantic, Mediterranean, Pacific and Indian oceans but is absent from polar regions (Fig. 91). It is recorded down to 1010 m off Portugal, 247 m in the Gulf of Guinea, 290 m off Japan and 902 m in the Arabian Sea. Its maximum abundance (89%) is on a marsh (Georgia, USA) but it is also abundant on carbonate sediments off New Caledonia, Algeria and southern England. It is epiphytic off Western Australia (Semeniuk, 2001). In a ria in northern Spain in high energy coarse sediments it is locally common down to 9 cm (Diz *et al.*, 2004). The mode of life is attached mobile: clinging to stable substrates using pseudopodia but also able to move freely through the sediment (Sturrock & Murray, 1981). The reproductive cycle was determined by Myers (1936). It is dimorphic and, under experimental conditions, the optimum temperature is 21°C with a minimum of 18 days to complete the full life cycle. At >26°C there is degeneration of some or all of the young while at 18°C the rate of reproduction is much reduced.

Stainforthia concava. The types are from Gullmar fjord, Sweden, where it was described as 'sparsely distributed' (Höglund, 1947, p. 258). It is now known to occur in a fjord on Svalbard and in shelf sediments from Iceland, Celtic Sea to the Gulf of Guinea including the western Mediterranean and Adriatic, the continental slope from Biscay to the Gulf of Guinea. There are isolated

Robertina and *Robertinoides* all spp.

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK				x	
39	Biscay				x	
43	Portugal					x
43	W Mediterranean		x			
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea				x	Max
10-30	S Atlantic					
35-56	S Atlantic					x

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada				x	
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					x
67	Weddell Sea					x

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					x
28	Baja California					
12	El Salvador-Nicaragua					x
35	Korea & Japan					
x	S China Sea				x	x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 86. *Robertina/Robertinoides* spp..*Robertina arctica*

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway			Max		
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					
43	Portugal					
43	W Mediterranean		x			
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 87. *Robertina arctica*.

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada				x	
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					x
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					Max
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 88. *Robertinoides charlottensis*.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK				x	
39	Biscay					
43	Portugal					
43	W Mediterranean					x
45	E Mediterranean				x	
20	NW Africa					
0	Gulf of Guinea					x
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea		Max		x	
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea				x	
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 89. *Siphonina* spp.

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					
56	S Scandinavia/Baltic					
43-45	Seas around UK					
39	Biscay					x
43	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 90. *Sphaeroidina bulloides*.

occurrences on the Canadian Arctic shelf, and continental slope off Iceland, tropical eastern Atlantic and Nicaragua; also a single record from a lagoon (Arcachon, France) (Fig. 92). Overall, the abundance is low with a single high value on the shelf off Algeria where it occurs at 67m in coarse grained cool-water carbonate sediment.

Stainforthia fusiformis. This is the most commonly occurring species of *Stainforthia*. Because of its small size it is more reliably recorded in >63 µm assemblages than in coarser fractions. It occurs from marginal marine to deep sea but is absent from marshes (Fig. 93). In marginal marine settings it is present in muddy sediments in the slightly brackish areas of estuaries and lagoons off NW Europe and the eastern seaboard of the USA. Although it occurs in Swedish and Norwegian fjords, it is in the latter that it reaches high abundance with mean values >40% and maximum occurrences of 88–98%. In shelf seas it extends from NW Europe to the Gulf of Guinea and in some areas reaches abundances >70% (Skagerrak, central North Sea, English Channel, Celtic Sea) and >65% off NW Africa. It occurs off southern France and in the Adriatic. In the NW Atlantic it occurs from the Arctic as far south as Cape Hatteras, USA. In the deep sea it is present in small numbers not only in the North Atlantic but also in the South China Sea, the Arabian Sea (Indian Ocean) and the

Spirillina vivipara

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic					
56	Seas around UK		x			
43-45	Biscay		x			
39	Portugal					x
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA	Max			x	
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea				x	
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean				x	x
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 91. *Spirillina vivipara*.

Scotia and Ross seas off Antarctica. It has not yet been recorded from the Pacific.

In the North Sea it may reproduce throughout the year (Murray, 1992). This species lives infaunally. In the southern North Sea on medium to fine sand substrates it occurs down to 25 cm but the majority of occurrences are at <5 cm (Moodley, 1990). In the Adriatic it is restricted to the top 2 cm (Barmawidjaja *et al.*, 1992).

This is an opportunistic species which is able to live at salinities >28, in sulphidic oxygen-depleted sediments (<2 ml l⁻¹ O₂) rich in organic matter (Alve, 1990; 1994; 1995; 2003; Bernhard & Bowser, 1999; Mojtabah *et al.*, 2009). In a two-year experiment, where the fauna was deprived of fresh phytodetritus, *S. fusiformis* decreased in abundance (Alve, 2010). It was a very successful colonizer in experiments (Alve, 1999). It migrated vertically from an initial maximum of 0.5–2 cm to the top 0.5 cm and even epifaunally on to worm tubes in response to experimentally altered oxygen conditions and did not tolerate oxygen levels <0.2 ml l⁻¹ (Alve & Bernhard, 1995). It is able to inhabit stressed environments subject to natural disturbance and it may also be able to do so where the disturbance is due to trawling (Alve & Murray, 1997). In a review, Alve (2003) concluded that it occupies three very different settings: beneath hydrographic fronts, e.g. Celtic Sea and Skagerrak; physically disturbed sediments, e.g. heavily

Stainforthia concava

EAST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					
65	Iceland-Norwegian Sea					
55-59	S Scandinavia/Baltic			x		
56	Seas around UK				x	
43-45	Biscay					x
39	Portugal					
43	W Mediterranean				Max	
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					

WEST ATLANTIC

~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada				x	
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD

~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					x
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
	Red Sea/Arabian Gulf					
10	Indian Ocean					
28	S Africa					
15-30	Australia					
65	Antarctic					

Fig. 92. *Stainforthia concava*.

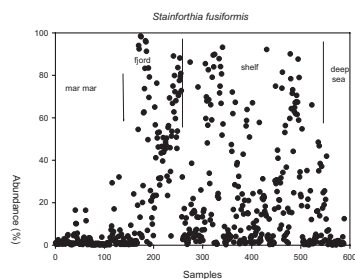
trawled North Sea and areas where sewage is dumped; ephemeral dysoxic/anoxic basins, e.g. fjords. It is the ability to cope with environmental stress rather than the control of any single environmental parameter that enables it to predominate in these areas.

Stainforthia loeblichii. This species was distinguished from *S. concava* because it is 'somewhat larger and by the lack of a distinct apical spine'; however, Feyling-Hanssen (1964, p. 308) considered the possibility that the two species may be the same. The types are from the Late Quaternary of the Oslo area, Norway. Although this species has a restricted distribution in cool waters in the Northern Hemisphere, from fjord, shelf and continental slope of the Arctic Ocean to western Norway (433 m) and the Grand Banks off Canada (330 m), it has moderate abundance in several areas. In two northern fjords on Svalbard abundances >10% occur in basins with water temperatures of 1.4 to -0.3°C but the only factor showing good correlation with abundance is salinity (34.66, Hald & Korsun, 1997). In subarctic Malangen fjord, Norway, a single occurrence >10% occurs in the inner part in waters of 6.0 to 6.9°C and salinity 34–34.75 (Husum & Hald, 2004). On the Grand Banks it occurs in water with a temperature of ~4°C with a highest abundance of 33% (Sen Gupta, 1971).

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					x
56	S Scandinavia/Baltic			Max		
43-45	Seas around UK					
39	Biscay					x
43	Portugal					x
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					x
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					x
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					x
15-30	S Africa					
65	Australia					
	Antarctic					

Fig. 93. *Stainforthia fusiformis*.

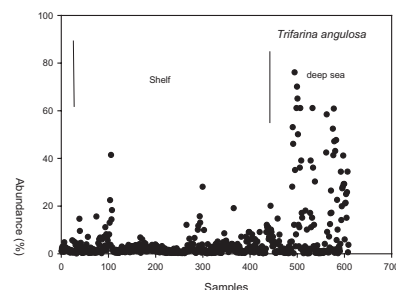
In the Barents Sea it reaches 12% on the continental slope at 433 m and with a TOC flux of $21 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Ivanova *et al.*, 2008). Thus, the distribution of *S. loeblichii* is geographically more confined than that of *S. concava* and it seems to be restricted to somewhat cooler waters. There is no information on downcore occurrence but is likely to be infaunal.

***Trifarina angulosa*.** Although there are occasional occurrences in marginal marine and fjord settings this is essentially a shelf and upper slope species and that is where it has its highest mean and maximum abundances (12% and 76%, respectively). It is found in all oceans except the Indian Ocean (Fig. 94). It is epifaunal and favours shelf break areas where the sediment is sand to gravel under the influence of bottom currents

EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70-60	Arctic Ocean					
65	N & W Norway					
55-59	Iceland-Norwegian Sea					Max
56	S Scandinavia/Baltic				x	
43-45	Seas around UK					
39	Biscay					x
43	Portugal				x	
45	W Mediterranean					
20	E Mediterranean					
0	NW Africa					
10-30	Gulf of Guinea					
35-56	S Atlantic					x

WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA				x	
40-25	E USA					x
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

REST OF WORLD						
~ lat.	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
48	Pacific Canada					
47-33	Pacific USA					
28	Baja California					
12	El Salvador-Nicaragua					
35	Korea & Japan					
x	S China Sea					
5	Banda Sea					
40	New Zealand					
18	Atolls					
10	Red Sea/Arabian Gulf					
28	Indian Ocean					
15-30	S Africa					
65	Australia					
	Antarctic					

Fig. 94. *Trifarina angulosa*.

(Mackensen *et al.*, 1993; 1995; Harloff & Mackensen, 1997) and oxic conditions (Schönfeld, 2001). The flux rate of organic carbon tolerated in the Gulf of Guinea is $8.7\text{--}89.2 \text{ g m}^{-2} \text{ a}^{-1}$ (Altenbach *et al.*, 2003).

***Trifarina fluens*.** The types are from Alaska and are said to differ from *T. angulosa* in having a more ornamented test, more irregular and inflated later chambers and not being consistently triangular in cross-section. There are 74 records compared with 621 for *T. angulosa*. All occurrences are from the Arctic Ocean and northern North Atlantic, from fjords, shelf and deep sea. It reaches its maximum abundance in the Norwegian Sea (Fig. 95). It is clearly a cold-water species.

Trifarina fluens						
EAST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
	Arctic Ocean					
70-60	N & W Norway					Max
65	Iceland-Norwegian Sea					Max
55-59	S Scandinavia/Baltic					
56	Seas around UK					
43-45	Biscay					
39	Portugal					
43	W Mediterranean					
45	E Mediterranean					
20	NW Africa					
0	Gulf of Guinea					
10-30	S Atlantic					
35-56	S Atlantic					
WEST ATLANTIC						
~ lat. N-S	Area	Marsh	Marg mar	Fjords	Shelf	Deep sea
70	E Greenland					
73	Arctic Canada					
50-43	Canada					
45-40	E USA					
40-25	E USA					
30	N Gulf of Mexico					
25-18	S Gulf of Mexico					
18-12	Caribbean Sea					
5	French Guiana					
24-31	Brazil					
38-54	Argentina					
58	Scotia Sea					
67	Weddell Sea					

Fig. 95. Trifarina fluens.

NOTE ADDED IN PROOF

After this paper had been accepted for publication and during the press editing phase, Andrew Gooday supplied the author with a pdf of the reference Gooday & Jorissen (2012). This paper discusses various aspects of biogeography of deep sea foraminifera based on mainly presence/absence data for living and dead forms. It has useful discussion of the controls on deep-sea biogeographical patterns and on future issues.

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REFERENCES

Ahrens, M.J., Graf, G. & Altenbach, A.V. 1997. Spatial and temporal distribution of benthic foraminifera in the Northeast Water Polynya, Greenland. *Journal of Marine Systems*, **10**: 445–465
Altenbach, A.V., Pflaumann, U., Schiebel, R., Thies, A., Timm, S. & Trauth, M. 1999. Scaling percentages and distributional patterns of benthic foraminifera with flux rates of organic carbon. *Journal of Foraminiferal Research*, **29**: 173–185.
Altenbach, A.V., Lutze, G.F., Schiebel, R. & Schönfeld, J. 2003. Impact of interrelated and interdependent ecological controls on benthic

foraminifera: An example from the Gulf of Guinea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **197**: 213–238.
Alve, E. 1990. Variations in estuarine foraminiferal biofacies with diminishing oxygen conditions in Drammensfjord, SE Norway. In Hemleben, C., Kaminski, M.A., Kuhnt, W. & Scott, D.B. (Eds), *Paleoceanography and taxonomy of agglutinated foraminifera*. Kluwer, Dordrecht, 661–694.
Alve, E. 1994. Opportunistic features of the foraminifer *Stainforthia fusiformis* (Williamson): Evidence from Frierfjord, Norway. *Journal of Micropaleontology*, **13**: 24.
Alve, E. 1995. Benthic foraminiferal distribution and recolonization of formerly anoxic environments in Drammensfjord, southern Norway. *Marine Micropaleontology*, **25**: 169–186.
Alve, E. 1999. Colonization of new habitats by benthic foraminifera: A review. *Earth-Science Reviews*, **46**: 167–185.
Alve, E. 2003. A common opportunistic foraminiferal species as an indicator of rapidly changing conditions in a range of environment. *Estuarine, Coastal and Shelf Science*, **57**: 501–514.
Alve, E. 2010. Benthic foraminiferal response to absence of fresh phyto-detritus: a two year experiment. *Marine Micropaleontology*, **76**: 67–75.
Alve, E. & Bernhard, J.M. 1995. Vertical migratory response of benthic foraminifera to controlled oxygen concentrations in an experimental mesocosm. *Marine Ecology Progress Series*, **116**: 137–151.
Alve, E. & Goldstein, S.T. 2003. Propagule transport as a key method of dispersal in benthic foraminifera. *Limnology and Oceanography*, **48**: 2163–2170.
Alve, E. & Goldstein, S.T. 2010. Dispersal, survival and delayed growth of benthic foraminiferal propagules. *Journal of Sea Research*, **63**: 36–51.
Alve, E. & Murray, J.W. 1994. Ecology and taphonomy of benthic foraminifera in a temperate mesotidal inlet. *Journal of Foraminiferal Research*, **24**: 18–27.
Alve, E. & Murray, J.W. 1997. High benthic fertility and taphonomy of foraminifera: a case study of the Skagerrak, North Sea. *Marine Micropaleontology*, **31**: 157–175.
Alve, E. & Murray, J.W. 1999. Marginal marine environments of the Skagerrak and Kattegat: a baseline study of living (stained) benthic foraminiferal ecology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **146**: 171–193.
Alve, E. & Nagy, J. 1986. Estuarine foraminiferal distributions in Sandebukta, a branch of Oslo Fjord. *Journal of Foraminiferal Research*, **16**: 261–284.
Alve, E., Murray, J.W. & Skei, J. 2011. Deep-sea benthic foraminifera, carbonate dissolution and species diversity in Hardangerfjord, Norway: an initial assessment. *Estuarine, Coastal and Shelf Science*, **92**: 90–102.
Anderson, S. 1994. Area and endemism. *Quarterly Review of Biology*, **69**: 451–171.
Angel, M. 1995. Rarity: A biological conundrum. *Ocean Challenge*, **5**: 8–9.
Barmawidjaja, D.M., Jorissen, F.J., Puskaric, S. & Van De Zwaan, G.J. 1992. Microhabitat selection by benthic foraminifera in the northern Adriatic Sea. *Journal of Foraminiferal Research*, **22**: 297–317.
Barras, C., Fontanier, C., Jorissen, F. & Hohenegger, J. 2010. A comparison of spatial and temporal variability of living benthic foraminiferal faunas at 550m depth in the Bay of Biscay. *Micropaleontology*, **56**: 275–295.
Belasky, P. 1996. Biogeography of Indo-Pacific larger foraminifera and scleractinian corals: a probabilistic approach to estimating taxonomic diversity, faunal similarity, and sampling bias. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **122**: 119–141.
Berkeley, A., Perry, C.T., Smithers, S.G. & Horton, B.P. 2008. The spatial and vertical distribution of living (stained) benthic foraminifera from a tropical, intertidal environment, north Queensland, Australia. *Marine Micropaleontology*, **69**: 240–261.
Bernhard, J.M. 2000. Distinguishing live from dead foraminifera: methods review and proper applications. *Micropaleontology*, **46** (Suppl. 1): 38–46.

- Bernhard, J.M. & Bowser, S.S. 1999. Benthic foraminifera of dysoxic sediments: chloroplast sequestration and functional morphology. *Earth-Science Reviews*, **46**: 149–165.
- Berthold, W.U. 1976. Test morphology and morphogenesis in *Patellina corrugata* Williamson. *Journal of Foraminiferal Research*, **6**: 167–185.
- Blanc-Vernet, L. 1969. Contribution à l'étude des Foraminifères de Méditerranée. *Recueil des travaux de la station marine d'Endoume*, **64**: 1–281.
- Bubenshchikova, N., Nürnberg, D., Lembe-Jene, L. & Pavlova, G. 2008. Living benthic foraminifera of the Okhotsk Sea: faunal composition, standing stock and microhabitats. *Marine Micropaleontology*, **69**: 314–333.
- Bugge, T., Befring, S., Belderson, R.H., Eidvin, T. & Jansen, E. 1987. A giant three-stage slide off Norway. *Geo-Marine Letters*, **7**: 191–198.
- Buzas, M.A. 1965. The distribution and abundance of foraminifera in Long Island Sound. *Smithsonian Miscellaneous Collections*, **149**: 1–89.
- Buzas, M.A., Smith, R.K. & Beem, K.A. 1977. Ecology and systematics of foraminifera in two *Thalassia* habitats, Jamaica, West Indies. *Smithsonian Contributions to Paleobiology*, **31**: 1–139.
- Buzas-Stephens, P. & Buzas, M.A. 2005. Population dynamics and dissolution of foraminifera in Nueces Bay, Texas. *Journal of Foraminiferal Research*, **35**: 248–258.
- Buzas-Stephens, P., Buzas, M.A. & Elliott, B.A. 2011. Foraminiferal population response to fluctuating inflow into Nueces Bay, Texas. *Journal of Foraminiferal Research*, **41**: 14–21.
- Cao, Y., Williams, D. & Williams, N.E. 1998. How important are rare species in aquatic community ecology and bioassessment? *Limnology and Oceanography*, **43**: 1403–1409.
- Cearreta, A. 1988. Population dynamics of benthic foraminifera in the Santoña estuary, Spain. *Revue de Paléobiologie*, **2**: 721–724.
- Cearreta, A. 1989. Foraminiferal assemblages in the ria of San Vicente de la Barquera (Cantabria, Spain). *Revista Española de Micropaleontología*, **21**: 67–80.
- Collen, J.D. & Newell, P. 1999. *Fissurina* as an ectoparasite. *Journal of Micropaleontology*, **18**: 110.
- Cooper, W.C. 1961. Intertidal foraminifera of the California and Oregon coast. *Contributions from the Cushman Foundation for Foraminiferal Research*, **12**: 47–63.
- Culver, S.J. & Buzas, M.A. 1999. Biogeography of neritic foraminifera. In Sen Gupta, B.K. (Ed.), *Modern foraminifera*. Kluwer, Dordrecht, 93–102.
- Culver, S.J. & Horton, B.P. 2005. Infaunal marsh foraminifera from the outer banks, North Carolina, USA. *Journal of Foraminiferal Research*, **35**: 148–170.
- Cushman, J.A. 1922. The Foraminifera of the Atlantic Ocean, Part 3. Textulariidae. *United States National Museum Bulletin*, **104**: 149pp.
- Daniels, C.H. 1970. Quantitative ökologische Beobachtungen an Foraminiferen im Limski kanal bei Rovinj/Jugoslawien (nördliche Adria). *Göttinger Arbeiten zur Geologie und Paläontologie*, **8**: 1–109.
- Debenay, J.P. 2000. Foraminifers of tropical paralic environments. *Micropaleontology*, **46** (Suppl. 1): 153–160.
- Debenay, J.P. & Payri, C.E. 2010. Epiphytic foraminiferal assemblages on macroalgae in reefal environments of New Caledonia. *Journal of Foraminiferal Research*, **40**: 36–60.
- Debenay, J.P., Eichler, B.B., Bonetti, C. & Coelho, C. 1996. Foraminifers, biomarkers in the mangrove swamps of Bertioiga (Sao Paulo, Brazil). *Anais da Reunião Especial da SBPC: Ecossistemas Costeiros – do conhecimento à gestão*. SBPC, Florianópolis, 448pp.
- Debenay, J.P., Guiral, D. & Parra, M. 2002. Ecological factors acting on the microfauna in mangrove swamps. The case of foraminiferal assemblages in French Guiana. *Estuarine, Coastal and Shelf Science*, **55**: 509–533.
- Debenay, J.P., Guiral, D. & Parra, M. 2004. Behaviour and taphonomic loss in foraminiferal assemblages of mangrove swamps of French Guiana. *Marine Geology*, **208**: 295–314.
- De Rijk, S.D. 1995. Salinity control on the distribution of salt marsh foraminifera (Great Marshes, Massachusetts). *Journal of Foraminiferal Research*, **25**: 156–166.
- De Rijk, S.D. & Troelstra, S.R. 1999. The application of a foraminiferal actuo-facies model to salt marsh cores. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **149**: 59–66.
- Diz, P., Francés, G., Costas, S. & Alejo, I. 2004. Distribution of benthic foraminifera in coarse sediments, Ría de Vigo, NW Iberian margin. *Journal of Foraminiferal Research*, **34**: 258–275.
- Donnici, S. & Serandrei Barbero, R. 2002. The benthic foraminiferal communities of the northern Adriatic continental shelf. *Marine Micropaleontology*, **44**: 93–123.
- Duchemin, G., Jorissen, F., Andieux-Loyer, F., Le Loc'h, F., Hily, C. & Phillipon, X. 2005. Living benthic foraminifera from 'La Grande Vasière', French Atlantic continental shelf: Faunal composition and microhabitats. *Journal of Foraminiferal Research*, **35**: 198–218.
- Duchemin, G., Fontanier, C., Jorissen, F.J., Barras, C. & Griveaud, C. 2007. Living small-sized (63–150µm) foraminifera from mid-shelf to mid-slope environments in the Bay of Biscay. *Journal of Foraminiferal Research*, **37**: 12–32.
- Duleba, W. & Debenay, J.P. 2003. Hydrodynamic circulation in the estuaries of Estação ecológica Juréa-Itatins, Brazil, inferred from the foraminifera and thecamoebian assemblages. *Journal of Foraminiferal Research*, **33**: 62–93.
- Eichler, B.B., Debenay, J.P., Bonetti, C. & Duleba, W. 1995. Répartition des foraminifères benthiques dans le zone sud-ouest du système estuarien-lagunaire d'Iguape-Cananéia (Brésil). *Boletim do Instituto Oceanográfico de USP, São Paulo*, **43**: 1–17.
- Ellison, R.L. & Murray, J.W. 1987. Geographical variation in the distribution of certain agglutinated foraminifera along the North Atlantic margins. *Journal of Foraminiferal Research*, **17**: 123–131.
- Erbacher, J. & Nelskamp, S. 2006. Comparison of benthic foraminifera inside and outside a sulphur-oxidizing bacterial mat from the present oxygen-minimum zone off Pakistan (NE Arabian Sea). *Deep-Sea Research I*, **53**: 751–756.
- Fatela, F., Moreno, J., Moreno, F. et al. 2009. Environmental constraints of foraminiferal assemblages distribution across a brackish tidal marsh (Caminha, NW Portugal). *Marine Micropaleontology*, **70**: 70–88.
- Feyling-Hanssen, R.W. 1964. Foraminifera in Late Quaternary deposits from the Oslofjord area. *Norges Geologiske Undersøkelse*, **225**: 1–383.
- Finlay, B.J. 2002. Global dispersal of free-living microbial eukaryote species. *Science*, **296**: 1061–1063.
- Fontaneto, D. 2011. *Biogeography of Microscopic organisms. Is Everything Small Everywhere?* Cambridge University Press, Cambridge, 365pp.
- Fontanier, C., Jorissen, F.J., Licari, L., Alexandre, P., Anschutz, P. & Carbonel, P. 2002. Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. *Deep-Sea Research I*, **49**: 751–785.
- Fontanier, C., Jorissen, F.J., Chaillou, G., David, C., Anschutz, P. & Lafon, V. 2003. Seasonal and interannual variability of benthic foraminiferal faunas as 550 m depth in the Bay of Biscay. *Deep-Sea Research I*, **50**: 457–494.
- Fontanier, C., Jorissen, F.J., Chailou, G., Anschutz, P., Gremare, A. & Givéaud, C. 2005. Live foraminiferal faunas from a 2800 m deep lower canyon station from the Bay of Biscay: faunal response to focussing of refractory organic matter. *Deep-Sea Research I*, **52**: 1189–1227.
- Fontanier, C., Jorissen, F., Anschutz, P. & Chaillou, G. 2006. Seasonal variability of benthic foraminiferal faunas at 1000 m depth in the Bay of Biscay. *Journal of Foraminiferal Research*, **36**: 61–76.
- Fontanier, C., Jorissen, F., Geslin, E., Zaragosi, S., Duchemin, G., Laversin, M. & Gaultier, M. 2008a. Live and dead foraminiferal faunas from Saint-Tropez Canyon (Bay of Fréjus): observations based on in situ incubated cores. *Journal of Foraminiferal Research*, **38**: 137–156.

- Fontanier, C., Jorissen, F.J., Lansard, B. *et al.* 2008b. Live foraminifera from the open slope between Grand Rhône and Petit Rhône Canyons (Gulf of Lions, NW Mediterranean). *Deep-Sea Research I*, **55**: 1532–1553.
- Forwick, M., Vorren, T.O., Hald, M. *et al.* 2010. Spatial and temporal influence of glaciers and rivers on the sedimentary environment in Sassenfjorden and tempelfjorden, Spitsbergen. In Howe, J.A., Austin, W.E.N., Korsun, S. & Paetzel, M. (Eds), *Fjord Systems and Archives*. Geological Society, London, Special Publications, **344**: 163–193.
- Frontalini, F. & Coccioni, R. 2008. Benthic foraminifera from heavy metal pollution monitoring: a case study from the central Adriatic coast of Italy. *Estuarine, Coastal and Shelf Science*, **76**: 404–417.
- Frontalini, F., Busi, C., Da Pelo, S., Coccioni, R., Cherchi, A. & Bucci, C. 2009. Benthic foraminifera as bio-indicators of trace element pollution in the heavily contaminated Santa Gilla lagoon (Cagliari, Italy). *Marine Pollution Bulletin*, **58**: 858–877.
- Gaston, K.J. 1997. What is rarity? In Kunin, W.E. & Gaston, K.J. (Eds), *The Biology of Rarity. Causes and Consequences of Rare-common Differences*. Chapman & Hall, London, 31–47.
- Gilpin, M.E. & Soulé, M.E. 1986. Minimum viable populations: processes of species extinction. In Soulé, M.E. (Ed.), *Conservation Biology: the Science of Scarcity and Diversity*. Sinauer, Sunderland, USA, 19–34.
- Goldstein, S.T. 1999. Foraminifera: a biological overview. In Sen Gupta, B.K. (Ed.), *Modern Foraminifera*. Kluwer, Dordrecht, 37–55.
- Goldstein, S. & Alve, E. 2011. Experimental assembly of foraminiferal communities from coastal propagule banks. *Marine Ecology Progress Series*, **437**: 1–11.
- Goldstein, S.T. & Harben, E.B. 1993. Taphonomic implications of infaunal foraminiferal assemblages in a Georgia salt marsh, Sapelo Island. *Micropaleontology*, **39**: 53–62.
- Gooday, A.J. 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *Journal of Oceanography*, **58**: 305–332.
- Gooday, A.J. & Jorissen, F.J. 2012. Benthic foraminiferal biogeography: controls on global distribution patterns in deep-water settings. *Annual Review of Marine Science*, **4**: 237–262. <http://dx.doi.org/10.1146/annurev-marine-120709-142737>
- Graf, G. 2003. Ecosystem functioning and biodiversity: bioengineering. In Wefer, G., Lamy, F. & Mantoura, F. (Eds), *Marine Science Frontiers for Europe*. Springer-Verlag, Berlin, 243–250.
- Grassle, J.F. & Sanders, H. 1973. Life histories and the role of disturbance. *Deep-Sea Research*, **20**: 643–659.
- Griveaud, C., Jorissen, F. & Anschutz, P. 2010. Spatial variability of live benthic foraminiferal faunas on the Portuguese margin. *Micropaleontology*, **56**: 297–322.
- Hald, M. & Korsun, S. 1997. Distribution of modern benthic foraminifera from fjords of Svalbard, European Arctic. *Journal of Foraminiferal Research*, **27**: 101–122.
- Harloff, J. & Mackensen, A. 1997. Recent benthic foraminiferal associations and ecology of the Scotia Sea and Argentine Basin. *Marine Micropaleontology*, **31**: 1–29.
- Haward, N.J.B. & Haynes, J.R. 1976. *Chlamys opercularis* as a mobile substrate for foraminifera. *Journal of Foraminiferal Research*, **6**: 30–38.
- Hayek, L.C. & Buzas, M.A. 2010. *Surveying Natural Populations. Quantitative Tools for Assessing Biodiversity* (2nd edn). Columbia University Press, New York, 590pp.
- Haynes, J.R. 1973. 1973. Cardigan Bay Recent foraminifera (Cruises of R.V. *Antur*, 1962–1964). *Bulletin of the British Museum (Natural History) Zoology*, Suppl. 4, 245pp.
- Haynes, J.R. 1981. *Foraminifera*. MacMillan, London, 433pp.
- Hayward, B.W., Holzmann, M., Grenfell, H.R., Pawlowski, J. & Triggs, C.M. 2004. Morphological distinction of molecular types in *Ammonia* – towards a taxonomic revision of the world’s most commonly misidentified foraminifera. *Marine Micropaleontology*, **50**: 237–271.
- Heinz, P., Ruscmeier, W. & Hemleben, C. 2008. Living benthic foraminiferal assemblages at the Pacific continental margin of Costa Rica and Nicaragua. *Journal of Foraminiferal Research*, **38**: 215–227.
- Heip, C., Brandt, A., Gattuso, J.P. *et al.* 2003. Ecosystem functioning and biodiversity. In Wefer, G., Lamy, F. & Mantoura, F. (Eds), *Marine Science Frontiers for Europe*. Springer-Verlag, Berlin, 289–302.
- Hess, S. & Jorissen, F.J. 2009. Distribution patterns of living benthic foraminifera from Cap Breton Canyon, Bay of Biscay: faunal response to sediment instability. *Deep-Sea Research I*, **56**: 1555–1578.
- Hess, S., Jorissen, F.J., Venet, V. & Abu-Zied, R. 2005. Benthic foraminiferal recovery after recent turbidite deposition in Cap Breton Canyon, Bay of Biscay. *Journal of Foraminiferal Research*, **35**: 114–129.
- Höglund, H. 1947. Foraminifera in the Gullmar Fjord and the Skagerak. *Zoologiska Bidrag från Uppsala*, **26**: 1–328.
- Hohenegger, J., Pillar, W. & Baal, C. 1989. Reasons for spatial microdistributions of foraminifera in an intertidal pool (northern Adriatic Sea). *PSZNI, Marine Ecology*, **10**: 43–78.
- Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, 375pp.
- Husum, K. & Hald, M. 2004. Modern foraminiferal distribution in the sub-arctic Malangen Fjord and adjoining shelf, northern Norway. *Journal of Foraminiferal Research*, **34**: 34–48.
- Ikeya, N. 1970. Population ecology of benthic foraminifera in Ishikari Bay, Hokkaido, Japan. *Records of Oceanographic Works in Japan*, **10**: 173–191.
- Ivanova, E.V., Ovsepyan, E.A., Risebrobakken, B. & Vetrov, A.A. 2008. Downcore distribution of living calcareous foraminifera and stable isotopes in the western Barents Sea. *Journal of Foraminiferal Research*, **38**: 337–356.
- Kitazato, H., Shiramaya, Y., Nakatsuka, T. *et al.* 2000. Seasonal phytodetritus deposition and responses of bathyal benthic foraminiferal populations in Sagami Bay, Japan: preliminary results from “Project Sagami” 1996–1999. *Marine Micropaleontology*, **40**: 135–149.
- Klitgaard-Kristensen, D. & Sejrup, H.P. 1996. Modern benthic foraminiferal facies across the northern North Sea. *Sarsia*, **81**: 97–106.
- Knight, R. & Mantoura, R.F.C. 1985. Chlorophyll *a* and carotenoid pigments in foraminifera and their symbiotic algae: analysis in high-performance liquid chromatography. *Marine Ecology Progress Series*, **23**: 241–249.
- Koho, K.A., Kouwenhoven, T.J., De Stigter, H.C. & Van Der Zwaan, G.J. 2007. Benthic foraminifera in the Nazaré Canyon, Portuguese continental margin: sedimentary environments and disturbance. *Marine Micropaleontology*, **66**: 27–51.
- Korsun, S. & Hald, M. 1998. Modern benthic foraminifera off Novaya Zemlya tidewater glaciers. *Arctic and Alpine Research*, **30**: 61–77.
- Korsun, S. & Hald, M. 2000. Seasonal dynamics of benthic foraminifera in a glacially fed fjord of Svalbard, European arctic. *Journal of Foraminiferal Research*, **30**: 251–271.
- Kunin, W.E. 1997. Introduction: on the causes and consequences of rare-common differences. In Kunin, W.E. & Gaston, K.J. (Eds), *The Biology of Rarity. Causes and Consequences of Rare-common Differences*. Chapman & Hall, London, 3–11.
- Langer, M. 2000. Comparative molecular analysis of small-subunit ribosomal 18S DNA sequences from *Haynesina germanica* (Ehrenberg, 1840), a common intertidal foraminifer from the North Sea. *Neues Jahrbuch für Geologie und Paläontologie*, **11**: 641–650.
- Langer, M.R., Hottinger, L. & Huber, B. 1989. Functional morphology in low-diverse benthic foraminiferal assemblages from tidal flats in the North Sea. *Senckenbergiana Maritima*, **20**: 81–99.
- Lankford, R.R. & Phleger, F.P. 1973. Foraminifera from the nearshore turbulent zone, western North America. *Journal of Foraminiferal Research*, **3**: 101–132.
- Le Calvez, J. 1947. *Entosolenia marginata* (Walker and Boys), foraminifère apogamique ectoparasite d’une autre foraminifère: *Discorbis villardebouanus* (d’Orbigny). *Comptes rendus hebdomadaire des séances de l’Académie des Sciences, Paris*, **224**: 1448–1450.

- Le Campion, J. 1970. Contribution à l'étude des foraminifères du Bassin d'Arcachon et du proche océan. *Bulletin Institute Géologique du Bassin Aquitaine*, **8**: 3–98.
- Lee, A.J. & Ramster, J.W. 1981. *Atlas of the seas around the British Isles*. Ministry of Agriculture, Fisheries and Food, Lowestoft, England. Not paginated.
- Lee, J.J. 1980. Nutrition and physiology of the foraminifera. In Levandowsky, M. & Hunter, S.H. (Eds) *Biochemistry and Physiology of Protozoa* (2nd edn), Academic Press, New York, **3**: 43–66.
- Lee, J.J., Muller, W.A., Stone, R.J., McEnery, M.E. & Zucker, W. 1969. Standing crop of foraminifera in sublittoral epiphytic communities of a Long Island salt marsh. *Marine Biology*, **4**: 44–61.
- Lesen, A.E. 2005. Relationship between benthic foraminifera and food resources in South San Francisco Bay, California, USA. *Marine Ecology Progress Series*, **297**: 131–145.
- Licari, L.N., Schumacher, S., Wenzhöfer, F., Zabel, M. & Mackensen, A. 2003. Communities and microhabitats of living benthic foraminifera from the tropical east Atlantic: impact of different productivity regimes. *Journal of Foraminiferal Research*, **33**: 10–31.
- Linke, P. & Lutze, G.F. 1993. Microhabitat preferences of benthic foraminifera: a static concept or a dynamic adaptation to optimise food acquisition? *Marine Micropaleontology*, **20**: 215–234.
- Lipps, J.H. & DeLaca, T.E. 1980. Shallow-water foraminiferal ecology, Pacific Ocean. In Field, M.E., Bouma, A.H. *et al* (Eds), *Quaternary Depositional Environments of the Pacific Coast, Pacific Coast Paleogeography Symposium*. Society of Economic Paleontologists and Mineralogists, 325–340.
- Lister, J.J. 1895. Contributions to the life-history of the Foraminifera. *Philosophical Transactions of the Royal Society*, **B186**: 401–453.
- Loeblich, A.R. & Tappan, H. 1987. *Foraminiferal genera and their classification*. Van Nostrand Reinhold, New York, **1**: 970pp, **2**: 212pp.
- Ludwick, J.C. & Walton, W.R. 1957. Shelf-edge, calcareous prominences in northeastern Gulf of Mexico. *Bulletin of the American Association of Petroleum Geologists*, **41**: 2054–2101.
- Lueck, K.L.O. & Snyder, S.W. 1997. Lateral variations among populations of stained benthic foraminifera in surface sediments of the North Carolina continental shelf (U.S.A.). *Journal of Foraminiferal Research*, **27**: 20–41.
- Lutze, G.F. 1980. Depth distribution of benthic foraminifera on the continental margin off NW Africa. "Meteor" *Forschungs-Ergebnisse, Reihe C*, **32**: 31–80.
- Lutze, G.F., Mackensen, A. & Wefer, G. 1983. Foraminiferen der Kieler Bucht, 2. Salinitätsansprüche von *Elphidium* *scabra* (Williamson). *Meyniana*, **35**: 55–65.
- Maas, M. 2000. Verteilung lebendgefärbter benthischer Foraminiferen in einer intensivierten Sauerstoffminimumzone, Indo-Pakistanischer Kontinentalrand, nördliches Arabisches Meer. *Meyniana*, **52**: 101–129.
- Mackensen, A. 1985. *Verbreitung und Umwelt Benthische Foraminiferen in der Norwegischen See*. Kiel University, 126pp.
- Mackensen, A. & Douglas, R.G. 1989. Down-core distribution of live and dead deep-water benthic foraminifera in box cores from the Weddell Sea and California continental borderland. *Deep-Sea Research*, **36**: 879–900.
- Mackensen, A., Fütterer, D.K., Grobe, H. & Schmiedl, G. 1993. Benthic foraminiferal assemblages from the South Atlantic Polar Front region between 35 and 57°S: distribution, ecology and fossilization potential. *Marine Micropaleontology*, **22**: 33–69.
- Mackensen, A., Schmiedl, G., Harloff, J. & Giese, M. 1995. Deep-sea foraminifera in the South Atlantic Ocean. *Micropaleontology*, **41**: 342–358.
- Matera, N.J. & Lee, J.J. 1972. Environmental factors affecting the standing crop of foraminifera in sublittoral and psammolittoral communities of a Long Island salt marsh. *Marine Biology*, **14**: 89–103.
- McCann, K.S. 2000. The diversity–stability debate. *Nature*, **405**: 228–233.
- McCormick, J.M., Severin, K.P. & Lipps, J.H. 1994. Summer and winter distribution of foraminifera in Tomales Bay, northern California. *Cushman Foundation for Foraminiferal Research, Special Publication*, **32**: 69–101.
- Milker, Y., Schmiedl, G., Betzler, C., Römer, M., Jaramillo-Vogel, D. & Siccha, M. 2009. Distribution of recent foraminifera in shelf carbonate environments of the Western Mediterranean Sea. *Marine Micropaleontology*, **73**: 207–225.
- Mojtahid, M., Jorissen, F., Lansard, B., Fontanier, C., Bombled, B. & Rabouille, C. 2009. Spatial distribution of live benthic foraminifera in the Rhône prodelta: faunal response to a continental-marine organic matter gradient. *Marine Micropaleontology*, **70**: 177–200.
- Mojtahid, M., Griveaud, C., Fontanier, C., Anschutz, P. & Jorissen, F.P. 2010. Live benthic foraminiferal faunas along a bathymetric transect (180–4800m) in the Bay of Biscay (NE Atlantic). *Revue de Micropaléontologie*, **53**: 139–162.
- Moodley, L. 1990. Southern North Sea seafloor and subsurface distribution of living benthic foraminifera. *Netherlands Journal of Sea Research*, **27**: 51–71.
- Morvan, J., Debenay, J.P., Jorissen, F.J. *et al*. 2006. Patchiness and life cycle of intertidal foraminifera: implications for environmental and palaeoenvironmental interpretation. *Marine Micropaleontology*, **61**: 131–154.
- Murosky, M.W. & Snyder, S.W. 1994. Vertical distribution of stained benthic foraminifera in sediments of southern Onslow Bay, North Carolina continental shelf. *Journal of Foraminiferal Research*, **24**: 158–170.
- Murray, J.W. 1968. The living Foraminifera of Christchurch Harbour, England. *Micropaleontology*, **14**: 83–96.
- Murray, J.W. 1980. *The Foraminifera of the Exe Estuary*. Devonshire Association Special Volume, **2**: 89–115.
- Murray, J.W. 1983. Population dynamics of benthic foraminifera: results from the Exe estuary, England. *Journal of Foraminiferal Research*, **13**: 1–12.
- Murray, J.W. 1991. *Ecology and palaeoecology of benthic foraminifera*. Harlow, Longman, 397pp.
- Murray, J.W. 1992. Distribution and population dynamics of benthic foraminifera from the southern North Sea. *Journal of Foraminiferal Research*, **22**: 114–128.
- Murray, J.W. 2003. Foraminiferal assemblage formation in depositional sinks on the continental shelf margin west of Scotland. *Journal of Foraminiferal Research*, **33**: 101–121.
- Murray, J.W. 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press, Cambridge, 426pp.
- Murray, J.W. 2007. Biodiversity of living benthic foraminifera: how many species are there?. *Marine Micropaleontology*, **64**: 163–176.
- Murray, J.W. & Alve, E. 2000a. Major aspects of foraminiferal variability (standing crop and biomass) on a monthly scale in an intertidal zone. *Journal of Foraminiferal Research*, **30**: 177–191.
- Murray, J.W. & Alve, E. 2000b. Do calcareous dominated shelf foraminiferal assemblages leave worthwhile ecological information after their dissolution? In Hart, M.B. Kaminski, M.A. & Smart, C. (Eds), *Proceedings of the Fifth International Workshop on Agglutinated Foraminifera*, Plymouth England, September 1997. Grzybowski Foundation Special Publication, **7**: 311–331.
- Murray, J.W. & Alve, E. 2002. Benthic foraminifera as indicators of environmental change: marginal marine, shelf and upper slope environments. In Haslett, S.K. (Ed.), *Quaternary Environmental Micropalaeontology*. Arnold, London, 59–90.
- Murray, J.W. & Alve, E. 2011. The distribution of agglutinated foraminifera in NW European seas: baseline data for the interpretation of fossil assemblages. *Palaeontologia Electronica*, **14**(2): 14A 41p: palaeo-electronica.org.2011_2/248/index.html.
- Murray, J.W. & Bowser, S.S. 2000. Mortality, protoplasm decay rate, and reliability of staining techniques to recognise 'living' foraminifera: a review. *Journal of Foraminiferal Research*, **30**: 66–77.

- Myers, E.H. 1935a. The life history of *Patellina corrugata* Williamson a foraminifer. *Bulletin of the Scripps Institution of Oceanography, Technical Series*, **3**: 355–392.
- Myers, E.H. 1935b. Morphogenesis of the test and the biological significance of dimorphism in the foraminifer, *Patellina corrugata* Williamson. *Bulletin of the Scripps Institution of Oceanography, Technical Series*, **3**: 393–404.
- Myers, E.H. 1936. The life-cycle of *Spirillina vivipara* Ehrenberg with notes on morphogenesis, systematics and distribution of the foraminifera. *Journal of the Royal Microscopical Society*, **66**: 120–146.
- Nardelli, M., Jorissen, F.J., Pusceddu, A. *et al.* 2010. Living benthic foraminiferal assemblages along a latitudinal transect at 1000 m depth off the Portuguese margin. *Micropaleontology*, **56**: 323–344.
- Orbigny, A.d'. 1839. Foraminifères. In R. de la Sagna (Ed), *Histoire physique politique et naturelle de L' Ile de Cuva*, Paris, Artus Bertrand, 224 pp.
- Ozarko, D.L., Patterson, R.T. & Williamsn, H.F.L. 1997. Marsh foraminifera from Nanaimo, British Columbia (Canada): implications of infaunal habitat and taphonomic biasing. *Journal of Foraminiferal Research*, **27**: 51–68.
- Pavlyuk, O.N., Tarasova, T.S. & Trebukhova, Y.A. 2008. Foraminifera and Nematoda within the area of *Ahnfeltia tobuchiensis* Field in Stark Strait (Peter the Great Bay of the Sea of Japan). *Russian Journal of Marine Biology*, **34**: 151–158.
- Pawlowski, J. & Holzmann, M. 2008. Diversity and geographic distribution of benthic foraminifera: a molecular perspective. *Biodiversity and Conservation*, **17**: 317–328.
- Pawlowski, J., Fahrni, J., Lecroq, D. *et al.* 2007. Bipolar gene flow in deep-sea benthic foraminifera. *Molecular Ecology*, **16**: 4089–4096.
- Phleger, F.P. 1951. *Ecology of foraminifera, northwest Gulf of Mexico*. Part I. *Foraminiferal distribution*. Geological Society of America, Memoir, **46**: 1–88.
- Phleger, F.P. 1956. Significance of living foraminiferal populations along the central Texas coast. *Contributions from the Cushman Foundation for Foraminiferal Research*, **7**: 106–151.
- Phleger, F.P. 1966. Patterns of living marsh foraminifera in South Texas coastal lagoons. *Boletín de la Sociedad Geológica Mexicana*, **28**: 1–44.
- Phleger, F.P. & Lankford, R.R. 1978. Foraminiferal and ecological processes in the Alvarado Lagoon area, Mexico. *Journal of Foraminiferal Research*, **8**: 127–131.
- Phleger, F.B. & Parker, F.L. 1951. *Ecology of foraminifera, northwest Gulf of Mexico*. Part II *Foraminiferal species*. Geological Society of America Memoir, **46**: 1–64.
- Poag, C.W., Knebel, H.J. & Todd, R. 1980. Distribution of modern benthic foraminifera on the New Jersey outer continental shelf. *Marine Micropaleontology*, **5**: 43–69.
- Polovodova, I., Nikulina, A., Schönfeld, J. & Dullo, W.C. 2009. Recent benthic foraminifera in the Flensburg Fjord (Western Baltic Sea). *Journal of Micropalaeontology*, **28**: 131–142.
- Rabinowitz, D. 1981. Seven forms of rarity. In Syngé, H. (Ed.), *The Biological Aspects of Plant Conservation*. John Wiley, Chichester, 205–217.
- Rathburn, A.E., Levin, L.A., Held, Z. & Lohmann, K.C. 2000. Benthic foraminifera associated with cold methane seeps on the northern California margin: ecology and stable isotopic compositions. *Marine Micropaleontology*, **38**: 247–266.
- Saffert, H. & Thomas, E. 1998. Living foraminifera and total populations in salt marsh peat cores: Kelsey marsh (Clinton, CT) and the Great Marshes (Barnstable, MA). *Marine Micropaleontology*, **33**: 175–202.
- Schafer, C.T. 1982. Foraminiferal colonization of an offshore dump site in Chaleur Bay, New Brunswick, Canada. *Journal of Foraminiferal Research*, **12**: 317–326.
- Schafer, C.T. & Young, J.A. 1977. Experiments on mobility and transportability of some nearshore benthonic foraminifera species. *Geological Survey of Canada*, Paper 99-1C: 27–31.
- Schmiedl, G., Mackensen, A. & Müller, P.J. 1997. Recent benthic foraminifera from the eastern South Atlantic Ocean; dependence on food supply and water masses. *Marine Micropaleontology*, **32**: 221–230.
- Schmiedl, G., De Bovée, F., Buscail, R. *et al.* 2000. Trophic control of benthic foraminiferal abundance and microhabitat in the bathyal Gulf of Lions, western Mediterranean. *Marine Micropaleontology*, **40**: 167–188.
- Schönfeld, J. 2001. Benthic foraminifera and pore-water oxygen profiles: a re-assessment of species boundary conditions at the western Iberian margin. *Journal of Foraminiferal Research*, **31**: 86–107.
- Schönfeld, J. 2012. History and development of methods of Recent benthic foraminiferal studies. *Journal of Micropalaeontology*, **31**: 53–72.
- Schönfeld, J. & Numberger, L. 2007. The benthic foraminiferal response to the 2004 spring bloom in the western Baltic Sea. *Marine Micropaleontology*, **65**: 78–95.
- Schönfeld, J., Dullo, W.C., Pfannkucke, O. *et al.* 2011. Recent benthic foraminiferal assemblages in the Porcupine Seabight. *Facies*, **57**: 187–213.
- Schweizer, M., Polovodova, I., Nikulina, A. & Schönfeld, J. 2011. Molecular identification of *Ammonia* and *Elphidium* species (Foraminifera, Rotaliida) from the Kiel Fjord (SW Baltic Sea) with rDNA sequences. *Helgolander Marine Research*, **65**: 1–10. DOI 10.1007/s10152-010-0194-3.
- Scott, D.B. & Medioli, F. 1980. Quantitative studies of marsh foraminiferal distribution in Nova Scotia: implications for sea level studies. *Contributions from the Cushman Foundation for Foraminiferal research, Special Publication*, **17**: 1–58.
- Scott, D.B., Medioli, F.S. & Schafer, C.T. 1977. Temporal changes in foraminiferal distributions in Miramichi River estuary, New Brunswick. *Canadian Journal of Earth Sciences*, **14**: 1566–1587.
- Scott, D.B., Piper, D.J.W. & Panagos, A.G. 1979. Recent salt marsh and intertidal mudflat foraminifera from the western coast of Greece. *Rivista Italiana de Paleontologia*, **85**: 243–266.
- Scott, G.A., Scourse, J.D. & Austin, W.E.N. 2003. The distribution of benthic foraminifera in the Celtic Sea: the significance of seasonal stratification. *Journal of Foraminiferal Research*, **33**: 32–61.
- Seiglie, G.A. 1974. Foraminifera of Mayagüez and Añasco Bays and its surroundings. *Caribbean Journal of Science*, **14**: 1–58.
- Semeniuk, T.A. 2001. Epiphytic foraminifera along a climatic gradient, Western Australia. *Journal of Foraminiferal Research*, **31**: 191–200.
- Sen Gupta, B.K. 1971. The benthonic foraminifera of the tail of the Grand Banks. *Micropaleontology*, **17**: 69–98.
- Simpson, J.H. & Sharples, J. 2012. *Introduction to Physical and Chemical Oceanography of Shelf Seas*. Cambridge University Press, Cambridge, p. 11.
- Smart, C.W. & Gooday, A.J. 2006. Benthic foraminiferal trends in relation to an organic enrichment gradient on the continental slope (850 m water depth) off North Carolina (USA). *Journal of Foraminiferal Research*, **36**: 34–43.
- Southall, K.E., Gehrels, W.R. & Hayward, B.W. 2006. Foraminifera in a New Zealand salt marsh and their suitability as sea-level indicators. *Marine Micropaleontology*, **60**: 167–179.
- Steineck, P.L. & Bergstein, J. 1979. Foraminifera from Hommocks salt-marsh, Larchmont Harbor, New York. *Journal of Foraminiferal Research*, **9**: 147–158.
- Sturrock, S. & Murray, J.W. 1981. Comparison of low energy middle shelf foraminiferal faunas. Celtic Sea and Western English Channel. In Neale, J.W. & Brasier, M.D. (Eds), *Microfossils from Recent and fossil shelf seas*. Ellis Horwood, Chichester, 250–260.
- Szarek, R., Kuhn, W., Kawanura, H. & Kitazato, H. 2006. Distribution of recent benthic foraminifera on the Sunda Shelf (South China Sea). *Marine Micropaleontology*, **61**: 171–195.
- Szarek, R., Kuhn, W., Kawanura, H. & Nishi, H. 2009. Distribution of recent benthic foraminifera along continental slope of the Sunda Shelf (South China Sea). *Marine Micropaleontology*, **71**: 41–159.

- Thompson, L.B. 1978. Distribution of living benthic foraminifera, Isla de los Estados, Tierra del Fuego, Argentina. *Journal of Foraminiferal Research*, **8**: 241–257.
- Tobin, R., Scott, D.B., Collins, E.S. & Medioli, F. 2005. Infaunal benthic foraminifera in some North American marshes and their influence on fossil assemblages. *Journal of Foraminiferal Research*, **35**: 130–147.
- Tsujimoto, A., Nomura, R., Yasuhara, M. & Yoshikawa, S. 2006. Benthic foraminiferal assemblages in Osaka Bay, southwestern Japan: faunal changes over the last 50 years. *Paleontological Research*, **10**: 141–161.
- Uchio, T. 1960. Ecology of living benthonic foraminifera from the San Diego, California, area. *Cushman Foundation for Foraminiferal Research, Special Publication*, **5**: 1–72.
- Van Der Zwaan, G.J. 1982. Paleocology of late Miocene Mediterranean foraminifera. *Utrecht Micropaleontological Bulletins*, **25**: 1–201.
- Walton, W.R. 1952. Techniques for recognition of living foraminifera. *Contributions from the Cushman Foundation for Foraminiferal Research*, **3**: 56–60.
- Wefer, G. 1976. Environmental effects on growth rates of benthic foraminifera (shallow water, Baltic Sea). *Maritime Sediments, Special Publication*, **1**: 39–50.
- Weinberg, J.R. 1991. Rates of movement and sedimentary traces of deep-sea foraminifera and Mollusca in the laboratory. *Journal of Foraminiferal Research*, **21**: 213–217.
- Williamson, W.C. 1848. On the recent species of the genus *Lagena*. *Annals and Magazine of Natural History, series 2*: 1–20.
- Williamson, W.C. 1858. *Recent Foraminifera of Great Britain*. Ray Society, London, 100pp.
- Wilson, B. 2007. Guilds of epiphytal foraminifera on fibrous substrates, Nevis, West Indies. *Marine Micropaleontology*, **63**: 1–18.
- Wilson, B. & Ramsook, A. 2007. Population densities and diversities of epiphytal foraminifera on nearshore substrates, Nevis, West Indies. *Journal of Foraminiferal Research*, **37**: 213–222.
- Wollenburg, J.E. & Mackensen, A. 1998. On the vertical distribution of the living (rose Bengal stained) benthic foraminifera in the Arctic Ocean. *Journal of Foraminiferal Research*, **28**: 268–285.