

# Experiments to determine the origin and palaeoenvironmental significance of agglutinated foraminiferal assemblages

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## ABSTRACT

The only modern environments which have primary agglutinated foraminiferal original dead assemblages (ODA) composed solely of forms with non-calcareous agglutinated tests are from two extremes, namely intertidal marshes or seas below the calcite compensation depth. Because of this, the interpretation of fossil agglutinated assemblages has so far remained enigmatic. Through dissolution experiments, we show that it is possible to derive secondary, solely agglutinated, well-preserved acid treated assemblages (ATA) from parent, calcareous-dominated ODAs from a wide range of environments (marginal marine, through shelf and slope, to deep sea). Furthermore, these ATAs mirror the ODAs in terms of species diversity. Areas that have been studied in more detail also reveal good agreement between the ODAs and ATAs concerning faunal boundaries. However, where the ODAs are highly dominated by a single opportunistic, calcareous species, the ATAs define more subenvironments. Consequently, the ATAs seem to reveal more ecological information. This new approach makes a promising advance in realising the palaeoecological potential of fossil agglutinated assemblages.

## INTRODUCTION

Fossil non-calcareous, organo- and ferro-agglutinated foraminiferal assemblages occur in Palaeozoic, Mesozoic and Tertiary rocks, sometimes in association with petroleum source rocks (e.g. Palaeogene of the North Sea, Jones, 1988; Charnock & Jones, 1990) and they are used in stratigraphic correlation (e.g. Morris & Dyer, 1990). Their earliest use in both these applications was by Grzybowski in the late 19th century (Czarniecki, 1993).

The palaeoecological significance of exclusively organo- and ferro-agglutinated fossil assemblages of foraminifera has until now been an enigma. In the two modern analogues (intertidal marshes and seas deeper than the calcite compensation depth), the biological secretion of calcareous material is difficult due to the undersaturation of the water with respect to calcium carbonate. If the fossil assemblages are primary, then this limits the palaeoecological interpretation to these two extremes. This led Scott *et al.* (1983) to pose the question: "The recent as the key to the past: does it apply to agglutinated foraminiferal assemblages?" For example, Jones (1988) considered that Palaeogene fossil agglutinated assemblages from the North Sea Viking Graben are primary and he reconstructed the environments of accumulation using a palaeoslope model based on geophysical data. An alternative hypothesis for agglutinated assemblages explored here is that some fossil examples are the secondary residue left from original, partially calcareous, foraminiferal assemblages which have undergone

syndepositional or diagenetic dissolution.

In order to resolve this problem, we have carried out experimental studies. We took primary modern original dead assemblages (ODA) and gently dissolved them in weak acid to give secondary acid-treated assemblages (ATA) which consist entirely of agglutinated foraminifera. It is clear that for ODAs with a very low percentage of agglutinated foraminifera, this is the only practicable way of making quantitative studies of the agglutinated component in order to build up a data base on their abundance and distribution. Furthermore, it has the advantage that agglutinated forms with a calcareous cement are destroyed as they would be if the dissolution was natural.

Previously published results from the NE Atlantic and Hamble inlet, near Southampton, England (discussed below) offer a new insight into the understanding of agglutinated assemblages. The fundamental question is whether the fossil examples are primary or if they are secondarily derived from originally, partially calcareous assemblages through dissolution during diagenesis (Fig. 1). If the latter is the case, does the experimental approach simulate nature? With this in mind, we here report an extension of our studies to further clastic sedimentary environments off Europe. The aims are to compare geographic and ecological patterns of distribution of ODAs and the ATAs drawn from them, and to consider the palaeoecological value of the ATAs.

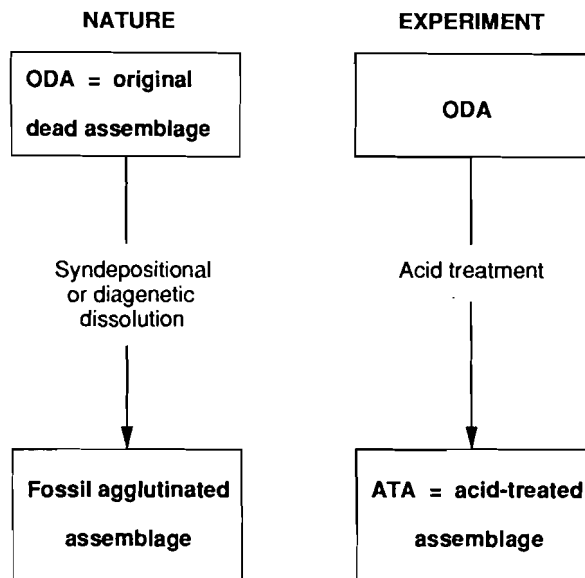


Fig. 1. Hypothetical relationships between ODAs and agglutinated assemblages.

## PREVIOUS STUDIES

### NE Atlantic ocean

Our first test of the possibility of experimentally deriving ATAs from ODAs by gently dissolving ODAs in acid was performed on 21 surface sediment samples from five separate areas in the NE Atlantic (Murray & Alve, 1994). At this initial stage, samples were deliberately chosen from a wide range of environments covering a water depth range from outer shelf (160 m) to abyssal plain (4660 m). The experiment confirmed our hypothesis: even though the agglutinated component made up less than 10% of the ODAs in most samples (in some cases less than 2%), most of them yielded highly diverse, statistically significant ATAs. The Fisher alpha diversity values were, however, consistently somewhat lower in the ATAs. As expected, there were too few samples from each area to draw any firm conclusions about regional faunal distribution patterns of either ODAs or ATAs. However, a significant finding was that in the ATAs, trochamminids were abundant at all slope and abyssal depths and they were even dominant at 7 stations.

### Hamble inlet

The results derived from studying shelf to abyssal assemblages encouraged us to extend our studies to marginal marine environments. Eight samples from a marsh, intertidal and shallow subtidal (4-6 m water depth) areas in the Hamble inlet near Southampton, southern England, were processed in the same way as the NE Atlantic samples (Alve & Murray, 1994). All the ODAs were strongly dominated by calcareous taxa but, after acid treatment, they yielded ATAs rich in individuals. As for the shelf to abyssal plain, the marginal marine samples yielded slightly lower Fisher-alpha values for the ATAs than for the ODAs. Together with the diversity patterns, the faunal composition of

the ATAs gave reliable information for defining the three marginal marine depositional environments. This emphasized the potential interpretational value of assemblages that have undergone diagenetic alteration due to carbonate dissolution.

## MATERIAL AND METHODS

The sample material included in the study comprises: 10 samples from the southern North Sea, previously studied for their living and dead assemblages (Murray, 1992); 6 samples from the Forties area and 5 from the Ekofisk area of the northern North Sea, previously studied by Murray (1985); 18 samples from the western slope of the shelf basin of the Skagerrak (collected on University of Bergen cruise: 19/93 in July 1993); 4 samples from fjords in southern Norway (Fig. 2). All were initially processed by staining with rose Bengal, washed on a 63  $\mu\text{m}$  sieve and dried at 50°C. The foraminifera in the North Sea samples had previously been separated by flotation in trichloroethylene. First the living assemblage and ODA were picked from those samples that had not been analysed previously. A portion of the sample was then placed in acetic acid pH 2.5 for 2 hours or more (to remove the calcareous material), washed on a 63  $\mu\text{m}$  sieve and dried. In most cases the samples were sufficiently large to provide an ATA of around 250 individuals, but in five North Sea samples smaller numbers were retrieved (Table 1). Fragments of tubular and branching forms were treated as a separate category and are not included in the calculations (for discussion, see Murray & Alve, 1994). Two measures of diversity have been used. The alpha index of Fisher *et al.*, (1943) is an indicator of species richness which relates the number of species to the number of individuals without regard to their variations in abundance. The information function,  $H(S)$ , is a measure of heterogeneity and takes into account the evenness of the species abundances (Murray, 1991). The key agglutinated taxa are given in the faunal reference list and illustrated in Plate 1.

## INVESTIGATION AREAS

### Description of the environments

**North Sea.** The Forties area lies at approximately Lat. 57° 44'N, Long. 0° 54'E and has a depth of 100-130 m. The mean bottom water temperatures are 6.5°C (winter) and 7.0°C (summer) and the mean salinity is 35.1‰ throughout the year. During the summer, the surface waters develop thermohaline stratification (Lee & Ramster, 1981). The sediments are fine sands with a mud content of 10-39% (Hartley, 1979).

The Ekofisk area lies at approximately Lat. 56° 32'N, Long. 3° 13'E and has a depth of 70 m. The surface waters are thermally stratified in the summer and the bottom waters have a mean temperature of 5.5°C, salinity 35.0‰ (winter) and 7.0°C and 34.0‰ (summer) (Lee & Ramster, 1981). The sub

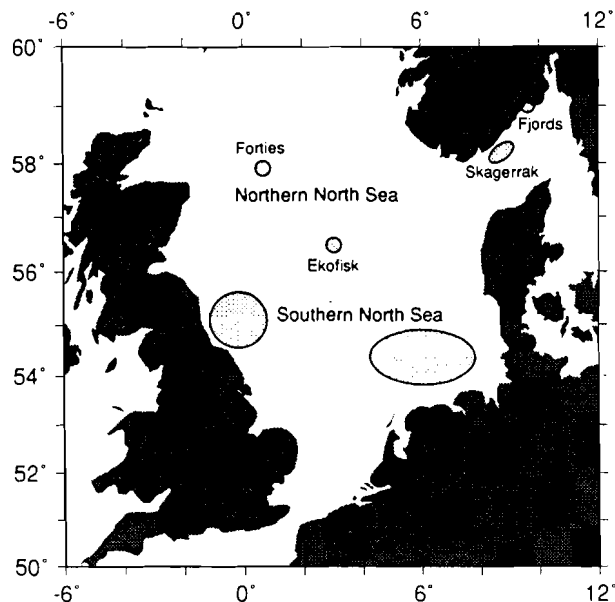


Fig. 2. Study areas in the North Sea, Skagerrak and Norwegian fjords.

strate is a slightly muddy, fine sand with 3.6-6.5% <63  $\mu\text{m}$  material and a median particle diameter of 130-140  $\mu\text{m}$  (Addy *et al.*, 1979).

The southern North Sea experiences summer bottom water temperatures of 8-14°C whereas in the winter values fall to around 5°C. The salinity varies from 34.0-34.8‰ (Lee & Ramster, 1981). The sediments are sands with minor amounts of silt (Murray, 1992).

**Skagerrak.** The Skagerrak forms an eastern continuation of the North Sea and is connected with the Baltic through the Kattegat. The water depth increases gradually from the shoreline towards the NW part of the Skagerrak, the Skagerrak Basin (maximum depth 700 m). This basin forms the deepest part of the Norwegian Channel. Atlantic Water enters the North Sea between the Orkney and Shetland Islands and some of it flows into the >200m parts of the Skagerrak via the Norwegian Channel. The Atlantic Water in the Skagerrak has salinities of >35.0‰, its temperature is generally between 6.0 and 6.5°C with occasional values below 5.0°C (Larsson & Rohde, 1979; Mork *et al.*, 1976) and it is well oxygenated (>95% saturation, Svansson, 1975). It is also very nutrient-rich (nitrates and phosphates) compared to the overlying Norwegian Coastal Current Water (Føyn & Rey, 1981). The organic carbon content in the Skagerrak sediments varies from <0.5 to >3%. Its occurrence is associated with the clay fraction with lowest values in the shallower, well-sorted sands and higher values in the moderately-sorted silts in the deeper parts of the area (Van Weering & Qvale, 1983). Bottom current velocities in the deeper parts of the Skagerrak are generally low (<10 cm/s) in contrast to the variable, but significantly higher (sometimes >30 cm/s), values at depths <100 m (Larsson & Rohde, 1979).

**Fjords.** The Grenlandsfjord system in southern Norway includes Langesundsfjord and Frierfjord (Fig. 2). The deep water of Langesundsfjord is separated from the southern fjord system and the Skagerrak by a sill at 50 m water depth and is generally renewed in winter. Before deep water renewals, the bottom water generally has an oxygen concentration of 2-3 ml/l. The more restricted Frierfjord has a maximum depth of around 100 m and is separated from Langesundsfjord by a sill at 23 m water depth. The deep water is renewed only every 1 to 3 years. Over the last century, anoxic conditions have predominated at water depths greater than 40-60 m but this has improved slightly during the last 10 years due to reduced organic pollution. The temperature at the sample sites is generally 5.5-6.9 and 5.8-6.1°C and the salinity is around 34.2-34.8 and 33.3-33.6‰ in Langesund and Frierfjord respectively (Rygg *et al.*, 1987). The sediments are silts and clays.

#### Previous foraminiferal studies

**North Sea.** The regional distribution of total benthic assemblages >63  $\mu\text{m}$  was described by Jarke (1961) and Gabel (1971). Living and dead assemblages >63  $\mu\text{m}$  were described from the Forties and Ekofisk areas (Murray, 1985) and southern North Sea (Murray, 1992). All these studies show that the dominant species in the Ekofisk and Forties areas and parts of the southern North Sea is *Stainforthia fusiformis* (recorded either as *Bulimina* or *Fursenkoina*) together with *Bulimina marginata* and *Hyalinea balthica* (as *Anomalina* in Jarke, 1961).

**Skagerrak.** Höglund (1947) provided a classic account of the taxonomy of the foraminifera from the Skagerrak and Gullmar Fjord. The distribution of total benthic assemblages >63  $\mu\text{m}$  was described by Jarke (1961) and Gabel (1971) and >125  $\mu\text{m}$  by Van Weering & Qvale (1983). For the area considered here, Jarke and Gabel recorded the dominant species as *Stainforthia fusiformis* (their *Bulimina*) together with *Bulimina marginata* and *Hyalinea balthica* (as *Anomalina* in Jarke, 1961) with an area of *Brizalina skagerrakensis* (as *Bolivina*). Van Weering and Qvale recognised five Q-mode factor assemblages of which factor 1 *Bolivina* cf. *B. robusta* (= *Brizalina skagerrakensis*) occupied the deepest part of the area studied here. The discrepancy between the two studies is almost certainly due to the different size fractions examined leading to the loss of *S. fusiformis* in the Van Weering and Qvale study.

**Fjords.** Nothing has yet been published on the foraminiferal distribution in Langesundsfjord and Frierfjord. Recently, however, sediment cores from various parts of Frierfjord have been analysed to document environmental changes, due to organic pollution, and foraminiferal responses to temporal

variations in oxygen conditions. At present, low diversity, living assemblages, strongly dominated by *S. fusiformis* (95-100%), occur at >50 m water depths in Frierfjord (Alve, 1994).

## RESULTS

### Original Dead Assemblages

**North Sea.** In all cases, the ODAs are dominated by calcareous foraminifera but there are differences in the proportion of agglutinated tests in the different areas (Table 1). Values are low in Forties (1-4%, mean 2%), moderate in Ekofisk (11-18%, mean 16%) and variable in the southern North Sea (generally <10% but up to 30%, mean 12%). Two main calcareous associations, named after the dominant species, are present: *Elphidium excavatum* and *Stainforthia fusiformis*.

The *Elphidium excavatum* ODA occurs over a depth range of 32-46 m in the southern North Sea (samples 3442-3446). *Elphidium excavatum* makes up 34-48% of the assemblage and the other common element is *Ammonia beccarii* (20-30%) (Murray, 1992). The *Stainforthia fusiformis* ODA is present in the southern North Sea (as *Fursenkoina*) at 45-98 m water depth (Murray, 1992), in the Ekofisk area at 70 m, and in the Forties area at 100-130 m (Murray, 1985). *Stainforthia fusiformis* occurs as living blooms throughout large areas of the southern and central North Sea and it is clearly an opportunistic species (Alve, 1994).

**Skagerrak.** Most of the ODAs from the slope of the Skagerrak Basin are dominated by calcareous taxa. The foraminifera can be divided into two main areas. From 266 to 534 m, samples are dominated either by *S. fusiformis* or *Pullenia osloensis* (Table 2). Other common species include *Cassidulina laevigata*, *Eggerelloides medius* and *Textularia tenuissima*. The Fisher alpha values are 10.5-18 and H(S) 1.8-3.1. The proportion of agglutinated tests is 8-47%, mean 30%. From 581 to 651 m, the dominant species is generally *Haplophragmoides bradyi* with common *E. medius*, *Saccammina* spp. and *Trochamminopsis pusillus*. The Fisher alpha values are 10.5-16 and H(S) 2.5-3.3. The proportion of agglutinated tests is 47-79%, mean 57%. Two further assemblages from 473 and 594 m are dominated by *Brizalina skagerrakensis*.

**Fjords.** *Stainforthia fusiformis* is the most abundant species at all fjord sites included in this study. The Langesund assemblage resembles those of the Skagerrak (shelf) in the frequent occurrence of *P. osloensis* and *C. laevigata* (Table 2). *Bulimina marginata* is the second most important species in the restricted Frierfjord. The Fisher-alpha values are 11-13, H(S) 2.7-3.0 and the proportion of agglutinated tests is 17-28%.

### Acid-Treated Assemblages

**North Sea.** The ATAs are more varied than the

ODAs from which they were derived. Their diversities (both the number of species and the Fisher alpha index) are, however, lower with only a few exceptions. The *Elphidium excavatum* ODA gave rise to an *Eggerelloides scabrus* ATA with 75-97% dominance of this species. The *Stainforthia fusiformis* ODA yielded ATAs with common *Reophax fusiformis*, *E. scabrus*, *Morulaepecta bulbosa* and *Clavulina obscura* with each being dominant in one or more ATAs (Table 1). In the Ekofisk area, there are *Leptohalysis catella* or *R. fusiformis* ATAs. Finally, in the Forties area there are *Adercotryma glomeratum* and *Eggerelloides medius* ATAs. These differences are summarised in Fig. 3.

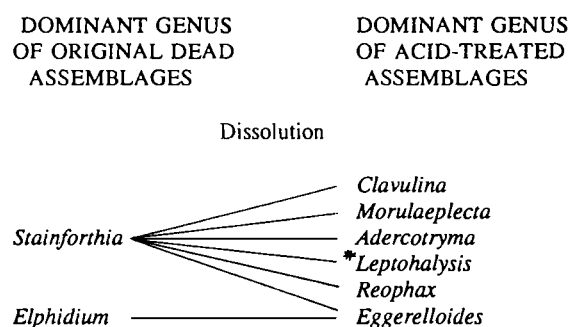


Fig. 3. North Sea. Two calcareous ODAs characterised by their dominant genera (left column) give rise to 6 agglutinated assemblages after acid-treatment (ATA) (right column). \* = fragile taxon unlikely to become fossilised.

**Skagerrak.** The samples can be divided into three geographic and depth-related areas: 266-359 m on the marginal shelf, 399-514 m on the basin slope, and 534-651 m in the deep basin (Table 2). The shelf assemblages are dominated by *T. tenuissima* with common *E. medius* and *Reophax micacea*, Fisher alpha 3-9 and H(S) 1.3-2.4. The basin slope is a transitional area with dominance of either *E. medius* or *T. tenuissima*, with common *Haplophragmoides bradyi*, Fisher alpha 4-8.5 and H(S) 2.0-2.4. The deep basin is dominated by *H. bradyi* with common *E. medius*, *Saccammina* spp. and *T. pusillus*, Fisher alpha 5.5-7 and H(S) 1.8-2.5.

**Fjords.** The two dominant species are *T. tenuissima* and *E. medius* with common *Adercotryma glomeratum*, *Recurvoides trochamminiforme* (in 2 samples) and *Spiroplectammina biformis* in the most restricted Frierfjord samples. The Fisher alpha values are 5.5-10 and H(S) 1.6-2.4 (Table 2).

## DISCUSSION

### Faunal distribution patterns

The samples from the North Sea and the Skagerrak provide, for the first time, a possibility to compare faunal distribution patterns of ATAs with those of their parent ODAs. Benthic foraminiferal ODAs are well known to reflect changing environmental conditions and numerous palaeoecological interpretations, especially of Cenozoic assemblages, have

been based on their distributional patterns. Generally, interpretations are based on the distribution of the most common taxa but what kind of information are we left with if the originally common species are diagenetically removed? In this study we investigate whether the residual assemblages remaining after dissolution of originally calcareous dominated ODAs hold equally significant palaeoecological information.

In the southern North Sea, the two main widely distributed calcareous ODAs are dominated by *S. fusiformis* in the western and by *E. excavatum* in the eastern area (Fig. 2). Between the two there is an area of *Eggerelloides scabrus* dominance. Furthermore, syndepositional dissolution of calcareous tests was recognised as active in the area (Murray, 1992). *Stainforthia fusiformis* is dominant in the Forties and Ekofisk areas. It thrives in organic-rich, restricted fjord environments (Alve, 1990), and it appears to be an opportunistic species which produces blooms over large areas (Alve, 1994).

The *E. excavatum* ODA in the southern North Sea gives rise to a single ATA with a high dominance of *E. scabrus*. In complete contrast, the widely distributed *S. fusiformis* ODA gives rise to numerous ATAs (Fig. 3). In the southern North Sea there are four different ATAs dominated by *R. fusiformis*, *E. scabrus*, *Morulaeplecta bulbosa* and *Clavulina obscura*, whereas in the Ekofisk area most of the ATAs are dominated by *R. fusiformis* with one *L. catella* ATA. In the Forties area, the ATAs are dominated either by *A. glomeratum* or *E. medius*. *Leptohalysis* is fragile and might not be preserved in the geological record. If that were so, the ATA would be dominated by *Eggerelloides*.

In the case of *S. fusiformis*, where the ODAs are dominated by a single, opportunistic species, the ATAs, which are dominated by several different species, seem to hold more ecological information. The reason for the strong dominance of *S. fusiformis* is uncertain but might be related to its rapid population growth in response to short-term increases in food supply. Similar opportunistic features with rapid growth- and turnover rates have not, so far, been reported for agglutinated forms.

The temperature range of the bottom waters is greatest (5-16°C) in the southern North Sea and decreases in Ekofisk (5.5-7.0°C) and Forties (6.5-7.0°C). The mud content of the sediment also shows a gradation from very low in the southern North Sea with an increase through Ekofisk to Forties. In summary, the southern North Sea is more variable with regard to substrate and hydrography and this is probably reflected in the higher numbers of ATAs relative to ODAs, whereas the more stable Forties and Ekofisk environments have fewer ATAs.

The relatively close spacing of the Skagerrak samples along environmental gradients makes possible a detailed comparative study of distributional patterns of the ODAs and ATAs. At depths of 266-534 m, two calcareous species (*P. osloensis*

and *S. fusiformis*) form essentially one ODA in which either species may be dominant. *Pullenia osloensis* is most frequent north of the Skagerrak basin, whereas *S. fusiformis* is most abundant to the south. By contrast, the ATAs can be divided into two groups (Fig. 4). From 266-359 m, there is a single, homogeneous *T. tenuissima* ATA, while from 399-534 m there is a transition zone where the *P. osloensis* and *S. fusiformis* ODAs give rise to ATAs dominated by one or other of *T. tenuissima*, *E. medius*, *H. bradyi* or *Trochamminopsis pusillus* (Fig. 5). In the area deeper than 581 m, the ODAs and ATAs are both dominated by the same two agglutinated taxa (*H. bradyi* and *E. medius*).

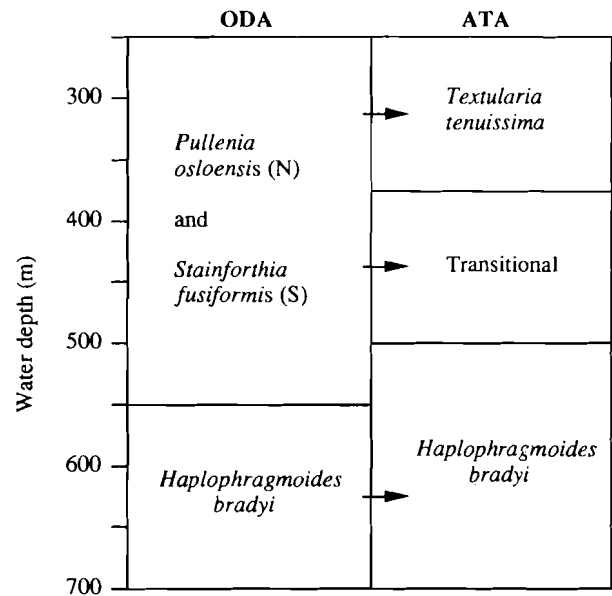


Fig. 4. Skagerrak. Depth distribution of main ATAs and their parent ODAs. N = North slope, S = South slope of Skagerrak Basin.

In spite of the different depths of the North Sea and Skagerrak, there are consistently more kinds of ATAs than ODAs in both areas. The general trend is, however, that main faunal boundaries between ODAs are reflected in the ATAs but the latter define more subenvironments.

The ODAs of the fjord samples are dominated by *S. fusiformis* and the ATAs by *T. tenuissima* (with one exception *E. medius*). The ATAs of the fjords resemble those of the Skagerrak margin more closely than those of the North Sea.

Tubular or branched foraminifera are found only in the Skagerrak Basin, where tube fragments are present in all samples. The number of fragments depends to a great extent on the fragility of different species. In the present case it implies that even though the maximum number of tube fragments is approximately the same in both shallower and deeper water samples (20-30 per 250 specimens of other taxa), the absolute abundance of tubular or branching forms is considerably higher in the deeper parts of the Skagerrak Basin. *Marsipella*

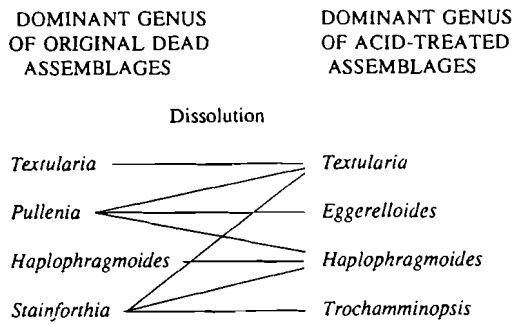


Fig. 5. Skagerrak. Two calcareous and two agglutinated ODAs characterised by their dominant genera (left column) give rise to 4 agglutinated assemblages after acid-treatment (ATA) (right column).

*spiralis* and *Rhabdammina scabra* occur between 266 and 404 m depth, whereas *Bathysiphon hirudinea* occurs at all depths below 300 m. Larger, more robust, coarse grained tubes of *Rhabdammina* spp. are most common at depths greater than 500 m.

### Diversity patterns

The relation between the ATA and the ODA from which it was derived by dissolution can be assessed through a comparison of their species diversity. The Fisher alpha values of the ODAs and ATAs of the North Sea, Skagerrak and fjords show a series of fields with some overlap (Fig. 6). The ODAs are more diverse in the Skagerrak and fjords than in the North Sea partly because of the initial higher proportion of agglutinated tests and, in the case of the Skagerrak, because of its greater environmental stability. The range of alpha for the ATAs is smaller but, nevertheless, there is broad similarity with that of the ODAs.

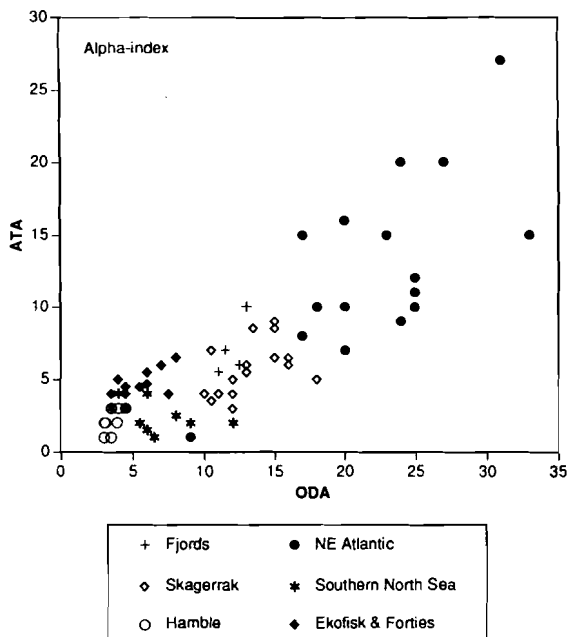


Fig. 6. Comparison of Fisher alpha values from NE Atlantic, Hamble, North Sea, Skagerrak and fjord ODAs and ATAs.

The pattern for H(S) is principally much the same but the field for the southern North Sea is large (Fig. 7). This is because the species evenness varies from high to low, reflecting the greater physical variability of the environments as previously discussed. Low H(S) values are caused by the high dominance of one species, for example, of *S. fusiformis* (>40%) in the Ekofisk and Forties ODAs and of *E. scabrus* (mainly >74%) in the southern North Sea ATAs. The evenness of species abundance in the Forties and Ekofisk ODAs and ATAs is similar (H(S) 1.4-2.1 and 1.7-2.3, respectively). The H(S) of the Skagerrak and fjords ODAs are generally high and only the shallower Skagerrak samples show overlap with the field for the North Sea. For depths of >359 m, the range of H(S) is similar (ODA 1.8-3.3, ATA 1.8-2.5) showing comparable species evenness.

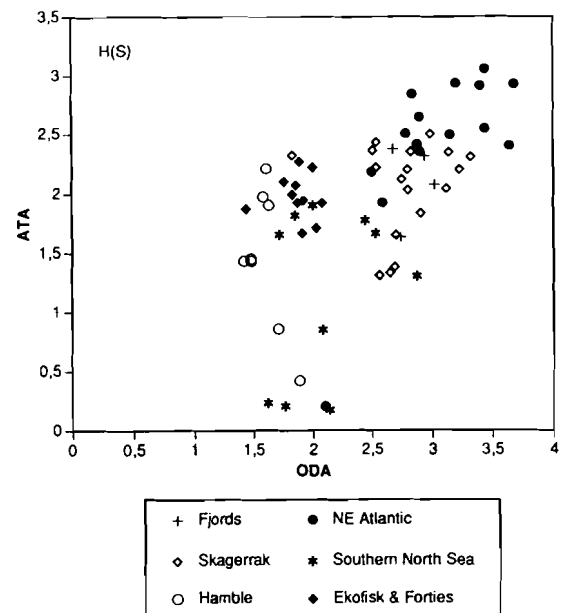


Fig. 7. Comparison of H(S) values from NE Atlantic, Hamble, North Sea, Skagerrak and fjord ODAs and ATAs.

In conclusion, although Fisher alpha and H(S) measure different aspects of diversity, both show a similar pattern of fields for the different geographic areas and environments.

A summary of the diversity relationships between the ODAs and ATAs is given in Figs. 8 and 9. For the Fisher alpha index, there is a progression from low diversity marginal marine, through shelf, fjords and shelf basin to bathyal and abyssal high diversity. The regression shows good correlation ( $r = 0.84$ ,  $n = 66$ ) between the ODA and ATA. The picture is similar for H(S) but not quite so clear-cut ( $r = 0.55$ ,  $n = 66$ ). There is more overlap between the fields for marginal marine and shelf seas, and between shelf basin, fjords and bathyal-abyssal and this is confirmed by the lower regression value. Nevertheless, both Fisher alpha and H(S) show the same overall trend. The importance of these

observations is that the diversity of the ATAs reflects that of the parent ODAs.

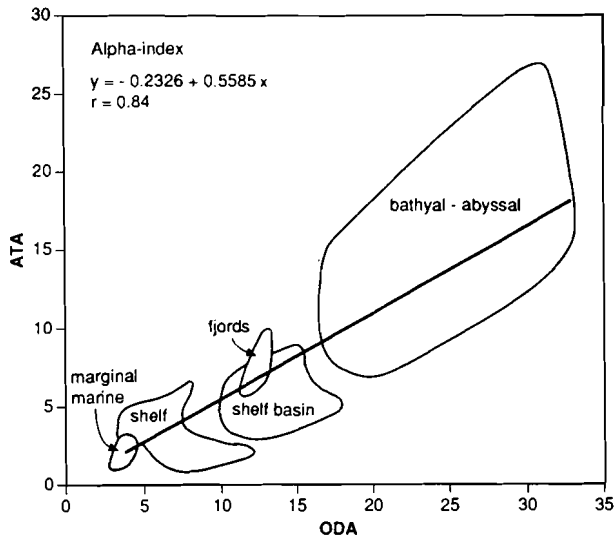


Fig. 8. Summary of Fisher alpha fields for different environments with a linear regression line.

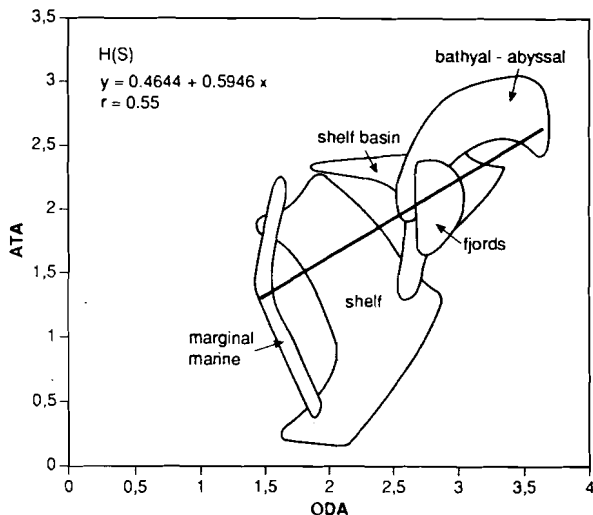


Fig. 9. Summary of H(S) fields for different environments with a linear regression line.

### Palaeoecological potential

This study shows that predominantly calcareous original dead assemblages (ODAs) give rise to abundant, secondary agglutinated assemblages (ATAs) following treatment with weak acid. The principal aim was to test whether such experiments would simulate the natural processes of dissolution and still give residual assemblages (ATAs) holding much of the ecological information of the parent ODA (Fig. 1). From the above discussion, it is evident that this holds true, for example, in terms of diversity as measured by the alpha index and information function. These trends seem to have a general relevance (except for carbonate environments) as they have applied to all the clastic environments studied so far. Thus we believe that the ATAs are comparable with some natural fossil assemblages. That is not to say that all fossil agglutinated assemblages are secondary, for some are

undoubtedly primary. Because the secondary assemblages retain so much ecological information, it follows that such fossil examples may have greater palaeoecological potential than has hitherto been realised. Although Murray (1991, p. 304) advised against attempting to carry out palaeoecological interpretations on severely dissolved assemblages this may have been unduly pessimistic. These new results suggest that, providing the ODAs had not previously been subjected to much alteration through transport, even totally agglutinated secondary assemblages may be used for palaeoecological interpretations (as in fields I-CC and II-CC of Murray, 1991, fig. 5.8).

### CONCLUSIONS

1. From this and our previous studies, we have shown that primary, calcareous dominated, original dead assemblages (ODAs), from a wide range of environments from intertidal to deep sea, can give rise to secondary agglutinated assemblages (ATAs) following treatment with weak acid. Only small, normal sized (20-40 cc wet sediment) samples are necessary to give statistically reliable counts of around 250 agglutinated individuals.
2. We are beginning to establish patterns of distribution and dominance of agglutinated taxa in areas where they are normally ignored because they are so heavily outnumbered by calcareous tests.
3. It is evident that some secondary agglutinated assemblages hold more ecological information than some primary calcareous ones. For example, the widespread *S. fusiformis* ODA gave rise to six different ATAs in the North Sea and a further three in the Skagerrak and Norwegian fjords.
4. The new results from the North Sea and Skagerrak show that the patterns of distribution of ODAs and ATAs are very similar with few assemblages in more stable environments and varied assemblages in transitional zones.
5. The diversity of the ATAs is generally, but not always, lower than that of the ODAs but, nevertheless, there is good agreement between the two.
6. ATAs show clearly defined diversity fields for different environments as is already known from studies of living and dead assemblages (Murray, 1991). For ATAs the Fisher alpha index seems to be better than H(S) in discriminating between environments.
7. Secondarily derived fossil agglutinated assemblages should now be considered as of potential palaeoecological significance.

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## FAUNAL REFERENCE LIST OF NORTH SEA AND SKAGERRAK AGGLUTINATED TAXA

- Adercotryma glomeratum* (Brady) = *Lituola glomerata* Brady, 1878
- Bathysiphon hirudinea* (Heron-Allen & Earland) = *Hippocrepinella hirudinea* Heron-Allen & Earland, 1932
- Clavulina obscura* Chaster, 1892
- Eggerelloides medius* (Höglund) = *Verneuilina media* Höglund, 1947
- Eggerelloides scabrus* (Williamson) = *Bulimina scabra* Williamson, 1858
- Haplophragmoides bradyi* (Robertson) = *Trochammina bradyi* Robertson, 1891
- Leptohalysis catella* (Höglund) = *Reophax catella* Höglund, 1947
- Marsipella spiralis* Heron-Allen & Earland, 1912
- Morulaepecta bulbosa* Höglund, 1947
- Recurvoides trochamminiforme* Höglund, 1947
- Reophax fusiformis* (Williamson) = *Proteonina fusiformis* Williamson, 1858
- Reophax micacea* (Cushman) = *Proteonina micacea* Cushman, 1918
- Rhadammina scabra* Höglund, 1947
- Spiroplectammina biformis* (Jones & Parker) = *Textularia agglutinans* d'Orbigny var. *biformis* Parker & Jones, 1865
- Textularia tenuissima* Earland, 1933      *Trochamminopsis pusillus* (Höglund) = *Trochammina pusilla* Höglund, 1947



Table 1. Faunal data for North Sea ODAs and ATAs (abundances of species  $\geq 5\%$ ).

| Area                           | Southern North Sea |      |      |      |      |      |      |      |      |      | Forties |      |      |      |      |       | Ekofisk |      |      |      |      |
|--------------------------------|--------------------|------|------|------|------|------|------|------|------|------|---------|------|------|------|------|-------|---------|------|------|------|------|
|                                | 3453               | 3454 | 3467 | 3468 | 3452 | 3456 | 3442 | 3443 | 3445 | 3446 | 2894    | 2895 | 2896 | 3136 | 3133 | 3143A | 3117    | 3118 | 3119 | 3120 | 3121 |
| Depth (m)                      | 98                 | 50   | 90   | 90   | 80   | 45   | 46   | 34   | 32   | 38   | 121     | 122  | 126  | 125  | 107  | 127   | 70      | 70   | 70   | 70   | 70   |
| <b>ODA</b>                     |                    |      |      |      |      |      |      |      |      |      |         |      |      |      |      |       |         |      |      |      |      |
| <i>Bulimina marginata</i>      | 10                 | 5    | 26   | 14   | 12   | 9    | 1    | 0    | 0    | 0    | 18      | 20   | 15   | 15   | 5    | 21    | 1       | 2    | 3    | 8    | 3    |
| <i>Cassidulina laevigata</i>   | 0                  | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 5       | 2    | 1    | 3    | 7    | 4     | 0       | 0    | 0    | 0    | 0    |
| <i>Cassidulina obtusa</i>      | 0                  | 3    | 2    | 1    | 1    | 6    | 0    | 0    | 0    | 0    | 2       | 3    | 5    | 4    | 5    | 5     | 16      | 8    | 11   | 8    | 8    |
| <i>Cibicides lobatulus</i>     | 11                 | 9    | 0    | 1    | 3    | 4    | 0    | 2    | 2    | 3    | 0       | 0    | 0    | 0    | 0    | 0     | 0       | 0    | 0    | 0    | 0    |
| <i>Eggerelloides scabrus</i>   | 0                  | 18   | 1    | 2    | 0    | 9    | 12   | 6    | 5    | 11   | 0       | 0    | 0    | 0    | 0    | 0     | 0       | 0    | 0    | 0    | 0    |
| <i>Elphidium excavatum</i>     | 9                  | 5    | 6    | 3    | 7    | 23   | 34   | 44   | 48   | 36   | 0       | 0    | 0    | 0    | 0    | 0     | 0       | 0    | 0    | 0    | 0    |
| <i>Epistominella vitrea</i>    | 4                  | 0    | 3    | 0    | 3    | 3    | 1    | 0    | 0    | 0    | 2       | 4    | 6    | 2    | 4    | 3     | 13      | 6    | 9    | 4    | 8    |
| <i>Hyalinea balthica</i>       | 8                  | 5    | 16   | 22   | 12   | 1    | 0    | 0    | 0    | 0    | 1       | 15   | 13   | 13   | 1    | 8     | 6       | 1    | 9    | 6    | 5    |
| <i>Leptohalysis catella</i>    | 0                  | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0       | 0    | 0    | 0    | 0    | 0     | 6       | 5    | 4    | 10   | 9    |
| <i>Reophax fusiformis</i>      | 0                  | 2    | 2    | 2    | 4    | 5    | 1    | 0    | 0    | 0    | 0       | 0    | 0    | 0    | 0    | 0     | 2       | 6    | 7    | 5    | 2    |
| <i>Stainforthia fusiformis</i> | 33                 | 20   | 33   | 44   | 49   | 23   | 3    | 1    | 0    | 1    | 49      | 41   | 46   | 43   | 54   | 43    | 45      | 65   | 48   | 52   | 50   |
| No. counted                    | 251                | 251  | 258  | 210  | 270  | 268  | 247  | 252  | 256  | 283  | 243     | 252  | 270  | 296  | 283  | 296   | 267     | 370  | 269  | 264  | 287  |
| No. species                    | 27                 | 37   | 21   | 14   | 22   | 30   | 23   | 21   | 22   | 24   | 27      | 22   | 24   | 24   | 28   | 27    | 22      | 17   | 18   | 16   | 18   |
| Agglutinated (%)               | 3                  | 30   | 7    | 9    | 6    | 22   | 16   | 6    | 6    | 11   | 3       | 1    | 2    | 3    | 4    | 1     | 11      | 15   | 15   | 19   | 18   |
| Alpha-index                    | 8                  | 12   | 4    | 3.5  | 6    | 9    | 6    | 5.5  | 5.5  | 6.5  | 7.5     | 6    | 5.5  | 6    | 8    | 7     | 4.5     | 3.5  | 4.5  | 4    | 4.5  |
| H(S)                           | 2.4                | 2.9  | 2.0  | 1.7  | 1.9  | 2.5  | 2.1  | 1.8  | 1.6  | 2.1  | 2.0     | 1.9  | 1.9  | 2.1  | 1.9  | 2.0   | 1.9     | 1.4  | 1.9  | 1.8  | 1.8  |
| <b>ATA</b>                     |                    |      |      |      |      |      |      |      |      |      |         |      |      |      |      |       |         |      |      |      |      |
| <i>Adercotryma glomeratum</i>  | 0                  | 0    | 0    | 0    | 3    | 0    | 0    | 0    | 0    | 0    | 39      | 47   | 34   | 36   | 19   | 34    | 8       | 5    | 6    | 4    | 5    |
| <i>Clavulina obscura</i>       | 17                 | 15   | 28   | 25   | 5    | 16   | 16   | 1    | 0    | 0    | 3       | 3    | 0    | 0    | 1    | 1     | 9       | 1    | 4    | 4    | 5    |
| <i>Eggerelloides medius</i>    | 0                  | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 14      | 27   | 29   | 32   | 32   | 41    | 0       | 0    | 0    | 1    | 0    |
| <i>Eggerelloides scabrus</i>   | 23                 | 57   | 27   | 22   | 2    | 35   | 75   | 96   | 96   | 97   | 0       | 0    | 0    | 0    | 0    | 0     | 0       | 3    | 2    | 0    | 1    |
| <i>Eggerelloides sp.</i>       | 0                  | 0    | 0    | 0    | 1    | 0    | 0    | 0    | 0    | 0    | 0       | 0    | 2    | 5    | 0    | 1     | 15      | 10   | 20   | 2    | 10   |
| <i>Leptohalysis catella</i>    | 0                  | 0    | 1    | 0    | 0    | 0    | 0    | 0    | 0    | 0    | 0       | 0    | 0    | 0    | 0    | 0     | 31      | 12   | 7    | 16   | 19   |
| <i>Reophax fusiformis</i>      | 35                 | 7    | 17   | 13   | 45   | 27   | 5    | 0    | 0    | 0    | 6       | 5    | 4    | 5    | 12   | 4     | 11      | 53   | 42   | 34   | 31   |
| <i>Morulæplecta bulbosa</i>    | 7                  | 11   | 11   | 32   | 19   | 9    | 0    | 0    | 0    | 0    | 7       | 3    | 1    | 4    | 3    | 0     | 0       | 0    | 0    | 1    | 0    |
| No. counted                    | 231                | 299  | 157  | 167  | 154  | 183  | 213  | 235  | 188  | 299  | 276     | 255  | 302  | 316  | 326  | 207   | 226     | 294  | 245  | 313  | 311  |
| No. species                    | 11                 | 8    | 14   | 11   | 17   | 11   | 8    | 9    | 8    | 5    | 22      | 18   | 19   | 22   | 26   | 21    | 16      | 17   | 15   | 21   | 19   |
| Alpha-index                    | 2.5                | 2    | 4    | 3    | 4    | 2    | 1.5  | 2    | 2    | 1    | 4       | 4.7  | 4.5  | 5.5  | 6.5  | 6     | 4       | 4    | 3    | 5    | 4.5  |
| H(S)                           | 1.8                | 1.3  | 1.9  | 1.7  | 1.8  | 1.7  | 0.9  | 0.2  | 0.2  | 0.2  | 2.2     | 1.7  | 1.9  | 1.9  | 2.3  | 1.7   | 2.1     | 1.9  | 1.9  | 2.1  | 2.0  |

Table 2. Faunal data for Skagerrak and fjord ODAs and ATAs (abundances of species  $\geq 5\%$ ).

| Area                                | Skagerrak |      |     |     |     |     |     |     |     |     |     |     |      |     |     |      |     |     |       | Fjords |       |       |  |
|-------------------------------------|-----------|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|-----|-----|------|-----|-----|-------|--------|-------|-------|--|
|                                     | 66        | 60   | 59  | 71B | 72  | 65  | 61  | 58  | 70  | 73  | 67  | 64  | 75   | 68  | 74B | 63   | 62  | 57  | 67-92 | 69-92  | 71-92 | 72-92 |  |
| Sample no.                          | 266       | 285  | 298 | 304 | 310 | 359 | 399 | 404 | 427 | 473 | 483 | 514 | 534  | 581 | 594 | 626  | 640 | 651 | 140   | 108    | 68    | 50    |  |
| Depth (m)                           | 266       | 285  | 298 | 304 | 310 | 359 | 399 | 404 | 427 | 473 | 483 | 514 | 534  | 581 | 594 | 626  | 640 | 651 | 140   | 108    | 68    | 50    |  |
| <b>ODA</b>                          |           |      |     |     |     |     |     |     |     |     |     |     |      |     |     |      |     |     |       |        |       |       |  |
| <i>Brizalina skagerrakensis</i>     | 0         | 4    | 7   | 3   | 3   | 1   | 8   | 5   | 8   | 22  | 0   | 0   | 1    | 5   | 21  | 1    | 3   | 5   | 0     | 1      | 0     | 0     |  |
| <i>Bulimina marginata</i>           | 0         | 0    | 1   | 0   | 1   | 0   | 1   | 0   | 0   | 1   | 0   | 0   | 0    | 1   | 0   | 0    | 0   | 0   | 9     | 5      | 12    | 22    |  |
| <i>Cassidulina laevigata</i>        | 3         | 10   | 15  | 8   | 12  | 4   | 11  | 5   | 6   | 10  | 1   | 2   | 4    | 1   | 6   | 1    | 7   | 9   | 9     | 10     | 7     | 5     |  |
| <i>Eggerelloides medius</i>         | 1         | 3    | 2   | 3   | 5   | 2   | 10  | 4   | 9   | 13  | 0   | 2   | 9    | 6   | 10  | 5    | 11  | 13  | 1     | 11     | 4     | 0     |  |
| <i>Haplophragmoides bradyi</i>      | 0         | 3    | 0   | 1   | 0   | 0   | 6   | 2   | 4   | 7   | 0   | 6   | 12   | 12  | 17  | 20   | 11  | 12  | 0     | 0      | 1     | 0     |  |
| <i>Hyalinea balthica</i>            | 0         | 0    | 1   | 1   | 1   | 0   | 1   | 0   | 1   | 1   | 0   | 0   | 0    | 0   | 0   | 0    | 0   | 0   | 4     | 10     | 7     | 3     |  |
| <i>Pullenia osloensis</i>           | 3         | 19   | 26  | 25  | 19  | 2   | 21  | 12  | 15  | 15  | 3   | 8   | 8    | 7   | 0   | 3    | 0   | 1   | 8     | 10     | 10    | 0     |  |
| <i>Saccammina</i> spp.              | 0         | 0    | 0   | 0   | 0   | 0   | 4   | 2   | 5   | 4   | 0   | 2   | 9    | 4   | 8   | 19   | 7   | 10  | 0     | 0      | 0     | 0     |  |
| <i>Stainforthia fusiformis</i>      | 39        | 12   | 4   | 8   | 15  | 45  | 8   | 19  | 3   | 3   | 65  | 43  | 25   | 10  | 2   | 3    | 9   | 1   | 19    | 13     | 19    | 38    |  |
| <i>Textularia tenuissima</i>        | 4         | 20   | 18  | 15  | 21  | 6   | 6   | 11  | 11  | 0   | 3   | 1   | 0    | 0   | 0   | 0    | 0   | 0   | 10    | 5      | 6     | 4     |  |
| <i>Trochamminopsis pusillus</i>     | 0         | 0    | 0   | 0   | 0   | 0   | 0   | 1   | 2   | 2   | 0   | 6   | 3    | 10  | 4   | 15   | 8   | 8   | 0     | 0      | 0     | 0     |  |
| No. counted                         | 288       | 272  | 273 | 262 | 261 | 255 | 262 | 256 | 261 | 253 | 283 | 294 | 258  | 275 | 257 | 258  | 260 | 288 | 290   | 304    | 274   | 347   |  |
| No. species                         | 47        | 35   | 38  | 38  | 36  | 44  | 33  | 48  | 47  | 42  | 38  | 46  | 41   | 45  | 39  | 34   | 47  | 43  | 36    | 41     | 40    | 40    |  |
| Agglutinated (%)                    | 18        | 36   | 26  | 32  | 31  | 18  | 35  | 30  | 42  | 35  | 8   | 29  | 47   | 52  | 51  | 79   | 47  | 54  | 19    | 28     | 23    | 17    |  |
| Alpha-index                         | 16        | 10.5 | 12  | 12  | 11  | 15  | 10  | 18  | 16  | 13  | 12  | 15  | 13.5 | 15  | 13  | 10.5 | 16  | 13  | 11    | 12.5   | 13    | 11.5  |  |
| H(S)                                | 2.8       | 2.7  | 2.6 | 2.7 | 2.7 | 2.5 | 2.8 | 3.1 | 3.1 | 2.8 | 1.8 | 2.5 | 2.8  | 3.2 | 2.9 | 2.5  | 3.3 | 3.0 | 2.7   | 3.0    | 2.9   | 2.7   |  |
| <b>ATA</b>                          |           |      |     |     |     |     |     |     |     |     |     |     |      |     |     |      |     |     |       |        |       |       |  |
| <i>Adercotryma glomeratum</i>       | 1         | 2    | 1   | 0   | 2   | 0   | 0   | 1   | 1   | 0   | 0   | 1   | 0    | 0   | 0   | 0    | 0   | 0   | 2     | 9      | 8     | 5     |  |
| <i>Eggerelloides medius</i>         | 11        | 12   | 17  | 8   | 16  | 9   | 23  | 15  | 23  | 33  | 0   | 7   | 16   | 16  | 11  | 11   | 16  | 18  | 10    | 33     | 27    | 2     |  |
| <i>Haplophragmoides bradyi</i>      | 0         | 15   | 6   | 9   | 2   | 2   | 25  | 20  | 14  | 18  | 0   | 14  | 32   | 30  | 34  | 23   | 22  | 23  | 1     | 1      | 2     | 0     |  |
| <i>Recurvoides trochamminiforme</i> | 0         | 1    | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0    | 0   | 0   | 0    | 0   | 0   | 3     | 18     | 2     | 9     |  |
| <i>Reophax micacea</i>              | 4         | 5    | 4   | 22  | 8   | 2   | 3   | 10  | 11  | 2   | 3   | 6   | 5    | 0   | 1   | 1    | 2   | 1   | 2     | 1      | 0     | 0     |  |
| <i>Saccammina</i> spp.              | 0         | 0    | 0   | 0   | 0   | 0   | 7   | 5   | 12  | 14  | 0   | 5   | 7    | 11  | 14  | 27   | 11  | 14  | 0     | 0      | 0     | 0     |  |
| <i>Textularia tenuissima</i>        | 35        | 60   | 62  | 49  | 64  | 40  | 8   | 31  | 15  | 9   | 39  | 5   | 0    | 0   | 1   | 0    | 0   | 1   | 62    | 19     | 34    | 25    |  |
| <i>Trochamminopsis pusillus</i>     | 0         | 0    | 1   | 0   | 0   | 2   | 15  | 5   | 7   | 9   | 2   | 34  | 14   | 17  | 14  | 16   | 20  | 12  | 0     | 0      | 8     | 0     |  |
| No. counted                         | 308       | 258  | 267 | 205 | 263 | 299 | 276 | 176 | 296 | 338 | 268 | 275 | 274  | 270 | 281 | 282  | 249 | 304 | 260   | 257    | 253   | 256   |  |
| No. species                         | 24        | 15   | 14  | 17  | 17  | 32  | 16  | 18  | 24  | 22  | 20  | 29  | 29   | 25  | 23  | 26   | 24  | 25  | 22    | 23     | 32    | 25    |  |
| Alpha-index                         | 6         | 3.5  | 3   | 4   | 4   | 9   | 4   | 5   | 6   | 5.5 | 5   | 8.5 | 8.5  | 6.5 | 6   | 7    | 6.5 | 5.5 | 5.5   | 6      | 10    | 7     |  |
| H(S)                                | 2.2       | 1.4  | 1.3 | 1.7 | 1.3 | 2.4 | 2.0 | 2.0 | 2.4 | 2.1 | 2.3 | 2.4 | 2.4  | 2.2 | 1.8 | 2.2  | 2.3 | 2.5 | 1.6   | 2.1    | 2.3   | 2.4   |  |

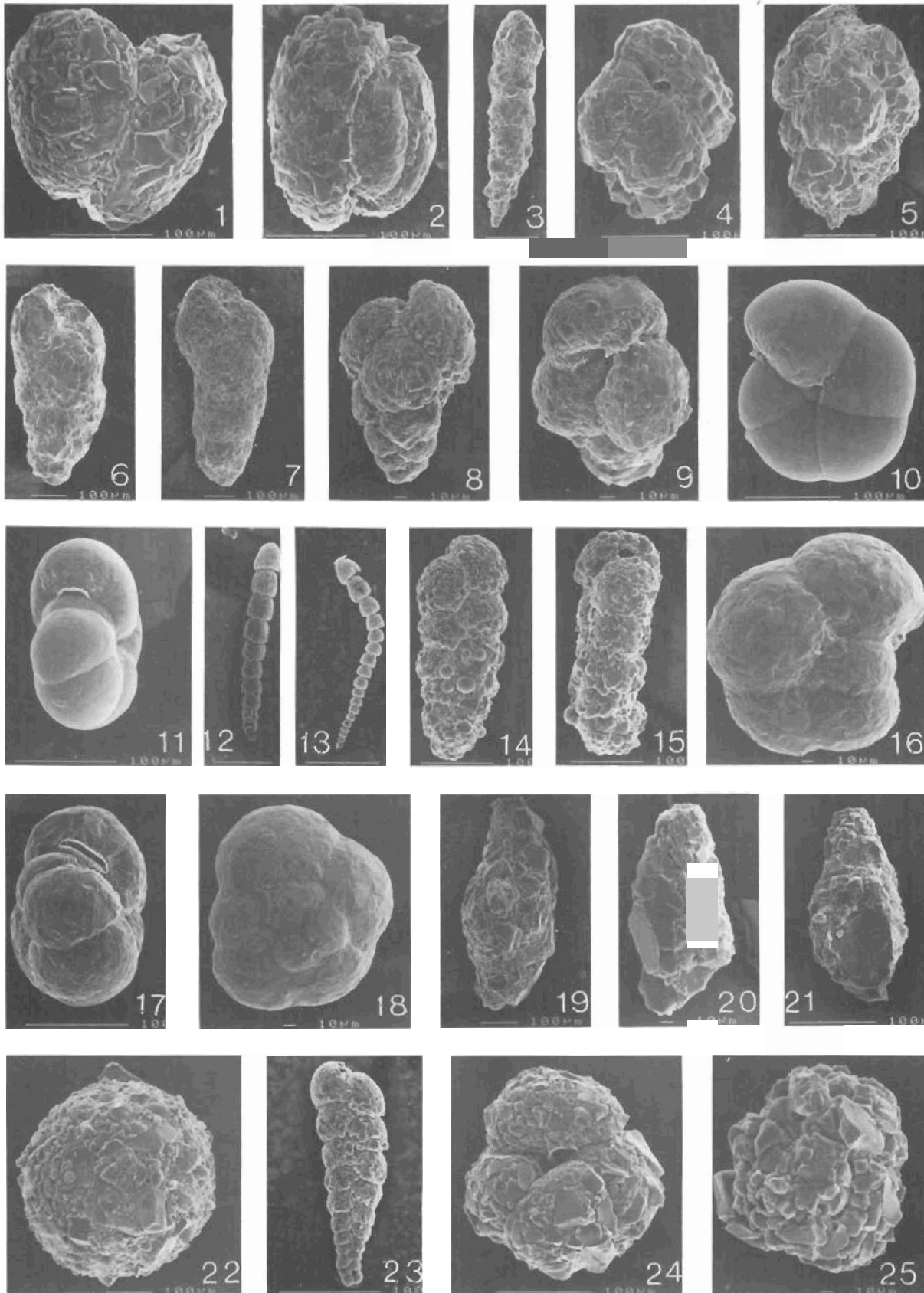


PLATE 1. Unlabelled scale bars are 100  $\mu\text{m}$ . Sample numbers are given in parentheses.

1,2. *Adercotryma glomeratum* (Brady) (2894). 3. *Clavulina obscura* Chaster (3454). 4,5. *Eggerelloides medius* (Höglund) (64-92). 6,7. *Eggerelloides scabrus* (Williamson) (3454). 8,9. *Eggerelloides* sp. (3118). 10,11. *Haplophragmoides bradyi* (Robertson) (Sk75). 12,13. *Leptohalysis catella* (3117). 14,15. *Morulaepecta bulbosa* Höglund (3454). 16-18. *Recurvroides trochamminiforme* Höglund (64-92). 19. *Reophax fusiformis* (Williamson) (3117). 20,21. *Reophax micacea* (Cushman) (Sk71B). 22. *Saccammmina* sp. (Sk75). 23. *Textularia tenuissima* Earland (Sk70). 24, 25. *Trochamminopsis pusillus* (Höglund) (Sk75).