

Response of deep-water agglutinated foraminifera to dysoxic conditions in the California Borderland basins

MICHAEL A. KAMINSKI¹, ANN BOERSMA², JAROSŁAW TYSZKA³, and ANN E.L. HOLBOURN¹

1. Research School of Geological and Geophysical Sciences, Birkbeck College and University College London, Gower Street, London WC1E 6BT, U.K.

2. Microclimates Research, 510 Gate Hill, Stoney Point, New York, 10980, USA

3. Institute of Geological Sciences, Polish Academy of Sciences, Senacka 3, 31-002 Kraków, Poland

ABSTRACT

Analysis of agglutinated benthic foraminifera from surface samples collected in the San Pedro and Santa Catalina Basins reveals a predictable relationship between the proportions of morphogroups with decreasing bottom water oxygen levels and with the TOC content of the surficial sediment. Living (Rose Bengal stained) foraminiferal faunas from dysaerobic environments display low diversity and high dominance, suggesting stressed conditions. There is an inverse relationship between oxygen and the relative abundance of deep infaunal morphogroups.

Samples collected from shallow stations above the oxygen minimum zone are comprised of epifaunal and shallow infaunal morphotypes. At intermediate depths (~500 m), there is a peak in the abundance of suspension-feeding and "climbing" forms (watchglass-shaped trochamminids attached to *Rhabdammina*). Specimens from intermediate stations display the largest overall size. Deeper in the San Pedro Basin the living fauna is dominated by a small, flattened, tapered, species that is interpreted as having a deep infaunal microhabitat. In the dysaerobic environments off California the greatest degree of faunal change occurs when bottom water dissolved oxygen values drop from 0.5 ml/l to 0.2 ml/l.

The effect of TOC content on the benthic fauna is demonstrated at two stations from the same depth in the San Pedro Basin. The station with the higher TOC content (4.2% vs. 2.9%) contains greater proportions of the small, deep infaunal morphotype. These faunal changes may be attributed to differences in the depth of the oxygenated zone within the sediment surface layer.

Agglutinated faunas from areas that experience seasonal anoxia are comprised of a large proportion of opportunistic forms such as *Reophax* and *Psammospaera*. These are the same taxa that colonised abiotic sediment trays in a recolonisation experiment in the Panama Basin. This study further demonstrates that agglutinated foraminiferal morphotypes respond in a similar manner to calcareous benthic foraminifera in dysaerobic environments.

INTRODUCTION

The deep water benthic foraminifera from black, dysaerobic shales have received a good deal of attention since the discovery in the 1970's that "oceanic anoxic events" have left a major impact on the sedimentary record in world ocean. There is little doubt that oxygen levels in the deep ocean have changed drastically in the past, owing to changes in thermohaline circulation and the opening and closing of oceanic gateways. There is an increasing amount of evidence to suggest that the fluctuating oxygen content of intermediate and deep waters may be one of the prime factors controlling the evolution of both planktonic foraminiferal (e.g. Leckie, 1989) and deep-sea benthic faunas at least since the Early Cretaceous (e.g. Kaiho, 1991; Kuhnt *et al.*, in press). Some morphological groups of calcareous benthic foraminifera display physiological adaptation to low-oxygen conditions (Bernhard, 1986). Among the foraminiferal morphologies typically observed in

oxygen-poor habitats are small size, flattened shapes, thin walls, and large pores (Sen Gupta & Machain-Castillo, 1993). However, recent studies of modern benthic foraminifera from oxygen-poor environments have concentrated mainly on calcareous forms (e.g. Hermelin, 1992) or on agglutinated taxa from Norwegian fjords (e.g. Alve, 1990). There is now experimental evidence to suggest that next to the bacteria, benthic foraminifera are perhaps more tolerant to anoxia than other organisms. In a landmark study, Bernhard (1993) determined that a number of benthic foraminiferal species (both calcareous and agglutinated) can survive 30 days of complete anoxia under laboratory conditions.

Deep-water agglutinated foraminifera (DWAFF) are often the only microfossils present in Cretaceous black shales recovered from ocean drilling sites in the world ocean. However, interpretations of their paleoecological significance are still based on a number of assumptions which must be tested by examin-

ing faunal patterns in modern dysoxic environments. Morphogroup analysis of DWAF assemblages from Mesozoic sediments (e.g. Nagy *et al.*, this volume) can provide insight into the presumed life habitats of foraminifera under dysaerobic conditions. By analogy with the morphotype model of calcareous benthic foraminifera developed by Corliss & Chen (1988), the dominant DWAF group in Mesozoic black shales is interpreted to have lived as infaunal detritivores. These infaunal organisms are undoubtedly adapted to reduced oxygen conditions within sediment pore waters, but their physiological adaptations to dysaerobic conditions is not well understood. These DWAF species normally possess a solid wall structure and it is unclear how the organisms can survive or improve gas exchange under low-oxygen conditions.

The purpose of this study is to test the morphogroup model by documenting DWAF biofacies in response to oxygen levels and organic carbon contents in a modern analogue of a restricted dysaerobic basin. The California borderland basins were selected for this study because the area offers the full range of dysaerobic conditions in a deep-water setting, the sedimentary environment of the region has been well documented, and through the kindness of R.G. Douglas, access to sample material was made available. The biofacies patterns of cal-

careous benthic foraminifera from the area have been studied previously (Douglas, 1987), thereby providing the opportunity to compare morphological trends in both groups of foraminifera.

STUDY AREA

The California Borderland forms the broad continental margin of southern California. Two or three parallel rows of submarine ridges and submarine banks separate 23 enclosed basins. Samples examined in this study were collected in the San Pedro, Santa Catalina, and San Nicolas Basins (Figure 1). The offshore San Nicolas Basin is a deep (greater than 1500m) basin with steep sides and irregular floor. The Santa Catalina Basin, which is intermediate in position, has steep sides and a relatively flat floor, but higher walls. Sediments in the basins are derived from both adjacent coastal rivers and from biogenic particles in this productive upwelling area. Calcium carbonate concentrations are generally low (30-5%) with contents <5% on the basin floors. Highest carbonate contents are typically found on bank tops and along the outer shelves where shell hash comprises a large portion of the sand fraction (Gorsline, 1992). Organic carbon contents in surface sediments range from 0.5 - 6% (Schwalbach & Gorsline, 1985).

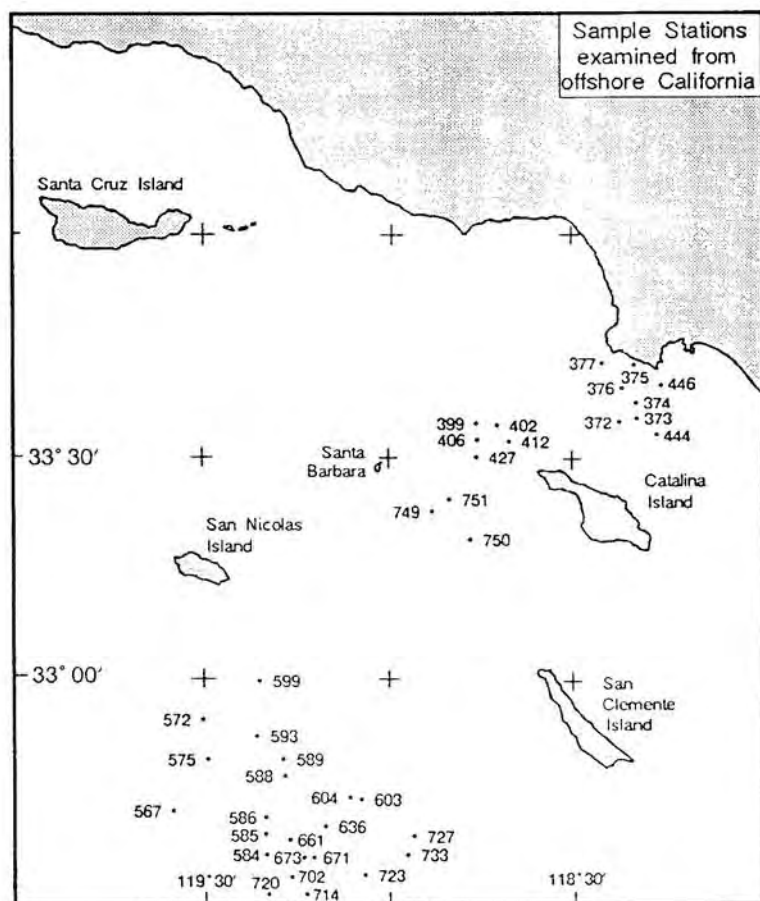


Figure 1. Sample stations from the California borderlands examined in this study.

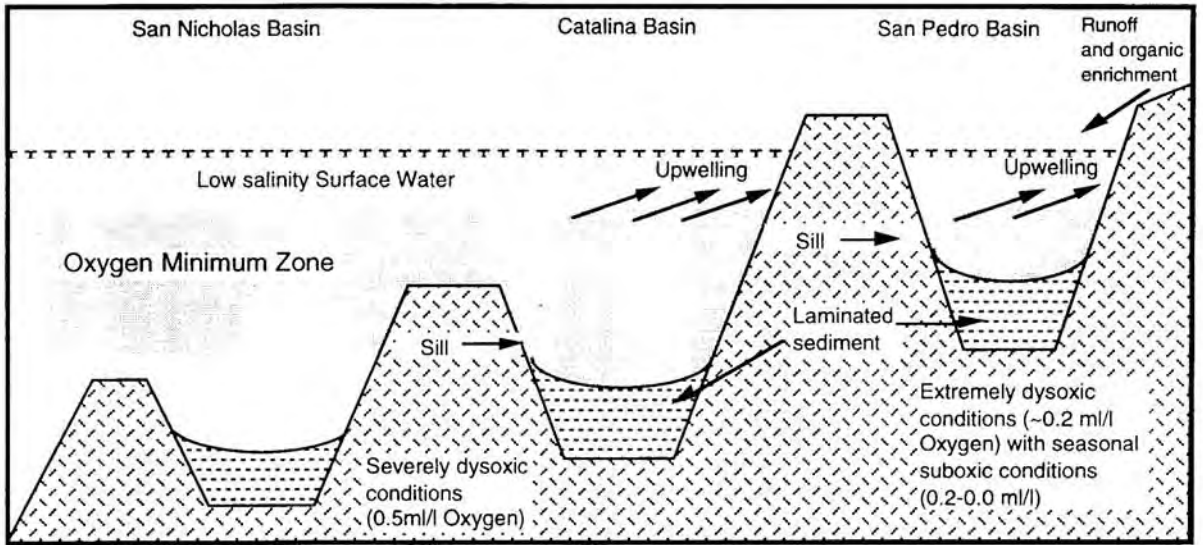


Figure 2. Environmental setting of the California borderlands basins, after Douglas (1987).

The surface circulation in the southern California bight is dominated by the interaction of the cool, southward-flowing California Current and the warm waters of the northward-flowing California Counter-current which hugs the coast. The study area is situated in the zone of mixing between the currents which is dominated by a large anticlockwise eddy known as the Southern California Eddy (Hickey, 1992). Localised upwelling occurs near the coast especially in the area of Point Conception north of Los Angeles, and in the lee of the islands. The spring bloom in the San Pedro Basin normally occurs in early April, whereas intense upwelling occurs between late April and early June, resulting in a large (nearly one order of magnitude) increase in foraminiferal flux observed in sediment traps (Thunell & Sautter, 1992). Deep circulation is restricted by sills that separate the basins. The study area has a strong oxygen minimum zone that begins in the lower thermocline layer, a consequence of the intense spring upwelling. Between 50 and 100m, oxygen values decrease rapidly to about 4 ml/l, then continue to decrease to about 1 ml/l at about 300m. Below sill depth in the Santa Catalina Basin the oxygen concentration falls to 0.5 ml/l, whereas closer to shore in the San Pedro Basin values periodically fall below 0.2 ml/l. The San Pedro Basin connects with the Santa Monica Basin, which has been fully anoxic for much of the Holocene (Pisias, 1978). The oceanographic setting of these three basins is summarised in Figure 2. The San Pedro Basin is not anoxic at present and its sediments are bioturbated. The basin has served as a dumping ground for drilling muds and cuttings from petroleum exploration in the area, but these have not significantly altered its bottom water oxygen content (Gorline, 1992).

MATERIAL & METHODS

The box-core samples used for this study were col-

lected in the winter of 1976-1977 by R.G. Douglas, and were previously picked for studies of calcareous benthic foraminifera. The surface sediment TOC and the dissolved oxygen content of bottom water was measured at each sample location (Figures 3, 4).

Throughout this study, we use the following terms describing oxygen levels in marine waters and sediments as defined by Tyson & Pearson (1991): oxic (>2.0 ml/l O_2); dysoxic (2.0-0.2 ml/l); suboxic (0.2 - 0.0 ml/l); and anoxic (0.0 ml/l).

Foraminiferal samples had been previously stained with Rose Bengal and sieved over a 63 μ m screen. We picked agglutinated foraminifera from aliquots of these dried washed residues. Unfortunately, the original volume of the samples is unknown, therefore the assemblage data gathered here are only useful for studying relative proportions of DWAF species. Likewise, the proportions of total foraminifera (calcareous and agglutinated) and total abundances in terms of volume are unknown. Specimens were picked from the >63 micron fraction and mounted on cardboard slides. These are housed in the micropaleontological collections of University College London. Selected specimens were photographed using a Zeiss-DSM-940 SEM at the Micropalaeontology Unit, UCL.

To interpret the relationship between DWAF assemblages and environmental parameters, we investigated the relative proportions of foraminiferal morphogroups. The morphogroup approach adopted here is based on the assumption that there is a relationship between foraminiferal test shape and the microhabitat preference of the organism with respect to life position and feeding behaviour. The shape classification adopted here is similar to the morphotypes used by Nagy *et al.* (this volume). We combined the abundance data into four classes: Tapered elongate forms such as *Reophax*, *Verneuilinulla*

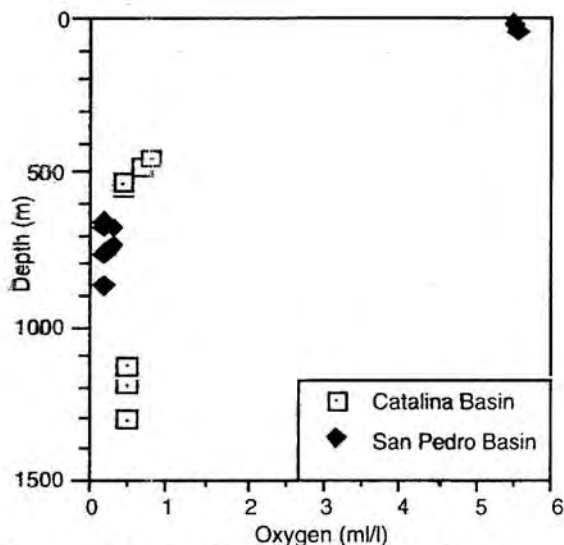


Figure 3. Relationship between dissolved oxygen and water depth at the sampled localities.

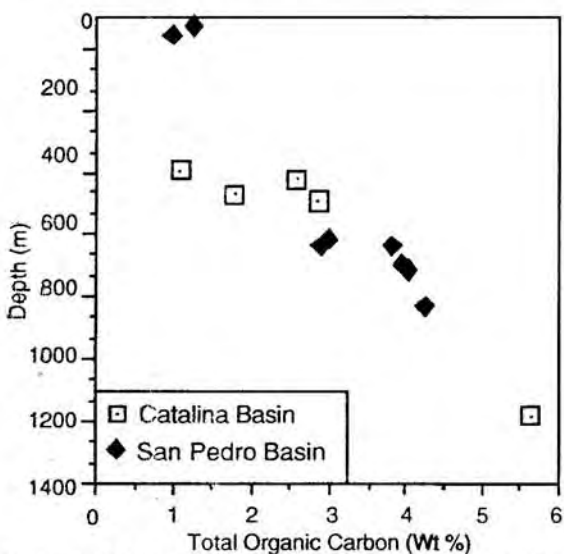


Figure 4. Relationship between TOC and water depth at the sampled localities.

and *Textularia* are regarded as "deep infauna". These forms have a streamlined shape, and are analogous in shape to the calcareous taxa *Chilostomella* and *Globobulimina* which were observed to live to a depth of 15 cm in normal deep marine sediments (Corliss, 1985). By the term "deep infaunal" we mean mobile forms that have the ability to live infaunally at the bottom tier of living foraminiferal species, but are not necessarily restricted to the deepest levels. In the Panama Basin, living *Reophax* specimens were observed as deep as 15cm (Kaminski et al., 1988). Bilaterally symmetrical forms such as *Haplophragmoides* and *Buzasina* are placed in the "intermediate infauna" group. These taxa are similar in shape to the planispiral calcareous species *Melonis barleeanum*, which Corliss (1985) found living at a depth of ca. 4cm. Spherical forms such as *Psammosphaera* are regarded as "shallow infauna", following the observation by Delaca (1986) that the genus *Astrammmina* lives

just below the sediment/water interface. "Mobile epifaunal" forms are the trochospiral forms and flat disk-shaped forms such as *Paratrochammina* and *Discammina*. The tubular forms such as *Marssipella* and *Rhabdammina* are placed in the group of sessile suspension feeders. Although tubular forms are present locally in the Santa Catalina Basin, this group displayed a patchy distribution and was omitted from the our analysis of morphogroups.

RESULTS

Despite our lack of control on the sample collection and processing, it is apparent that the DWAf from the San Pedro and Santa Catalina Basins display changes in size, dominance, taxonomic composition, and the proportion of morphogroups, as well as in the proportions of opportunistic species.

San Pedro Basin

The foraminiferal census data from the stations in the San Pedro Basin are presented in Table 1. The assemblages generally display low diversity (3 to 11 species) and variable dominance (measured as the proportion of the most common species), which reaches the high level of 95%. The stained faunas comprise four distinct assemblages: (1) faunas from shallow stations are dominated by *Haplophragmoides* and *Paratrochammina* spp. These stations also contain *Cyclammina cancellata* and calcareous-cemented forms such as *Gaudryina*; (2) a station at 672 m is dominated by a large species of *Verneuilinulla*; (3) a fauna with low dominance comprised of *Rhizammina*, *Bathysiphon*, *Reophax*, and *Labrospira* at 689 and 750m; and (4) a fauna strongly dominated by a diminutive species of organically-cemented *Textularia* at stations from 689, 768, and 874 m.

Santa Catalina Basin

The foraminiferal census data from the stations in the Santa Catalina Basin are presented in Table 2. Compared with the San Pedro Basin, the stations display intermediate TOC and O₂ values, and DWAf assemblages display moderate levels of dominance. Stained assemblages at these stations consist of: (1) a fauna dominated by a *Marsipella* sp., *Reophax excentricus*, and species of *Verneuilinulla* at stations above 500m depth; (2) a fauna dominated by *Reophax* (*R. bilocularis*, *R. dentaliniformis*, and *R. excentricus*) accompanied by *Psammosphaera fusca* at stations near 550m depth; and (3) At intermediate depths (~500m), there is a peak in the abundance of suspension-feeding and "climbing" forms (watchglass-shaped trochamminids attached to tubular forms). Specimens from intermediate stations display the largest overall size. A fauna with *Saccorhiza ramosa* was found at the deep stations. However, *Saccorhiza* also dominates the assemblage at 554m, where a species of *Lepidotrochammina* is found associated with it. Several taxa are common in one or two samples only, such as *Rhizammina irregularis*

Sample	Depth [m]	<i>Ammodiscus</i> sp.	<i>Bathysiphon</i> filiformis	<i>Buzasina</i> sp.	<i>Cyclamina</i> cancellata	<i>Gaudryina</i> arenacea	<i>Haplophragmoides</i> canariensis	<i>Hyperamina</i> laevigata	<i>Labrospira</i> scitula	<i>Labrospira</i> wiesneri	<i>Recurvoides</i> turbinatus	<i>Reophax</i> bilocularis	<i>Reophax</i> dentaliniformis	<i>Reophax</i> hispidus	<i>Reophax</i> micaceus	<i>Rhizammina</i> irregularis	<i>Saccorhiza</i> sp.	<i>Textularia</i> sp.	<i>Trochammina</i> sp.	<i>Verneuilinulla</i> ?/Matanzia	Total
24508-375	26	0	0	0	4	3	40	0	0	3	0	0	0	0	0	0	0	3	120	0	173
22621-443	54	0	0	0	0	15	131	0	0	0	0	14	0	0	0	0	0	16	66	0	242
24438-374	672	0	0	0	0	0	0	0	1	8	0	5	0	0	0	4	0	27	19	180	244
24440-377	689	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	264	0	13	279
24437-373	689	6	14	0	0	0	0	4	0	9	2	16	9	0	0	24	0	11	2	4	101
22910-444	750	5	6	2	0	0	0	2	0	20	0	13	13	2	0	28	0	11	0	15	117
24439-376	768	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	263	6	10	279
24436-372	874	0	0	0	0	0	0	0	1	4	0	2	0	0	5	0	0	296	23	1	332

Table 1. DWAF from the San Pedro Basin.

Sample	Depth [m]	<i>Ammobaculites</i> sp.	<i>Ammodiscus</i> sp.	<i>Bathysiphon</i> filiformis	<i>Cribrostomoides</i> subglobosus	<i>Discammina</i> compressa	<i>Hyperamina</i> laevigata	<i>Karrerulina</i> sp.	<i>Labrospira</i> scitula	<i>Labrospira</i> wiesneri	<i>Lepidotrochammina</i> sp.	<i>Marsipella</i> sp.	<i>Martinotiella</i> sp.	<i>Multifidella</i> pacifica	<i>Psamosphaera</i> fusca	<i>Recurvoides</i> contortus	<i>Recurvoides</i> turbinatus	<i>Reophax</i> bilocularis	<i>Reophax</i> dentaliniformis	<i>Reophax</i> excentricus	<i>Reophax</i> hispidus	<i>Rhizammina</i> irregularis	<i>Saccorhiza</i> sp.	<i>Verneuilinulla</i> ?/Matanzia	Total
24432-427	448	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	2	51	0	3	0	10	69	
24426-406	461	4	0	0	13	8	0	0	0	0	26	2	1	2	0	5	3	1	92	0	38	0	109	304	
24434-412	491	0	3	3	0	37	0	1	10	2	0	98	6	0	0	7	45	16	6	5	9	0	17	265	
24427-399	539	0	0	0	0	0	0	3	0	0	0	0	0	59	0	0	112	11	0	0	0	8	6	199	
24433-402	554	0	0	23	0	4	2	0	1	0	18	2	0	4	0	0	77	18	0	0	0	113	9	271	
23934-749	1202	0	0	0	0	0	0	0	2	3	0	0	0	0	1	4	0	4	1	4	0	62	57	138	
24582-751	1309	0	0	10	0	0	0	0	1	1	0	0	0	0	4	0	6	12	18	0	11	27	9	99	

Table 2. DWAF from the Santa Catalina Basin.

at 461m, *Discammina compressa* at 491m, *P. fusca* at 539m, and *Bathysiphon* sp. at 554 and 1309m.

Morphogroups

The data presented in Tables 1 and 2 were combined into morphogroups according to test shape to examine the relationship between the first-order faunal patterns and environmental parameters. In theory, we expect the proportion of infaunal detritivores to be positively correlated to the amount of food resources available to them. Corliss & Chen (1988) and other authors have pointed out the positive correlation between the proportion of the infaunal calcareous benthic morphogroup and the flux of organic matter to the sea floor. The California Borderlands data set therefore enables us to test the morphogroup model for agglutinated foraminifera.

The relative proportions of the stained DWAF in our samples vary in a predictable manner with regard to the bottom water oxygen content and total

organic content. At our sampled stations, the TOC content of the surficial sediment varies from <1% to ca. 4.5%. In the San Pedro and Catalina Basins, a positive relationship was observed between TOC and the relative proportions of the combined "intermediate infaunal" and "deep infaunal" morphogroups (Figure 4). At the same time there is a corresponding inverse relationship between TOC and the "shallow infaunal" group. Surprisingly, the "epifaunal" group displayed no clear trend in this data set. Two stations from the San Pedro Basin with high TOC values contained assemblages consisting of nearly 100% deep infaunal forms, whereas the two stations with low values contained a more equable mixture of the three morphogroups. The effect of TOC content on the benthic fauna is demonstrated at Stations 377 and 373 which were both collected at a depth of 689m in the San Pedro Basin. Although both stations experience the same bottom water oxygen content, Station 377 with the higher TOC content

(3.8% vs. 2.9%) contains greater proportions of the small, deep infaunal morphotype.

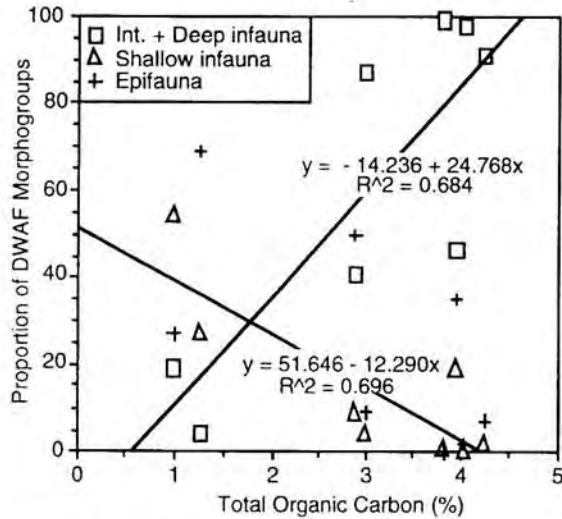


Figure 4. Relationship between TOC and DWAF morphogroups at the sampled localities.

When the proportions of DWAF morphogroups are compared with the bottom water dissolved oxygen contents measured at the sample station, a clear separation between dysoxic and fully oxygenated environments becomes apparent (Figure 5). Although we lack samples from the critical interval of rapid change in the lower thermocline layer, our samples reveal a marked contrast between the well-oxygenated surface layer and the severely to extremely dysoxic environments of the basins. Samples collected from shallow stations above the oxygen minimum zone are comprised of both epifaunal and shallow infaunal morphotypes. Deeper in the San Pedro Basin the living fauna is dominated by a small, flattened, tapered species of *Textularia* that is interpreted as having a deep infaunal microhabitat.

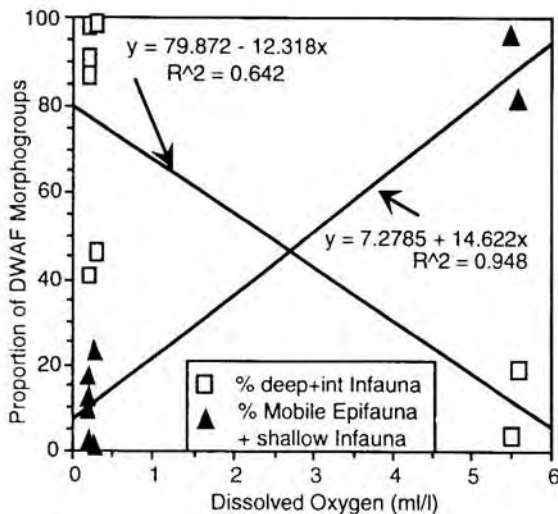


Figure 5. Relationship between bottom water oxygen content and DWAF morphogroups at the sampled localities.

In the dysaerobic environments off California the greatest change in benthic foraminiferal faunas occurs when bottom water dissolved oxygen values drop from 0.5 ml/l to 0.2 ml/l.

The dominant calcareous benthic taxa from the basin floors of the nearshore basins also belong to the elongate, tapered, "deep infaunal" morphogroup. Douglas (1987) described a biofacies with dominant *Fursenkoina apertura* (Uchio), *F. bramlettei* (Galloway & Morley), *F. seminuda* (Natland), *Cassidulinoides cornuta* (Cushman) and *Buliminella tenuata* (Cushman), with associated *Globobulimina affinis* (d'Orbigny) and *G. hoeglundi* (Uchio). Under normally oxygenated conditions, taxa such as *Globobulimina* have been observed to live as deep as 15cm below the sediment surface (Corliss, 1985), but in the dysoxic basins they are recovered from the sediment surface layer.

DISCUSSION

r-selection in dysoxic environments

In his discussion of marine benthic diversity Sanders (1968) regarded the severely to extremely dysoxic environments beneath the equatorial upwelling region off Peru as a prime example of a physically unpredictable, or highly stressed, habitat. In such an environment where physical conditions fluctuate widely and unpredictably, a "physically-controlled" benthic community is found which consists of a small number of opportunistic species living at the edge of their environmental tolerance. In this situation the carrying capacity of the environment is never reached, and diversity is controlled by the frequency of population reduction by stress (in this case, by periodic anoxia) relative to the reproduction rates of the benthic organisms. In the most extreme environments, both diversity and abundance is reduced further until abiotic conditions are reached. This model became known as the stability-time hypothesis (Sanders, 1968). The postulates of the model were depicted graphically by Sjoerdsma & van der Zwaan (1992), who used benthic foraminifera from the Adriatic as an example. In a test of the model, Sanders (1969) examined the diversity gradient across the upwelling zone in Walvis Bay. Sanders found that the diversity of macrofaunal organisms was lowest at the most severely dysoxic site in the transect (the bottleneck case of Sjoerdsma & van der Zwaan, 1992), and that macrofaunal abundance was as low as in oligotrophic areas of the deep ocean. In this setting, periodic anoxia causes mass mortality and any animals living in the area must be *r*-selected opportunists.

The only experimental study to data of recolonisation rates (a proxy for opportunism) in deep-sea agglutinated foraminifera was carried out at a 3,900m station in the Panama Basin (Kaminski *et al.*, 1988). At this station, three trays of abiotic sediment were placed on the sea floor for nine months in an effort to determine faunal recruitment rates. Species that colonised the trays were all agglutinated, and

mainly consisted of *Reophax dentaliniformis*, *R. excentricus*, *Psammosphaera fusca*, and *Cribrostomoides*. One surprising finding is that the opportunists at this station are mainly infaunal detritivores. The suspension-feeding tubular species did not colonise the trays.

The results of the recolonisation experiment in the Panama Basin are important for testing the species response models of Sanders (1968) and Sjoerdsma & van der Zwaan (1992). In our samples from the Catalina Basin, a large proportion of the stained DWAF population comprises forms that were identified as opportunistic by Kaminski *et al.* (1988) (Figure 6). At some stations in the Catalina Basin close to 80% of the stained DWAF are comprised of *Reophax dentaliniformis*, *R. excentricus*, and *Psammosphaera fusca*. These are large-sized taxa that are identical to those in the Panama Basin samples of Kaminski *et al.* (1988). *Reophax dentaliniformis* (in association with *R. bilocularis*) has also been observed to dominate an assemblage beneath the intense oxygen minimum zone off Oman (Hermelin, 1992).

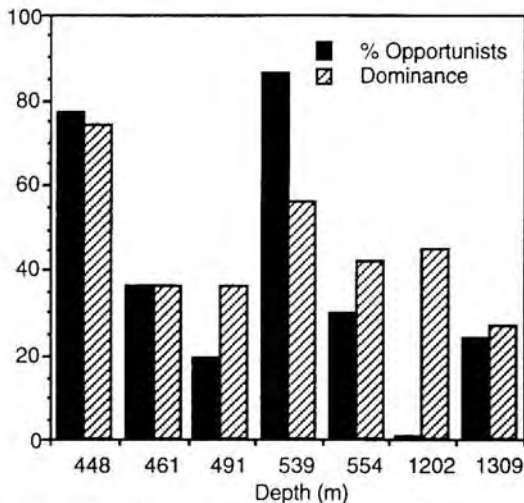


Figure 6. Proportion of opportunists and dominance (measured as the proportion of the dominant species) in samples from the Santa Catalina basin.

At the most severely dysoxic stations in the San Pedro Basin the diversity is low in agreement with the stability-time model. Douglas (1987) noted that species diversity drops to 6 or 7 species in the basinal areas with laminated sediments, and that individual species have patchy distributions and do not occur in every sample. In the deeper areas of the Santa Barbara Basin foraminiferal populations are low in summer because of extremely dysoxic to anoxic conditions (Bernhard & Reimers, 1991) and consist of about 85% *Nonionella stella*. However, autumn populations are high and dominated by three taxa with infaunal morphology: *Nonionella stella*, *Chilostomella ovoidea*, and "*Textularia earlandi*". The dominant "*Textularia sp.*" in our samples from the San Pedro Basin is no doubt the same species as the one observed by Bernhard & Reimers in the Santa Barbara

Basin, and can increase greatly in abundance within the span of three months. We speculate that this form must also be an r-selected species even though it was not one of the taxa recovered in the Panama Basin. However, this is a small species, and its presence in the San Pedro samples is due entirely to the choice of a smaller sieve size.

Response of DWAF to anoxia

The effects of anoxia on invertebrate macrofaunal communities have been studied by observing the response of benthos to the onset of anoxic conditions in shelf seas (e.g. Boesch & Rabalais, 1991; Stachowitsch, 1991). By analogy with previous studies of benthic foraminifera and other organisms from modern dysoxic environments, the California Borderlands data set enables us to construct a descriptive model relating the response of DWAF morphogroups to dysaerobic conditions. Although our data set lack information for the whole range of oxygen concentrations, end-member faunas can be clearly defined (Figure 7).

In many shelf seas anoxia occurs seasonally as a result of enhanced export production. Initially, the increased flux of organic matter to the sea floor may have an enrichment effect on the benthic communities, and benthic biomass rapidly increases. In the California Borderlands, the change in macrofaunal communities is observed at oxygen levels of 0.5 ml/l. Below this level infaunal burrowers disappear and the benthic community becomes dominated by surface-feeding polychaetes (Fauchild & Jones, 1979). As the dissolved oxygen of bottom waters is depleted, the oxycline within the sediments emerges close to the sediment/water interface. This reduces habitat space for infaunal organisms and may cause mortality of the more sensitive macrofaunal organisms, such as echinoderms and crustaceans. At times when dissolved oxygen in bottom waters becomes seriously depleted, burrowing organisms use such as polychaetes and holothurians normally exhume themselves, seeking more oxygenated waters at the sediment surface (Stachowitsch, 1991). In the northern Adriatic, where the strong summer thermocline causes seasonal dysoxia at the sea floor, the microhabitat separation of benthic foraminifera is minimal or non-existent in summer (Jorissen *et al.*, 1992), and even the "deep infaunal" group is found restricted to the surficial layer of the sediment. With further oxygen depletion, eventually the benthic invertebrate community is completely decimated. However, in the absence of grazing pressure by predators the numbers of resistant foraminifera may rapidly increase (Douglas, 1987). Bernhard & Reimers (1991) found that foraminiferal numbers on the slope of the seasonally anoxic Santa Barbara Basin can reach one to two orders of magnitude higher than in well-oxygenated environments. As oxygen depletion continues, the redox discontinuity may emerge to the sediment surface, which stimulates the growth of

mat-forming chemotrophic bacteria. Below a critical oxygen level, the numbers of foraminifera begin to decline (the bottleneck case of Sjoerdsma & van der Zwaan, 1992). Jorissen *et al.*, (1992) reported low benthic foraminiferal standing stocks in the most severely dysoxic organic-rich areas of the northern Adriatic. It is now clear, however, that some species of benthic foraminifera can inhabit sediments with anoxic pore waters (Bernhard & Reimers, 1991) and will survive at least month-long periods of complete anoxia (Bernhard, 1993). Bacterial mats may serve as a food for infaunal foraminiferal detritivores, since some infaunal species are known to ingest bacteria (Goldstein & Corliss, 1989; Bernhard & Bowser, 1992).

Mortality of benthic invertebrates caused by anoxia is rapid, occurring in a matter of days, but recovery is slow (Stachowitsch, 1991). In areas such as the New York Bight where anoxia is not seasonal, but a rare occurrence, benthic macrofaunal communities had not recovered after two years (Boesch & Rabalais, 1991). However, where anoxia is seasonal, the benthic communities consist of populations of opportunistic species which quickly re-establish themselves after the return of oxygenated conditions (Boesch & Rosenberg, 1981). In the Adriatic where bottom water oxygenation improves in autumn, the living benthic foraminiferal populations are first dominated by infaunal taxa (Jorissen *et al.*, 1992).

Apparently, the infaunal detritivores are more tolerant to low oxygen conditions than the epifauna, and therefore are the first to benefit from the high availability of food once oxygen is no longer a limiting factor. As oxygenation improves further in winter, epifaunal taxa become established and the infauna can invade the deeper sediment layers.

A benthic community that experiences seasonal anoxia will be kept in an early stage of faunal succession because of the high frequency of mass mortality. This explains the occurrence of a DWAF community consisting of infaunal opportunistic species such as *Reophax* and *Psammosphera*, and the absence of tubular forms. Such a community bears a surprising resemblance to a DWAF assemblage described from the HEBBLE area off Nova Scotia (Kaminski, 1985), where frequent benthic storms cause disturbance to the benthic community. Regardless whether mortality is caused by substrate disturbance (in the case of the HEBBLE Area or in the recolonisation experiment in the Panama Basin) or by seasonal anoxia as in the California Borderland basins, the effect on benthic foraminiferal communities appears to be similar. Epifaunal and suspension-feeding morphogroups are at risk, and the living DWAF community is patchy and strongly dominated by opportunists with infaunal morphologies.

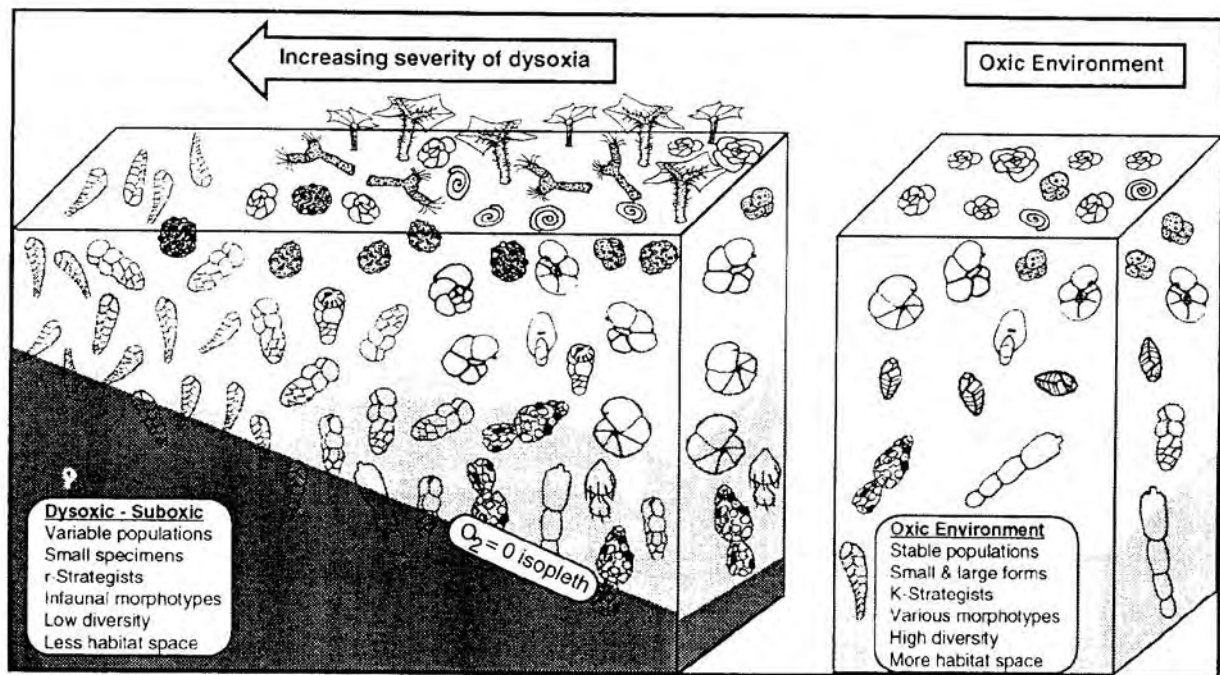


Figure 7. Conceptual morphogroup model relating the response of DWAF morphogroups to dysaerobic conditions in the California Borderland basins.

CONCLUSIONS

DWAF from seasonally dysaerobic environments off California are comprised mainly of opportunistic forms such as *Reophax* and *Psammosphaera*. The most severely dysaerobic stations in the San Pedro Basin are strongly dominated by a small, flattened, tapered "Textularia" interpreted as having a deep infaunal microhabitat. This faunal change occurs when bottom water oxygen values fall to 0.2 ml/l. In contrast, control stations from a well-oxygenated setting contain a variety of different morphogroups.

The finding of predominantly tapered, elongate DWAF morphotypes in dysaerobic environments agrees well with studies of the calcareous benthic foraminifera carried out by Douglas (1987).

ACKNOWLEDGEMENTS

The authors express their thanks to Dr. Lowell Stott for providing access to sample material and to Dr. Don Gorsline for chemical data. M.A.K. and A.B. were supported in part by the Deep-Water Benthic Forum Project, administered by W.A. Berggren at the Woods Hole Oceanographic Institution. A.E.L.H. acknowledges support of a research studentship from the Natural Environment Research Council. J.T. gratefully acknowledges support from a European Community TEMPUS Fellowship at University College London as well as grants from Stratigraphic Services International Ltd. and the Grzybowski Foundation. This is contribution number 45 of the Deep-Water Agglutinated Forum Project.

REFERENCES

- 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.) *Paleoecology, Biostratigraphy, Paleoceanography and Taxonomy of Agglutinated Foraminifera*. NATO ASI Series C 327, 661-694.
- Bernhard, J.M. 1986. Characteristic assemblages and morphologies of benthic foraminifera from anoxic, organic-rich deposits: Jurassic through Holocene. *Journal of Foraminiferal Research*, 16, 207-215.
- Bernhard, J.M. 1993. Experimental and field evidence of Antarctic foraminiferal tolerance to anoxia and hydrogen sulfide. *Marine Micropaleontology*, 20, 203-213.
- Bernhard, J.M. & Bowser, S.S. 1992. Bacterial biofilms as a trophic resource for certain benthic foraminifera. *Marine Ecology Progress Series*, 83, 263-272.
- Bernhard, J.M. & Reimers, C.E. 1991. Benthic foraminiferal population fluctuations related to anoxia: Santa Barbara Basin. *Biogeochemistry*, 15, 127-149.
- Boesch, D.F. & Rosenberg, R. 1981. Response to stress in marine benthic communities. In: Barrett, G.W. & Rosenberg, R. (Eds.) *Stress effects on Natural Ecosystems*. Wiley, New York, pp. 215-225.
- Boesch, D.F. & Rabalais, N.N. 1991. Effects of hypoxia on continental shelf benthos: comparisons between the New York Bight and the northern Gulf of Mexico. In: Tyson, R.V. & Pearson, T.H. (Eds.) *Modern and Ancient Continental Shelf Anoxia*. Geological Society Special Publication 58, 27-34.
- Corliss, B.H. 1985. Microhabitats of benthic foraminifera within deep-sea sediments: *Nature*, 314, 435-438.
- Corliss, B.H. & Chen, C. 1988. Morphotype patterns of Norwegian Sea deep-sea benthic foraminifera and ecological implications. *Geology*, 16, 716-719.
- DeLaca, T.E. 1986. The morphology and ecology of *Astraminina rara*. *Journal of Foraminiferal Research*, 16, 216-223.
- Douglas, R.G. 1987. Paleoecology of continental margin basins: a modern case history from the Borderland of southern California. In: Gorsline, D.S. (Ed.) *Deposition in active margin basins*. Pacific Section, SEPM, pp. 81-117.
- Gorsline, D.S. 1992. The geological setting of the Santa Monica and San Pedro Basins, California continental borderland. *Progress in Oceanography*, 30, 1-36.
- Hermelin, J.O.R. 1992. Variations in the benthic foraminiferal fauna of the Arabian Sea: a response to changes in upwelling intensity? In: Summerhayes, C.P., Prell, W.L., Emeis, K.C., *Upwelling Systems: Evolution since the Miocene*. Geological Society Special Publication, 64, 151-166.
- Hickey, B.M. 1992. Circulation over the Santa Monica - San Pedro Basin and shelf. *Progress in Oceanography*, 30, 37-115.
- Jorissen, F.J., Barmawidjaja, D.M., Puskaric, S. & Van der Zwaan, G.J. 1992. Vertical distribution of benthic foraminifera in the northern Adriatic Sea: The relation with the organic flux. *Marine Micropaleontology*, 19, 131-146.
- Kaiho, K. 1991. Global changes of Paleogene aerobic/anaerobic benthic foraminifera and deep-sea circulation. *Paleogeography, Palaeoclimatology, Palaeo-ecology*, 83, 65-85.
- Kaminski, M.A., Grassle, J.F. & Whitlatch, R.B. 1988. Life history and recolonization among agglutinated foraminifera in the Panama Basin. In: Gradstein, F.M. & Rögl, F., (eds.) *Proceedings of the 2nd International Workshop on Agglutinated Foraminifera*. *Abhandlungen der Geologischen Bundesanstalt, Wien*, 41, 229-244.
- Kuhnt, W., Moulade, M. & Kaminski, M.A. (in press). Oceanic events and evolution of Cretaceous abyssal foraminifera. Submitted to: Whatley, RC et al. (Eds.) *Proceedings of the "ODP and the Marine Biosphere" Conference, Aberystwyth, April 1994*.
- Leckie, R.M. 1989. A paleoceanographic model for the early evolutionary history of planktonic foraminifera. *Paleogeography, Paleoclimatology, Paleoecology*, 73, 107-138.
- Pisias, N.G. 1978. Paleoceanography of the Santa Barbara Basin during the last 8000 years. *Quaternary Research*, 10, 366-384.
- Sanders, H. 1968. Marine benthic diversity: a comparative study. *American Naturalist*, 102, 243-282.
- Schwabach, J.R. & Gorsline, D.S. 1985. Holocene sediment budgets for the basins of the California continental borderland. *Journal of Sedimentary Petrology*, 55, 829-842.
- Sen Gupta, B.K. & Machain-Castillo, M.L. 1993. Benthic foraminifera in oxygen-poor habitats. *Marine Micropaleontology*, 20, 183-201.
- Sjoerdsma, P.G. & van der Zwaan, G.J. 1992. Simulating the effect of changing organic flux and oxygen content on the distribution of benthic foraminifera. *Marine Micropaleontology*, 19, 163-180.
- Stachowitsch, M. 1991. Anoxia in the northern Adriatic Sea: rapid death, slow recovery. In: Tyson, R.V. & Pearson, T.H. (Eds.) *Modern and Ancient Continental Shelf Anoxia*. Geological Society Special Publication, 58, 119-129.
- Thunell, R., Sautter, L.R. 1992. Planktonic foraminiferal and stable isotopic indices of upwelling: a sediment trap study in the San Pedro Basin, Southern California Bight. In: Summerhayes, C.P., Prell, W.L., Emeis, K.C., *Upwelling Systems: Evolution since the Miocene*. Geological Society Special Publication, 64, 77-92.
- Tyson, R.V. & Pearson, T.H. 1991. Modern and ancient continental shelf anoxia: an overview. In: Tyson, R.V. & Pearson, T.H. (Eds.) *Modern and Ancient Continental Shelf Anoxia*. Geological Society Special Publication 58, 1-24.

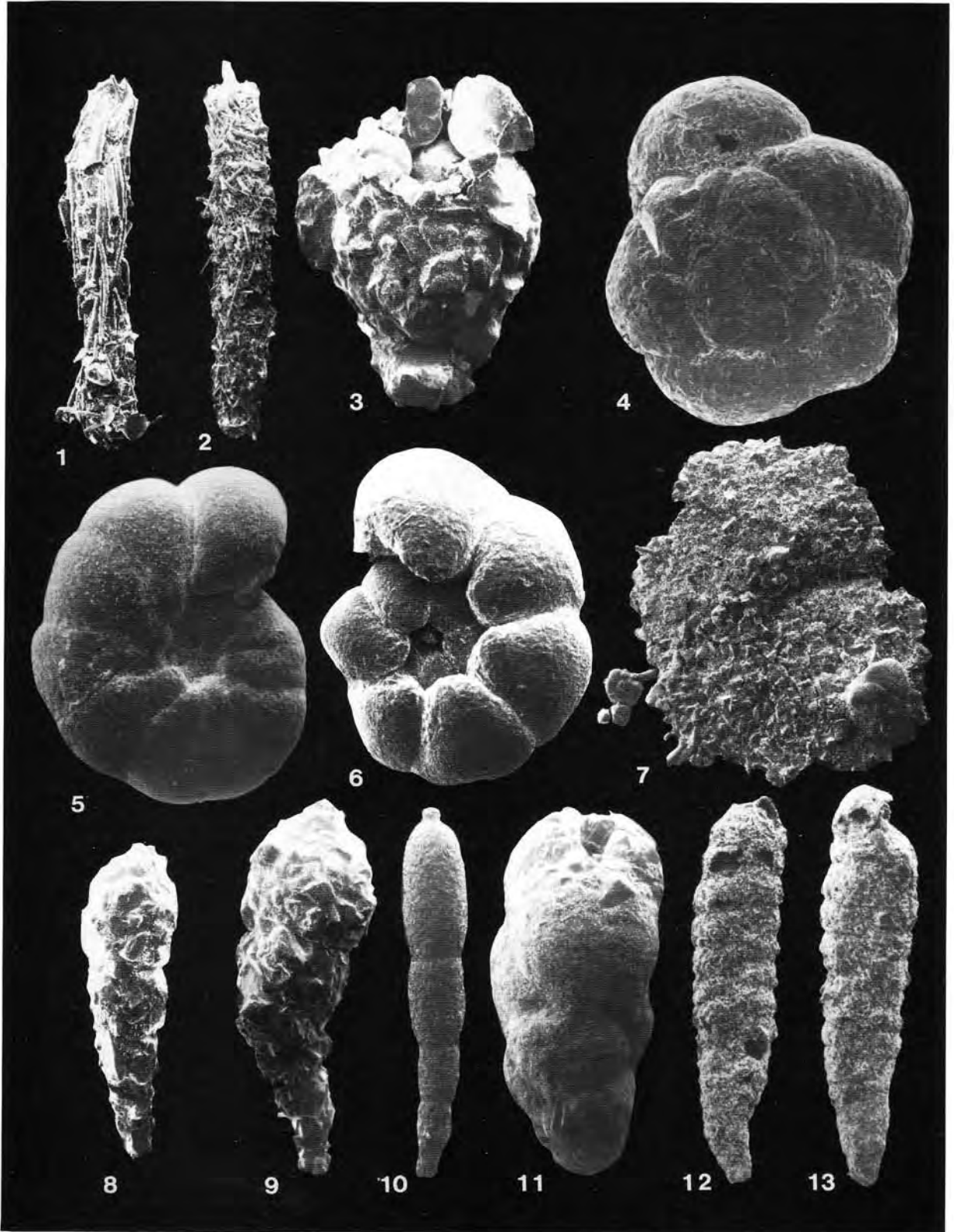


Plate 1. 1. *MarSSIPella* sp. x38. 2. *Rhizammina* sp., 24434-412, x20. 3. *Psammosphaera fusca* x30. 4. *Trochammina* sp. 22621-443, x150. 5. *Haplophragmoides canariensis* x60. 6. *Labrosphera wiesneri*, 22621-443, x55. 7. *Discammina compressa*, 24434-412, x30. 8. *Reophax excentricus*, 24432-427, x22. 9. *Reophax excentricus*, 24432-427, x16. 10. *Reophax dentaliniformis*, 24582-751, x18. 11. *Verneuillinulla?* sp., 24426-406, x38. 12-13. "*Textularia*" sp. 24436-372, x85.