UTRECHT MICROPALEONTOLOGICAL BULLETINS

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EDITOR

RECONSTRUCTION OF MARINE PALEOENVIRONMENTS

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RECONSTRUCTION OF MARINE PALEOENVIRONMENTS

Selection of papers presented at the meeting in Utrecht,
March 21–25, 1983

J. E. MEULENKAMP
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PREFACE

The international meeting on "Reconstruction of marine paleoenvironments; principles and methods" was held in Utrecht, the Netherlands, from March 21–25, 1983. It was organized by J. E. Meulenkamp with the assistance of other staff members of the Department of Stratigraphy and Micropaleontology of the State University of Utrecht. The meeting was sponsored by the Regional Committee on Mediterranean Neogene Stratigraphy of the I.U.G.S., by the International Nannoplankton Association and by the I.U.G.S. Working Group on the Paleogene/Neogene boundary.

The larger part of the programme consisted of talks by invited speakers from various disciplines of the earth sciences. Most of the invited speakers agreed to publish their contribution; the present U.M.B. volume includes 75% of the papers read during the plenary morning sessions.

The editing task was carried out with the assistance of G. J. van der Zwaan, W. J. Zachariasse, A. J. T. Romein and C. W. Drooger. Most of the figures were drawn or re-drawn by A. van Doorn, J. T. van Hinte and P. Hoonhout. Proof reading was carried out in Utrecht by a large group of department members.

Financial support from the Netherlands Ministry of Education (The Hague) enabled us to offer this bulletin at a moderate price.

INTRODUCTION

JOHAN E. MEULENKAMP

At the last, seventh International Congress on the Mediterranean Neogene (Athens, 1979) it was felt that future research activities of the Regional Committee on Mediterranean Neogene Stratigraphy (R.C.M.N.S.) should concentrate on ecostratigraphy. In the Mediterranean area refined biostratigraphic scales are available now, for instance through the achievements of I.G.C.P. Projects 74/25, Stratigraphic correlation of the Tethys – Paratethys Neogene, and 75/1, Accuracy in time. It is a logical, next step to attempt to understand these scales in terms of changes in magnitude of physical, chemical and biological processes of regional and global extent.

Following the definition given by the late Anders Martinsson in his 1973 Lethaia paper, ecostratigraphy implies "the construction of timeplanes with the greatest possible precision and frequency through environmentally-defined stratigraphic units". It also reads that this requires "a far-reaching systematical and ecological knowledge of the organisms and communities involved". Both statements illustrate the need to evaluate the principles of, and to develop the methods applied in, paleoecological and paleoenvironmental interpretations.

Paleoenvironmental interpretations based on the study of marine microfossils follow two different lines of approach, as can be detected from the literature. The first relies on the principle of uniformitarianism and the methods applied basically reflect a straightforward transfer of what is known about Recent ecology to the fossil record. Many conclusions on paleoclimatology and paleobathymetry express this line of approach. The other line consists of studies in which it is tried to reconstruct preference and tolerance patterns of fossil species and/or groups of species independent of Recent data. For this purpose fossil distribution patterns are compared with reconstructions of paleoenvironmental conditions, which in turn are based on the analyses of physical/chemical sediment properties and on paleogeography.

Both lines of approach may lead to similar conclusions on the life-habitat of marine organisms recovered from fossil strata, but often they appear to provide conflicting evidence, the more so if we go down in the historical record. It is evident that actualistic data alone cannot offer unambiguous paleoenvironmental interpretations.

Recent advances in the application of isotope chemistry to (paleo)environmental analyses have resulted in a remarkable progress in paleoceanography and paleoclimatology. The opportunities offered by isotope chemistry to understand the ecology and to unravel paleoecological aspects of marine micro-organisms, disclose an enormous field of research. However, there are still many problems to be solved, for instance those concerning the interpretation of oxygen isotope data in terms of "absolute" temperature and salinity, those related to the carbon isotope chemistry of marine organisms, and the complex problem known as "vital effect".

The composition of clay minerals in marine sediments basically reflects the type of paleosoils on neighbouring landmasses, which, in turn, is a measure for paleoclimatic conditions. Thus clay mineralogy may be an "independent" tool in paleoclimatic interpretations of marine sequences. Occasionally, however, it appears difficult to discriminate between climate-induced changes in the composition of clay mineral associations and the effects caused by tectonic processes. To date we are only at the beginning of unravelling in detail the possible common response of clay mineral associations and of marine organisms to paleoenvironmental processes.

It is beyond doubt that progress in paleoecology and in paleoenvironment-directed research will largely depend on co-variate analyses of different groups of microfossils and on a more profound calibration of the results obtained by physical, chemical and paleontological methods. With this in mind we considered it appropriate to organize the Utrecht meeting for a review of the "state of the art". We feel confident that the selection of papers brought together in this volume will not only be of interest to those involved in Mediterranean research, but that it equally will serve as a stimulus of other research in paleoecology, paleoclimatology, paleoceanography, and, in particular, in ecostratigraphy of the Late Cenozoic.

THE GLOBAL SIGNIFICANCE OF REGIONAL MEDITERRANEAN NEOGENE PALEOENVIRONMENTAL STUDIES

WILLIAM W. HAY

ABSTRACT

There is growing evidence that prior to the Oligocene the deep waters of the ocean were warm rather than cold as they are at present. Warm saline bottom water formation takes place in marginal and shelf seas in arid regions. Such downwelling waters contain only about half as much dissolved oxygen as modern deep waters formed in the polar regions. The Mediterranean and Red Seas are modern analogs for pre-Oligocene oceans.

INTRODUCTION

It has recently become apparent that the structure of the modern ocean may be a poor analog for the oceans of Eocene and earlier times. The two major aspects of oceanic circulation are the wind driven surface circulation, which is strongly influenced by changes in both wind patterns and distributions of land and sea, and the thermohaline circulation which affects the deep water of the oceans. Changes in the surface currents are important in controlling the paleobiogeographic distributions of organisms both in the sea and on the adjacent land areas, but changes in the thermohaline circulation affect the global distribution of nutrients, oxygen, and carbon dioxide in the deep waters of the oceans. It is the thermohaline circulation that controls productivity in the surface waters, oxidation or preservation of organic matter in deep sea sediments, and dissolution of carbonate in the deep sea.

It has long been realized that changes in the surface currents are an inherent part of paleogeographic interpretation, but although discussed by Chamberlin in 1906, it is only in the past few years that the broad geologic significance of thermohaline circulation patterns radically different from those of the present have become evident and explored by a series of papers: Fischer and Arthur (1977), Berry and Wilde (1978), Kraus et al. (1978), Arthur and Natland (1979), Arthur and Kelts (1979), Thierstein (1979), Peterson (1979), Holser et al. (1980), Weissert (1981), Peterson et al. (1981), Southam et al. (1981), Brass et al. (1982), Wilde and Berry (1982), Southam et al. (1982), Southam et al. (in press), and Hay (in press). The Mediterranean and Red Seas are the only modern analogs for ancient oceans, hence paleoenvironmental studies of these areas have global significance for the interpretation of pre-Neogene deposits.

The structure of the modern ocean is dominated by cold deep waters which form about 95% of the total mass. The warm surface waters which contain all except the polar surface currents are only about 5% of the ocean mass. At present the deep waters are rich in nutrients (PO_4, NO_3, SiO_2, and in greater depths, O_2). The deep waters are in motion; early modelling efforts (Broecker, 1971, 1974) used a downwelling/upwelling rate equivalent to 2 m per year over the entire ocean to describe mixing of the surface and deep reservoirs in a two-box model. Assuming an average depth of 3200 m this gave a "residence time" of 1600 years for the deep water. In the same models, the river input of fresh water to the ocean is equivalent to 10 cm per year over the entire ocean. The concentration of the principal limiting nutrient, phosphorus, in river water, surface ocean water and deep ocean water is approximately 45, 10 and 225 p.p.b. respectively.

The surface ocean water is depleted of nutrients by the organisms growing there. It is evident that the main supply of nutrients to the surface ocean waters is from upwelling of deep waters rather than river inputs. In spite of their naive nature, the dynamics of simple two-box models following these assumptions have yielded insight into the basics of behavior of the dynamic system linking physical oceanographic mixing processes, ocean chemistry, and biological productivity (Southam and Hay, 1976, 1977).

The real ocean is much more complex than the simple two-box models. An initial attempt to explore this complexity was the three-layer model proposed by Wyrtki (1962) to investigate the oxygen minimum zone, which, of course, cannot be represented in two-box models.

A new evaluation of rates of thermohaline mixing in the ocean has been presented by Stuiver et al. (1983), based on C^{14} data from a large number of stations in the ocean as part of the GEOSECS (Geochemical Sections) program. The new residence times for deep water in the major ocean basins are only about one-third what Broecker, and Southam and Hay had assumed. Consequently, the rate of return of deep water through upwelling is more rapid than had been assumed. Figure 1 indicates the fluxes, residence times and upwelling rates determined by Stuiver et al. (1983).

The system is even more complex than these models would indicate because the deep water is formed by creation of dense water at several sites. The Atlantic has the largest number of sources: the western side of the Norwegian Sea, off SE Greenland, and the Labrador Sea are all sources in the north; the Weddell Sea in the Antarctic region is the main southern source. The Bellingshausen and Ross Seas are other possible sources of deep water formation in the Antarctic. In addition to these sources of cold deep water, the Mediterranean outflow of warm saline water is a significant source of deep water in the northern Atlantic. Water from each of these sources forms at a different rate, and each source has its own characteristics with regard to biolimiting chemicals. These peculiarities have been discussed by Broecker (1983), and illustrated by the oceanic sections showing temperature, salinity, density, and concentrations of certain elements in the GEOSECS Atlantic Expedition atlas (Bainbridge, no date).

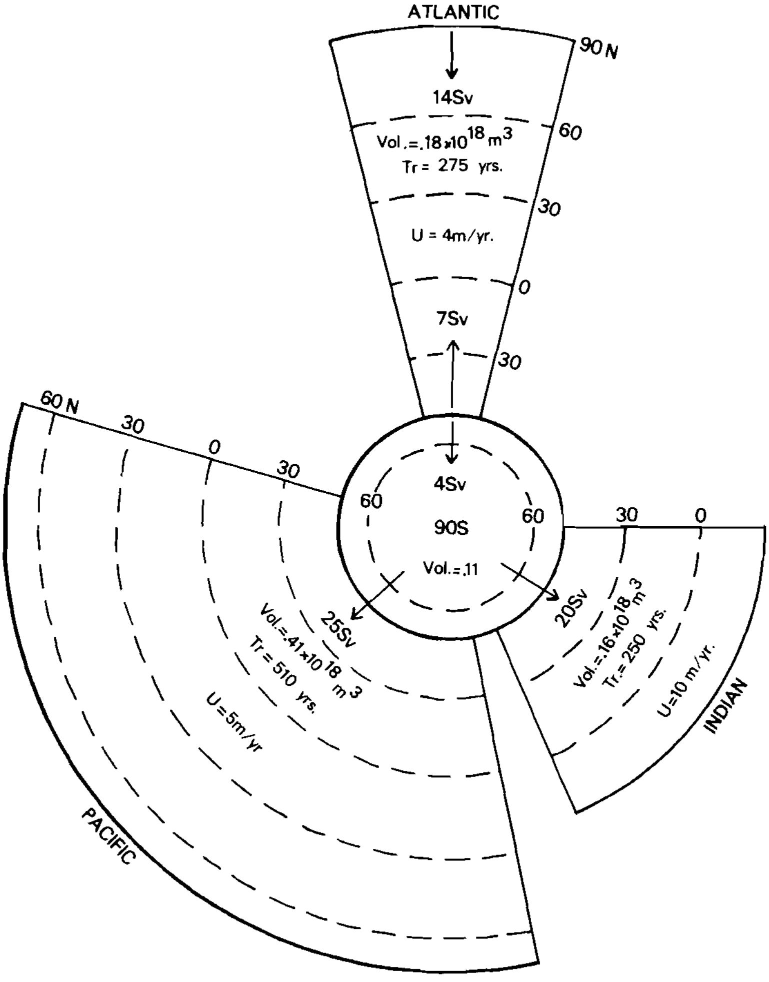


Fig. 1 Volumes (V) in 10^{18} m^3, fluxes of deep water in Sverdrups (Sv = 10^6 m^3/sec), residence times (Tr) in years, and basinwide upwelling rates (U) in meters per year for the Atlantic, Indian, and Pacific oceans north of 50°S and the circumpolar ocean south of 50°S (after Stuiver et al., 1983).

Some of the data for the GEOSECS western Atlantic N-S section are shown in simplified form in figure 2. The major deep water masses are indicated on the salinity section. Two wedges of water having Antarctic sources extend north. The lowest is Antarctic Bottom Water (AABW) with its source in the Weddell Sea. The upper wedge is Antarctic Intermediate Water (AAIW), formed in the region of the Antarctic convergence; it is much less dense. Extending south from the Norwegian-Greenland sea is a thick wedge of

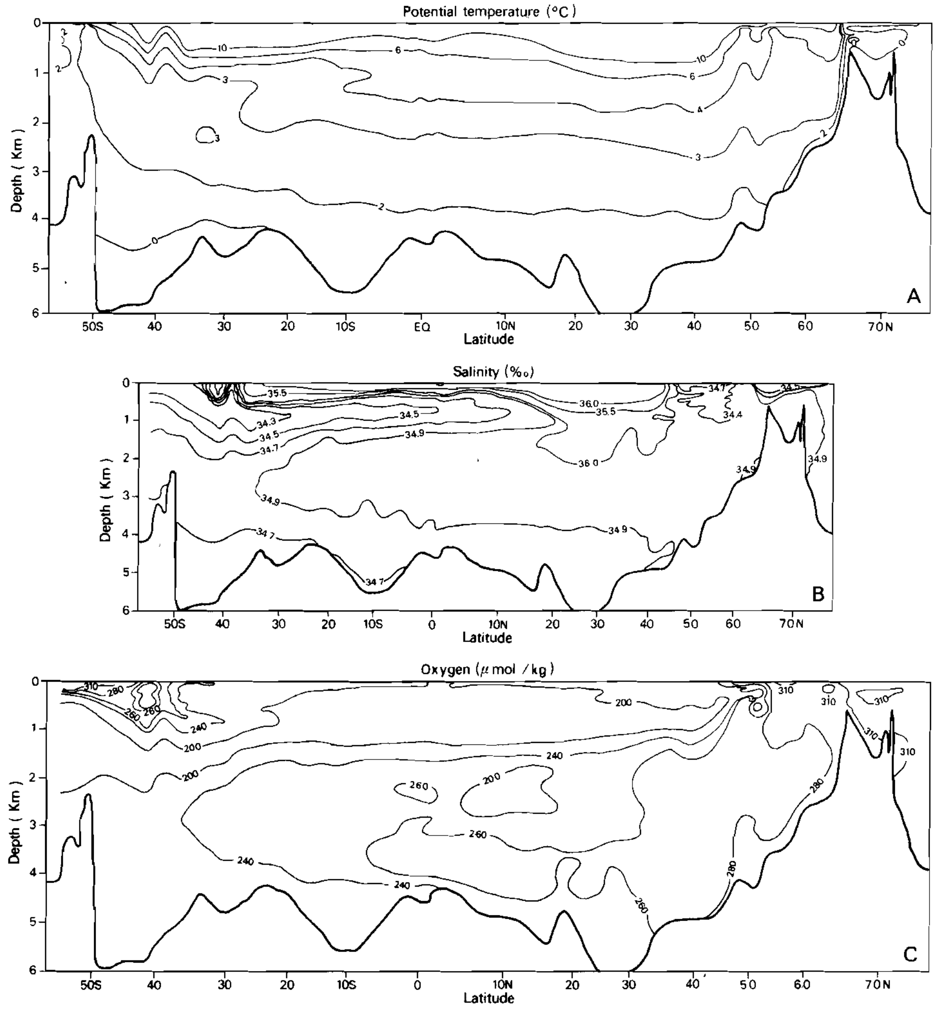
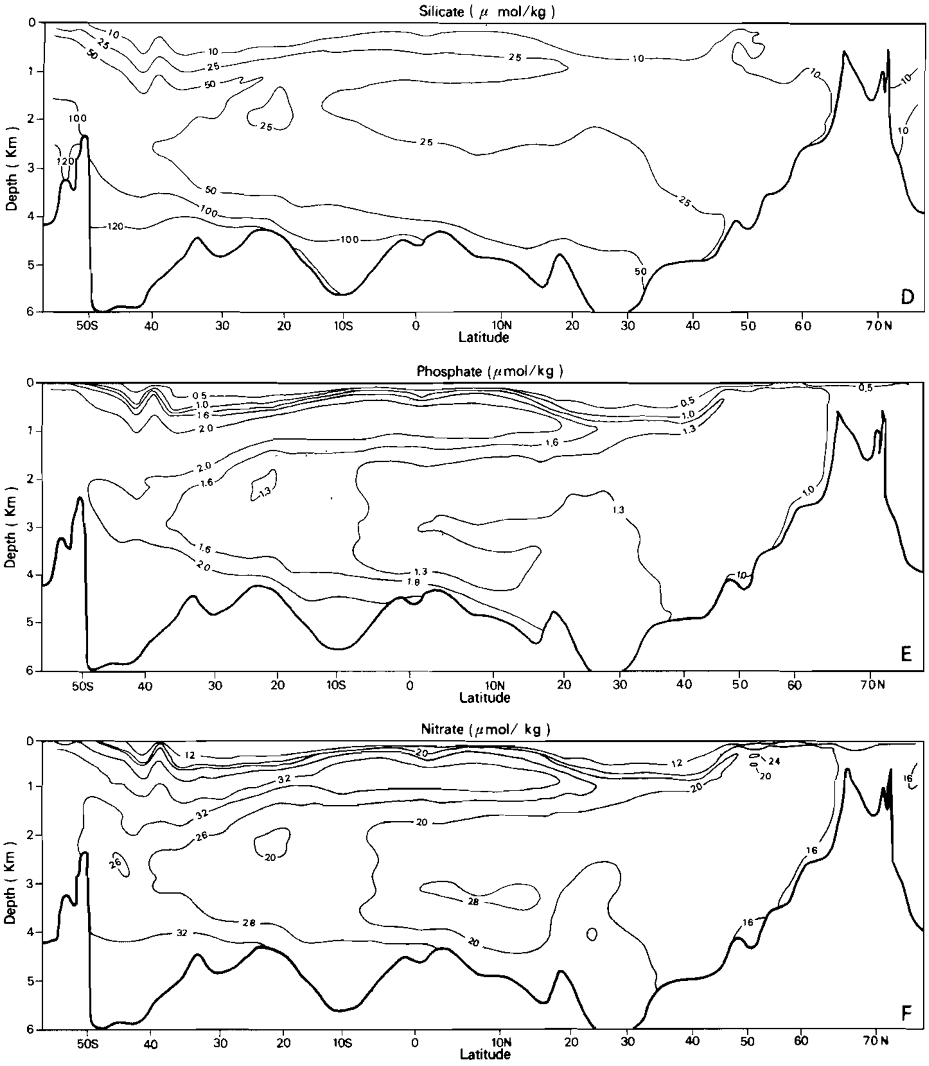


Fig. 2 Simplified N – S sections of the western Atlantic after Bainbridge (no date). A. Potential temperature; B. Salinity; C. Oxygen; D. Silicate; E. Phosphate; F. Nitrate.

North Atlantic Deep Water (NADW). The differences between these major Atlantic water masses are evident from inspection of figure 2.

Both Antarctic water masses are rich in phosphate and nitrate, but AAIW is depleted in silica while AABW is enriched in silica. NADW is relatively O_2 rich but is depleted in phosphate, nitrate and silica. Each of these water mass sources has different characteristics, depending on the nature of the surface water at each of the source sites.



The downwelling of surface water to form deep water at specific sites is only half of the cycling process. The deep water is returned to the surface through mixing and upwelling. The general rate of upwelling calculated from the data of Stuiver et al. (1983), exclusive of local turnover in the Antarctic circumpolar ocean, is equivalent to 5.8 m of water over all of the oceans

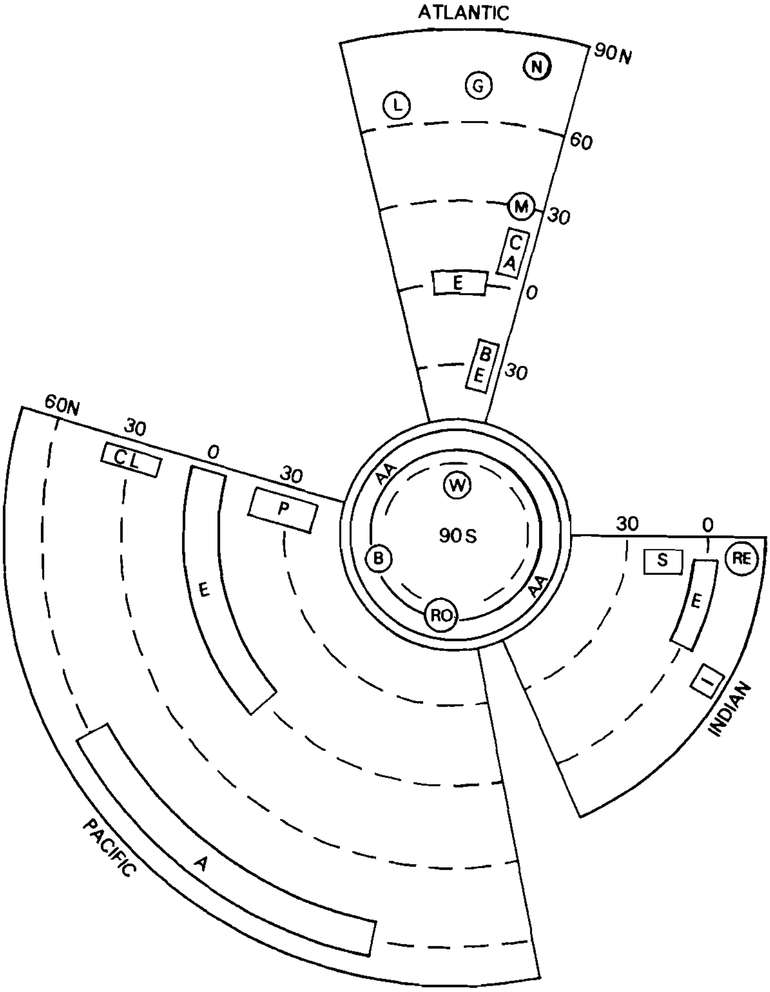


Fig. 3 Sites of formation of deep water and sites of upwelling. Deep water formation sites: N = Norwegian-Greenland Sea, G = off SE Greenland, L = Labrador Sea, W = Weddell Sea, B = Bellingshausen Sea, RO = Ross Sea, M = Mediterranean Sea (warm salty water), RE = Red Sea (warm salty water). Major sites of upwelling: E = Equatorial divergence, A = Subarctic divergence (Pacific), AA = Antarctic divergence, CL = California Current, P = Peru Current, CA = Canary Current, BE = Benguela Current, S = Somali Current, I = Southwest India.

north of 50° S each year, but water is not returned to the surface everywhere at the same rate (see fig. 1).

The deep ocean water masses, which have their sources mostly peripheral to the Atlantic, become homogenized and mix as they become more and more distant from their source, as shown in figure 3. Return to the surface water is through general basinwide vertical eddy diffusion processes and through concentrated vertical flow at specific upwelling sites. Upwelling occurs as an active process at sites in the open ocean where the winds cause oceanic divergences, and along continental margins where winds parallel to the shore induce Ekman transport of the water offshore. At present the oceanic upwelling systems are equatorial, along the eastern margins of the ocean basins at 20°–30° N and S, and in the subpolar divergence regions at 60° N and S, although in the northern hemisphere the subpolar upwelling is limited to the Pacific. The most active sites of upwelling on continental margins are along the eastern margins of the ocean basins in the zones of the easterly trade winds, with the upwelling intensified where the winds parallel the shoreline. The relative proportions of deep water upwelled at continental margins and in the open ocean, and the proportion of deep water returned to the surface through general vertical eddy diffusion processes are unknown.

THE "MESOZOIC" (PRE-OLIGOCENE) OCEAN

Before the Oligocene cooling of the oceans' deep water, discovered by Emiliani (1961) and subsequently documented in a series of papers (Douglas and Savin, 1971, 1973, 1975; Kennett et al., 1974; Shackleton and Kennett, 1974; Savin et al., 1975; Boersma and Shackleton, 1977a, b; van Andel et al., 1977; Savin, 1977, 1982; Savin and Yeh, 1981) the oceans were very different. Because this different ocean was characteristic of the world at least through the interval Triassic – Eocene it is referred to hereafter as the Mesozoic ocean. Until very recently there were few data to indicate any thing other than generally warmer bottom water temperatures, and for the Mesozoic such data were exceedingly sparse because pristine benthic foraminiferal tests which have not undergone recrystallization and oxygen isotope reequilibration are very rare.

Saltzman et al. (1981), Saltzman and Barron (1982) and Barron et al. (in press) have found that the shells of *Inoceramus* are especially resistant to recrystallization, and commonly retain their original isotopic composition. They have published the first data which give insight into the thermal structure of the Mesozoic ocean; figure 4 compares a modern and Cretaceous cross section of the South Atlantic based on their data.

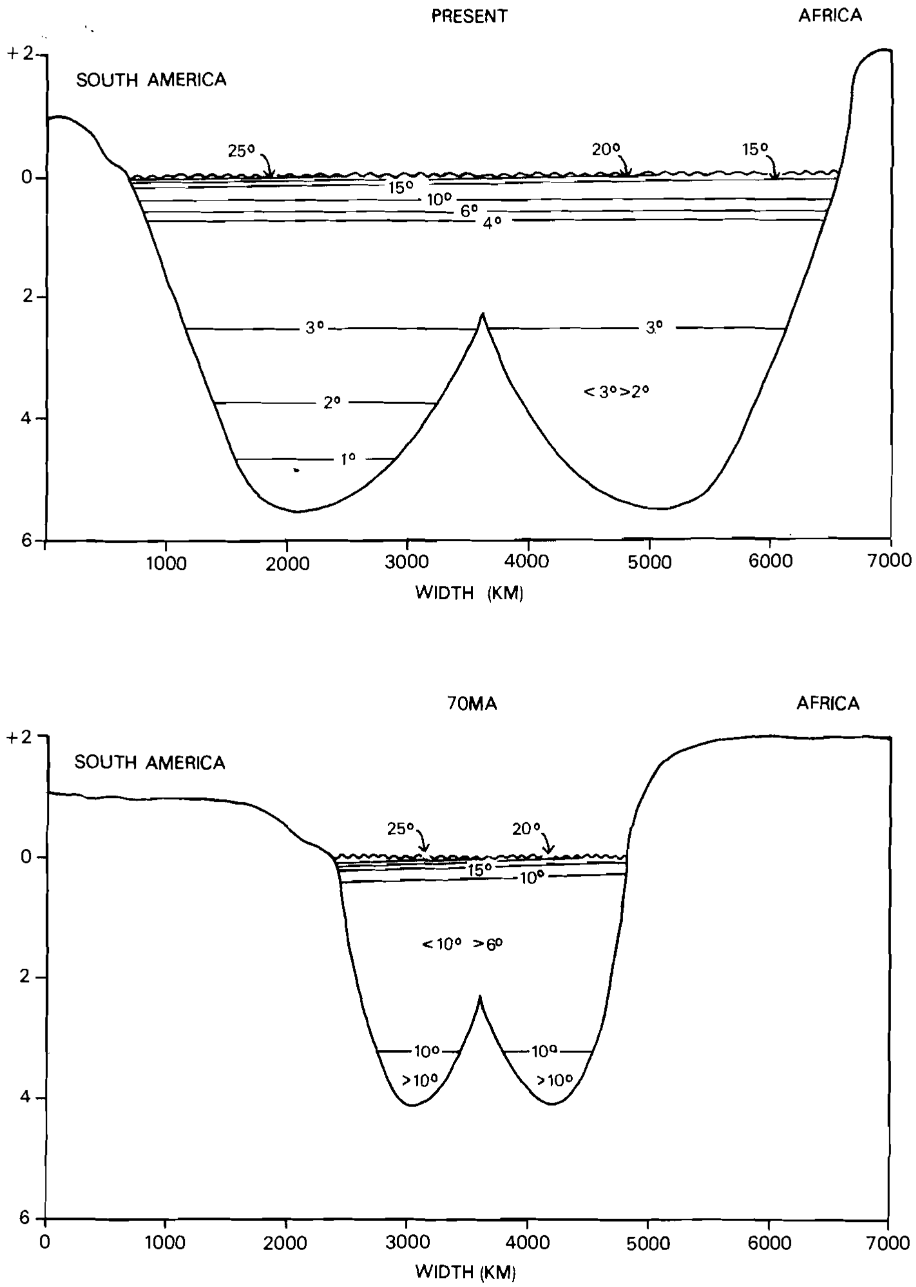


Fig. 4 Comparison of modern and Late Cretaceous E–W sections across the South Atlantic in the Brazil and Angola Basins showing the thermal structure of the water. Modern section after Gorshkov, 1977; Cretaceous section after Saltzman and Barron, 1982.

Fundamental to understanding the structure of the Mesozoic Ocean is knowledge of how deep water may be formed. Figure 5 shows the relationships between temperature, salinity, density, and oxygen content. It is evident that density is most sensitive to temperature changes in warmer, less saline waters. As the waters become more saline or cooler, density is little affected by temperature but is very sensitive to changes in salinity. For surface water to sink it must become denser than the underlying water, and for this to happen the surface water must be isolated in such a way that it can become cooler or more saline or both. Interaction with the atmosphere

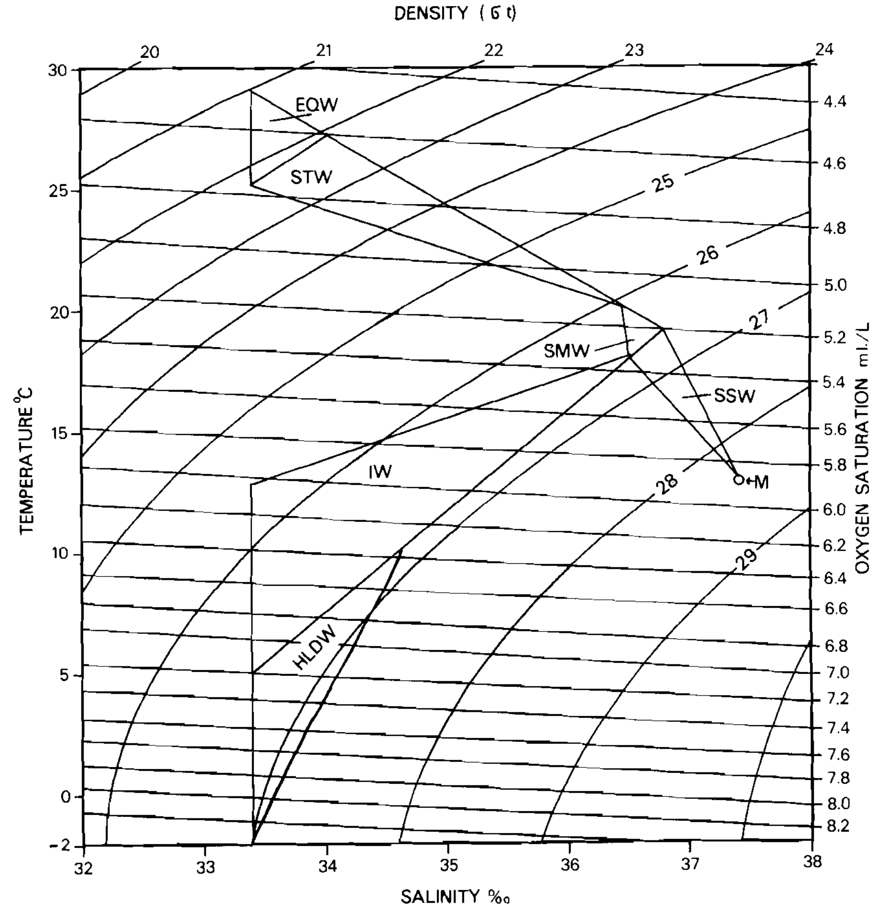


Fig. 5 Relationships between salinity, temperature, density, and oxygen saturation, with major modern masses indicated (after Wilde and Berry, 1982). EQW = Equatorial water, STW = Subtropical water, SMW = Salinity maximum water (open ocean), SSW = Shelf sea water, M = Mediterranean water, IW = Intermediate water, HLDW = High latitude deep water.

can produce either of these effects. Chilling of the water by very cold air can cause it to sink just as can increase in salinity of the ocean water due to formation of relatively less salty sea ice. Increase in salinity due to evaporation can also produce dense water which will sink. It is obvious that the shallower the sea and the more isolated it is from the main body of the ocean, the more likely it becomes that water will be differentiated as a distinct water mass. Hence, the sites of deep water formation are due to geographic accidents and may not be readily apparent in our present rudimentary state of knowledge of paleogeography.

The dense water formed by ocean – atmosphere interaction at the surface will sink as a negatively "buoyant plume" in the terminology of Peterson (1979). Whether the dense water will become oceanic deep water depends on the buoyancy flux, which is the product of the excess of density of the water in the plume over the density of the surrounding ocean water and the rate at which the dense water is produced at the surface (Kraus et al., 1978; Peterson, 1979; Peterson et al., 1981; Brass et al., 1982). As Peterson (1979) has demonstrated, there is a very delicate balance between competing dense water plumes, and the plume which has the higher buoyancy flux fills the deep ocean. The competition between plumes from different Atlantic sources is apparent in figure 2.

At the present time the densest surface water in the world forms in the eastern Mediterranean. The dense Mediterranean outflow in the bottom of the Straits of Gibraltar flows as a density plume into the Atlantic, entraining the surrounding waters as it sinks. At present the volume of the outflow of Mediterranean water is about 1 Sverdrup, too small to permit it to become the deep water of the Atlantic; it does not have an adequate buoyancy flux. By the time the Mediterranean plume has reached 1500 m depth it has entrained so much lighter water that it flows out horizontally, but it is still a distinctive water mass which can be traced over a broad area of the North Atlantic. Kraus et al. (1978) estimated that if the volume outflow of the Mediterranean was increased by a factor of three it would achieve a buoyancy flux adequate to become the deep water of at least part of the Atlantic.

In the Mesozoic, formation of dense water is likely to have taken place in shallow marginal seas in the arid zone, where increase in salinity of the water could make it much denser than that of the adjacent ocean. The topographic relief of the land to the windward of the shelf sea may be important in enhancing the evaporative capacity of the air (Hay et al., 1982). Obvious sites of deep water formation might be basins in which evaporites but not bittern salts occur, indicating reflux of brine to the ocean (Arthur and Kelts, 1979; Holser et al., 1980; Arthur and Natland, 1979). However, it is apparent that the largest buoyancy flux will occur when hypersaline waters are formed and refluxed just before sulfates and other salts are precipitated. It will also be apparent that sites of fresh water input to the ocean are a critical factor, freshening the surface waters and preventing dense water formation (Hay, in press).

Buoyancy plumes may have a short life, and may not operate continuously. Deep water formation in the Labrador Sea apparently stopped for much of the decade of the 1970's (Rooth, in press) probably due to freshening of the surface waters. On longer time scales, buoyancy plumes are delicately balanced, and their relative strengths can be expected to vary with local and global climatic variations. Mesozoic buoyancy plumes are likely to have had lower buoyancy fluxes than the present polar plumes, and to have been very delicately balanced. They could exist only because there were no strong polar sources. It is likely that in the Mesozoic oceans there were many more competing sources than today and consequently that there was more local differentiation of the bottom waters. Many individual oceanic basins may have had local bottom water sources.

The chemistry of Mesozoic warm saline bottom waters was significantly different from modern deep waters in that the warm saline waters had initial low O_2 and CO_2 contents, but were relatively rich in PO_4 and NO_3 as are modern deep waters. Dissolved SiO_2 should have been greater because of generally higher SiO_2 availability due to extensive tropical weathering (Hay and Southam, 1977).

The motion of the warm saline bottom waters formed in the arid regions near 30° N and S would have been governed by the principles of baroclinic and geostrophic flow and the coriolis effect. In each hemisphere they would form currents flowing poleward along the eastern margins of the basins. This is in contrast to the present situation where waters formed in the polar regions flow equatorward along the western sides of the basins. There would be a tendency for upwelling to occur in the ice free polar regions, particularly the Arctic where easterly winds would promote upwelling around the margin of the Arctic basin. The probability of this form of circulation is further suggested by recent climate modelling studies of the Cretaceous by Thompson and Barron (1981), Barron et al. (1981), and Barron (1981, 1983).

It is widely assumed that the episodes of anoxia in the ocean basins during the Mesozoic must have been the result of slower thermohaline circulation. The coupled oxygen, carbon, phosphorus system modelled by Southam et al. (1982, and in press) is a further development of Wyrtki's (1962) three-layer model for the oxygen minimum. It indicates that because of the interactions within the system, for thermohaline circulation scenarios involving warm saline bottom water, it is a state of more vigorous circulation that is more likely to become anoxic.

IMPORTANCE OF THE NEOGENE MEDITERRANEAN AND RED SEAS

The Mediterranean and Red Seas are the only parts of the world ocean which behave in a "Mesozoic way". These seas are close analogs, but differ from those of the Mesozoic in several minor ways:

1) Salinity of the world ocean was higher in the Mesozoic; salt extractions associated with continental rifting have reduced oceanic salinity by perhaps 20% (Holser et al., 1978; Southam and Hay, 1982), and produced a number of unique changes (Arthur and Kelts, 1979).

2) General global temperatures were higher; in particular, polar temperatures are thought to have been much warmer than at present. If the poles were ice free, the mean annual temperature there must have been above 0°C.

3) The Ca/Mg ratio of the ocean was probably different; hydrothermal flow through the mid-ocean ridge system related to breakup of Pangaea and sea floor spreading consumes Mg and releases Ca. At the present time the river input of Mg is approximately equal to that consumed in the mid-ocean ridge system.

4) Other things being equal, a warmer Mesozoic ocean would have held less CO_2, and the atmospheric content of CO_2 can be expected to have been significantly higher.

Despite these minor differences, the Mediterranean and Red Seas offer promising analogs to the Mesozoic Ocean. They demonstrate much more rapid cycling than the modern ocean, and show that with salinity-driven thermohaline circulation sites of deep water formation and of upwelling need not be far apart. The Mediterranean has demonstrated a capacity for the development of periodic anoxia, as discussed by Williams et al. (1978), Williams and Thunnell (1979), and Cita and Grignani (1982). We need to know much more about the oceanography, micropaleontology, and sedimentology of the Mediterranean and Red Seas in order to understand what we observe in ancient marine deposits.

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RECONSTRUCTION OF MEDITERRANEAN LATE CENOZOIC HYDROGRAPHY BY MEANS OF CARBON ISOTOPE ANALYSES

COLETTE VERGNAUD-GRAZZINI

ABSTRACT

A tentative reconstruction of the Late Cenozoic hydrography of the Mediterranean is proposed, which is based on carbon isotope analyses planktonic and benthic foraminiferal carbonate. A Late Burdigalian tectonic event caused the closure of the connections with the Indo-Pacific. From that time onward the Mediterranean circulation patterns underwent repeated, fundamental changes, which were closely related to the climatic evolution and to tectonic processes shaping the geometry of the basin. It seems unlikely that the Late Cenozoic flux of Mediterranean waters was sufficiently high to have been of influence on the formation of NADW.

INTRODUCTION

Variations in the composition of carbon isotopes of planktonic and benthic foraminiferal carbonate have proved to be a useful tool in the reconstruction of the paleohydrography of the Atlantic, the Pacific and the Indian Oceans. Little is known, however, about the evolution of the hydrography of the Mediterranean and about the exchanges between Mediterranean and Atlantic watermasses since Middle Miocene time. Hence, speculations on the contribution of the Mediterranean outflow to the formation of North-Atlantic Deep Water (Reid, 1979), or on the effects of eustatic sea-level fluctuations and/or tectonics on the inflow – outflow balance between the Mediterranean and the Atlantic may not corroborate with the paleohydrological evidence inferred from the $\delta^{18}O$ and $\delta^{13}C$ records of Mediterranean foraminifera.

It is evident that Mediterranean watermasses have been strongly affected by global climatic changes and by tectonically-controlled paleogeographic reorganisations which have occurred since the late Early Miocene. Such changes are in part reflected by the $\delta^{18}O$ isotopic record; additional information may be obtained from $\delta^{13}C$ variations in benthic and planktonic foraminiferal calcite. Mainly on the basis of the carbon isotope record it will be tried in this contribution to arrive at a tentative reconstruction of the Late Cenozoic hydrography of the Mediterranean, in particular with respect to the Middle Miocene, the Early Messinian, the Early Pliocene and the Late Quaternary.

PRINCIPLES OF CARBON ISOTOPE CHEMISTRY

Amongst the nutrient-related tracers, only the $\delta^{13}C$ of total dissolved inorganic carbon (ΣCO_2) can be recorded in an authigenic carbonate precipitate (Kroöpnick et al., 1972; Williams et al., 1977). In the equation

$$\Sigma CO_2 = [CO_2] + [HCO_3^-] + [CO_3^{--}] + [H_2CO_3]$$

it may be assumed that dissolved bicarbonate is the major component of ΣCO_2 in sea water. Therefore, the $\delta^{13}C$ of the ΣCO_2 approximates the $\delta^{13}C$ of bicarbonate and, as a consequence, that of calcite. The ^{13}C values of calcites precipitating in isotopic equilibrium with the acqueous carbon reservoir can be calculated by means of the equation (Emrich et al., 1977)

$$\delta^{13}C_{\text{equil. CaCO}_3} = \delta^{13}C_{\text{dissolved bicarbonate}} + 1.85 + 0.035\ (T - 20),$$

in which T is the water temperature in °C.

Craig (1970), Kroopnick (1971) and Duplessy (1972) demonstrated that the carbon isotope composition of the total dissolved inorganic carbon (ΣCO_2) can be regarded as a valuable marine hydrographic tracer. Natural variations in the $\delta^{13}C$ of the marine ΣCO_2 can mainly be attributed to the effects of two processes. One is linked to the apparent oxygen utilisation (AOU), which, in its turn, is related to the progressive oxydation of organic matter. The second process concerns changes in the volumes of exchangeable CO_2 reservoirs.

Apparent oxygen utilisation

The $\delta^{13}C$ values of the ΣCO_2 in the open ocean display a depth gradient (see fig. 1), similar to those of phosphate, nitrate, and apparent oxygen

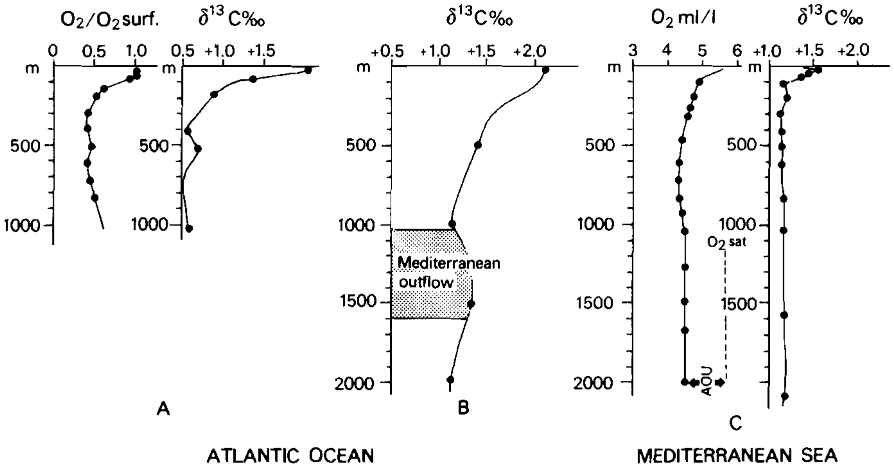

Fig. 1 Oxygen content and $\delta^{13}C$ profiles at three stations. A) Atlantis Station, Atlantic Ocean; B) Charcot Station, west of Gibraltar; C) Korotneff Station, Ligurian Sea.

utilisation. Increasing oxidation of organic matter with increasing depth causes an increase of the concentration of the ΣCO_2, nitrate and phosphate, and a decrease of the concentration of dissolved O_2 and of the $\delta^{13}C$ of the ΣCO_2. In deep waters longer residence times favour the addition of $\delta^{13}C$ depleted carbon to the dissolved bicarbonate by the oxidation of organic matter and by the dissolution of carbonate. This accounts for the relation between the residence time of deep watermasses and the $\delta^{13}C$ values of the ΣCO_2: the greater the residence time, the lower the $\delta^{13}C$ of the ΣCO_2.

Changes in the volumes of exchangeable CO_2 reservoirs

Each CO_2 reservoir has its characteristic carbon isotope composition; the most important reservoirs are atmospheric CO_2 ($\delta^{13}C \simeq - 7^0/_{00}$), marine bicarbonate ($\delta^{13}C \simeq + 2^0/_{00}$), fossil carbonate on land, organic carbon in marine sediments, carbon in the continental and in the marine biomasses, fossil organic carbon on land, and volcanic gases. Since exchange of CO_2 takes place between these reservoirs, it can be expected that changes in one reservoir cause changes in another. For instance, a change in the volume of the marine organic carbon reservoir ($\delta^{13}C \simeq - 20^0/_{00}$) relative to that of the terrestrial organic carbon reservoir ($\delta^{13}C \simeq - 25^0/_{00}$) may produce an important shift in $\delta^{13}C$ values (Shackleton, 1977). Alternatively, Broecker (1982) argued that the $0.7^0/_{00}$ decrease in $\delta^{13}C$ values of marine carbonates during the last glacial episode should be explained in terms of the transfer of organic carbon from the continental shelf towards the deep sea.

The exchange between dissolved CO_2 in surface waters and the atmospheric CO_2 reservoir varies with latitude. This is due to the effect temperature has on the solubility of CO_2, and it accounts for the decrease of the $\delta^{13}C$ of the ΣCO_2 from low to high latitudes. The $\delta^{13}C$ of the surface water ΣCO_2 near continents is also affected by runoff, which brings meteoric waters into the basin, waters that are enriched in compounds of terrestrial origin with low $\delta^{13}C$ values.

It can be concluded that changes in the volume of CO_2 reservoirs affect the $\delta^{13}C$ of both the deep and the shallow water ΣCO_2. In addition, shallow water $\delta^{13}C$ values can be strongly influenced by local processes. The $\delta^{13}C$ values of the deep water ΣCO_2 provide information on the residence time.

MODERN MEDITERRANEAN HYDROGRAPHY AND THE CARBON ISOTOPE RECORD

General patterns

The modern Mediterranean has a negative water-budget (evaporation exceeds precipitation) and an anti-estuarine circulation. The water-loss is compensated by the inflow of Atlantic waters across the Straits of Gibraltar. Through the excess-evaporation the density of the Mediterranean water increases, which generates convection. Therefore, the deeper parts of the Mediterranean contain denser, surface-derived water. This deep, more saline water spills over at the Gibraltar sill and generates a shallow-in, deep-out circulation pattern (fig. 2).

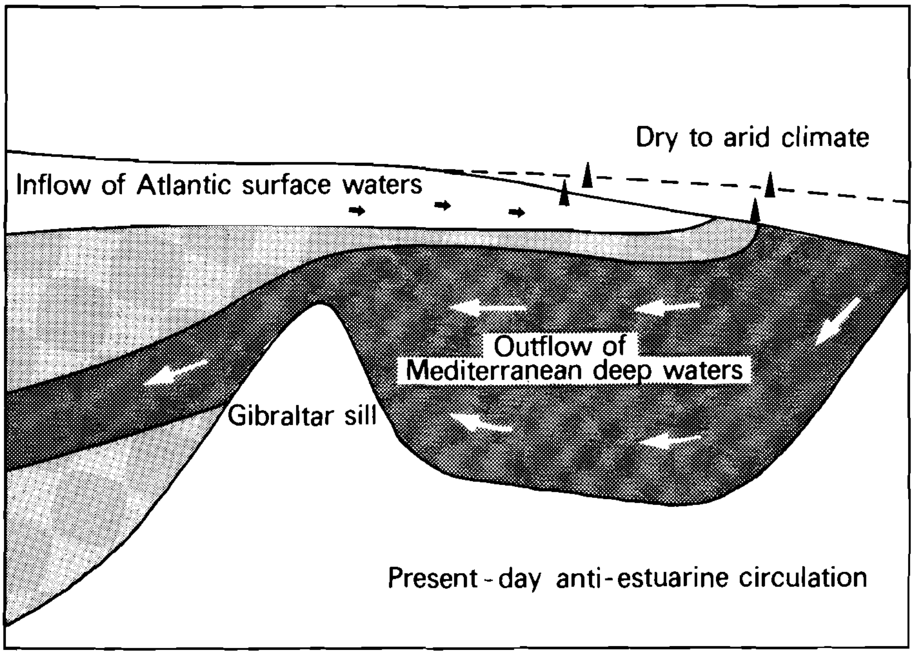

Fig. 2 Circulation pattern across the Straits of Gibraltar.

Deep water formation and the $\delta^{13}C$ of the ΣCO_2

Production of bottom waters is one of the characteristic features of the modern Mediterranean. The formation of bottom water is seasonally controlled and it occurs only at two sites during winter time: in the northern part of the Adriatic Sea ($T = 11°C$, $S = 38.3‰$) and off southern France, in the Gulf of Lion ($T = 12.6°C$, $S = 38.4‰$). Intermediate waters are formed during winter time in the Levantine Sea and in the Aegean Sea (fig. 3).

The deep water that is formed in the western Mediterranean can be identified and traced across the Gibraltar sill into the Atlantic, where it sinks down to the depth of hydrostatic equilibrium (between 800 and 1200 metres). Although it mixes with Atlantic water, the outflowing Mediterranean water can nevertheless be traced over a considerable distance because of higher salinity, low oxygen content, high $\delta^{18}O$ and low $\delta^{13}C$ values of the ΣCO_2 (see fig. 1).

Deep Adriatic water flows across the sill at the Strait of Otranto into the Ionian Basin. There it mixes with the intermediate water of the Levantine Basin; together the two watermasses form deep eastern Mediterranean water. This deep water consists of 7/8 Adriatic and of 1/8 Levantine waters.

Since the Mediterranean deep waters are formed in the Mediterranean itself, they are younger than Atlantic deep waters at the same latitude, which originally were formed at high latitudes. As a consequence, the $\delta^{13}C$ values of the ΣCO_2 of deep Mediterranean waters are higher than those from the Atlantic. Furthermore, there are differences in the $\delta^{13}C$ depth gradients between the Mediterranean and the Atlantic. In the Mediterranean this gradient is very small: from + $1.5^0/_{00}$ in the surface waters to + 1.2 to $1.3^0/_{00}$ in the deep waters (fig. 1), i.e. it amounts to + $0.3^0/_{00}$. This value is lower than that known from the Atlantic, which displays a $\delta^{13}C$ gradient of the ΣCO_2 of + $0.5^0/_{00}$.

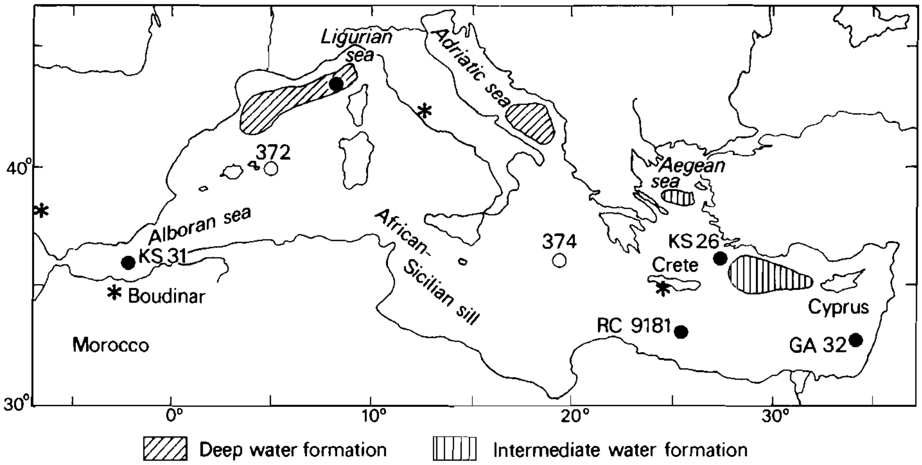

Fig. 3 Location of Mediterranean deep sea cores (●), deep sea drilling sites (○), land-based sections (★), deep water sources (////), and intermediate water sources (||||).

Carbon isotopes and modern Mediterranean foraminifera

The difference between deep water calcite from the Atlantic and the Mediterranean is shown by the $\delta^{13}C$ ratios of benthic foraminifera (table 1, fig. 4). As demonstrated by Graham et al. (1981) the $\delta^{13}C$ values of *Planulina* (about $+ 1^0/_{00}$) are very close to the $\delta^{13}C_{\Sigma CO_2}$ values of Atlantic deep waters. Unfortunately *Planulina* (and also *Cibicides*) are present in the oxygen-poor waters of the Mediterranean in too small a number to perform reliable isotopic analyses; the opposite is true for specimens of *Uvigerina*. To arrive at comparable data, however, the $\delta^{13}C$ values of *Uvigerina* have to be adjusted to those of *Planulina*, which can be done in the way described by Graham et al. (1981):

$$\delta^{13}C\ \textit{Planulina} - \delta^{13}C\ \textit{Uvigerina} = + 0.77^0/_{00}.$$

	Species	Site, core or location	Measured $\delta^{13}C$ values	$\delta^{13}C$ values adjusted to *Planulina*
Mediterranean Sea	*Uvigerina mediterranea*1)	GA32, off Israel	+ 0.90	+ 1.67
	U. mediterranea	Ligurian Sea		
		90 m	+ 0.36	+ 1.13
		340 m	+ 0.30	+ 1.07
		800 m	+ 0.35	+ 1.12
		920 m	+ 0.59	+ 1.36
		Straits of Sicily	+ 0.68	+ 1.45
		GES73, KS57	+ 0.52	+ 1.29
	Planulina ariminensis	Ligurian Sea	+ 1.30	+ 1.30
	average			+ 1.32
Atlantic Ocean	*U. mediterranea*	Faegas 82	+ 0.43	+ 1.20
			+ 0.02	+ 0.79
	Planulina spp.2)	AII 94-99-24	+ 1.02	+ 1.02
		CHN 82-51-21	+ 1.21	+ 1.21
		TRI 121-37	+ 1.25	+ 1.25
		CHN 96-44	+ 0.83	+ 0.83
		AII 31-12-12	+ 1.07	+ 1.07
		CHN 115-77	+ 0.98	+ 0.98
		AII 31-14-144	+ 0.47	+ 0.47
		AII 31-11-11	+ 0.77	+ 0.77
		CHN 115-11-10	+ 0.89	+ 0.89
		A64-9 core 25	+ 1.07	+ 1.07
	average			+ 0.96

Table 1 Carbon isotopic composition of benthic foraminifera from Recent sediments of the Atlantic and the Mediterranean. 1) after Luz, 1979; 2) after Graham et al., 1981.

The adjusted values of Mediterranean *Uvigerina* are represented in table 1. The values show that they are indeed close to, and thus may reflect, the $\delta^{13}C$ values of the deep water ΣCO_2.

The planktonic foraminiferal species *Globigerinoides ruber* is generally abundant in the eastern Mediterranean, as well as in some parts of the western Mediterranean (Cifelli, 1974). $\delta^{13}C$ values of *G. ruber* are summarized in table 2. The average value (+ 1.5°/oo) is very close to those of the $\delta^{13}C$ of the ΣCO_2 of the surface waters.

On the basis of the presently available data one may postulate the following gradients:

$$\Delta_1 = \delta^{13}C_{\text{plankt. Medit.}} - \delta^{13}C_{\textit{Planulina}\text{ Med.}} = +\ 0.2^{0}/_{00}$$
$$\Delta_2 = \delta^{13}C_{\textit{Planulina}\text{ Med.}} - \delta^{13}C_{\textit{Planulina}\text{ Atl.}} = +\ 0.3^{0}/_{00}$$

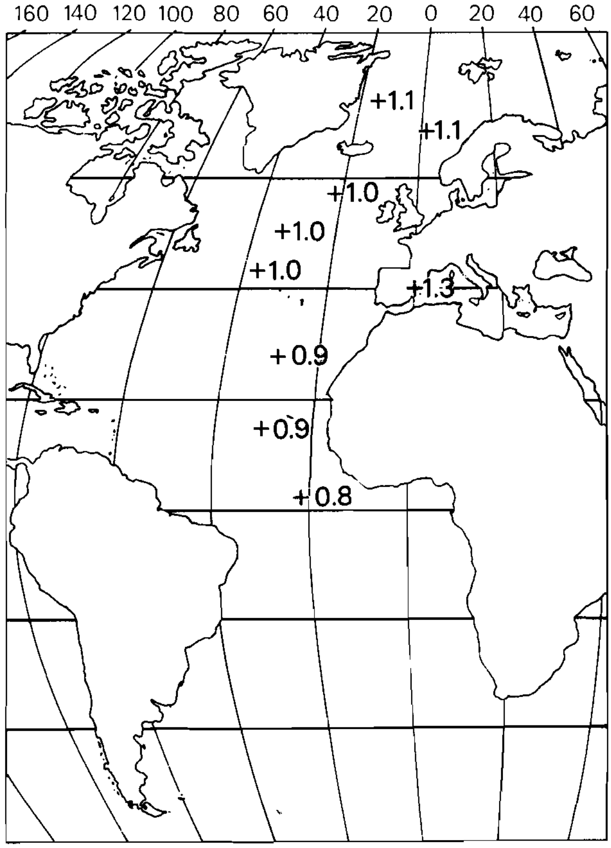

Fig. 4 Modern $\delta^{13}C_{\Sigma CO_2}$ values of deep water in the Mediterranean and in the Atlantic.

	Site or core location	$\delta^{13}C$	
Western Mediterranean	Balearic Basin1)	+ 1.41	
	Ligurian Sea	+ 0.83	
	Straits of Sicily	+ 1.29	
		+ 1.60	
		+ 0.42	
		+ 1.55	
	average	+ 1.18	
Eastern Mediterranean	core KS092)	+ 1.57	
	South Crete	+ 1.44	
	Core RC9-1813)	+ 1.37	
	Core V10-674)	+ 1.57	
	Core KS525)	+ 1.06	
	Surface sediments off Israel6)	+ 1,57	+ 1.41
		+ 1.76	+ 1.29
		+ 1,54	+ 0.86
		+ 1.86	+ 1.67
		+ 1.94	+ 1.31
		+ 1.71	+ 0.58
		+ 1.78	+ 1.62
		+ 1.78	+ 0.84
		+ 1.62	+ 1.32
		+ 1.81	+ 1.59
		+ 1.81	+ 1.60
		+ 1.74	+ 1.53
		+ 1.64	+ 1.33
	average		+ 1.53

Table 2 Carbon isotopic composition of *G. ruber* in the western and in the eastern Mediterranean. 1) after Leclaire and Vergnaud-Grazzini, 1972; 2) after Cita et al., 1977; 3) after Vergnaud-Grazzini and Herman-Rosenberg, 1969; 5) after Znaidi, 1982; 6) after Weiner, 1975.

The reconstruction of these gradients through time provides information pertinent to the paleocirculation patterns and to the deep water formation in the Late Cenozoic Mediterranean.

ATLANTIC LATE CENOZOIC CARBON ISOTOPE PATTERNS

Carbon isotope data of deep water benthic formatinifera are available from DSDP sites of low to mid-latitudes (Shackleton and Cita, 1979; Rabussier-Lointier, 1980; Graham et al., 1981). These data are given in table 3.

The $\delta^{13}C_{\Sigma CO_2}$ values, inferred from the $\delta^{13}C$ values of *Planulina* and *Cibicides*, display a pattern of overall decrease since the Middle Miocene. The highest values were obtained for Early Miocene benthic foraminifera recovered from several sites (Shackleton and Kennett, 1975; Vergnaud-Grazzini and Rabussier-Lointier, 1980). A rapid shift of considerable magnitude has been reported by Keigwin (1979), Vincent et al. (1980) and Bender and Graham (1981) for the Late Miocene of the Atlantic, Pacific and Indian Oceans. This drop of $0.7^{0}/_{00}$ on the average is known as the global "6.2 Ma carbon shift".

During full glacial conditions in the Pleistocene, which especially are recorded in the isotopic stages 2, 6 and 12 (Vergnaud-Grazzini and Saliège, in press) the $\delta^{13}C$ values of the ΣCO_2 decreased by 0.5 to $0.7^{0}/_{00}$ (Shackleton, 1977; Streeter and Shackleton, 1977; Boyle and Keigwin, 1982; Broecker, 1982; Curry and Lohmann, 1982; Vergnaud-Grazzini and Saliège, in press). As is shown in table 3, variations in the $\delta^{13}C$ values of the ΣCO_2 during the Neogene are of the same order as those recorded for the Pleistocene glacial –

Core location		Stratigraphic level	Benthic $\delta^{13}C$ values (*Planulina*-adjusted)	Average
"Modern" Sediments		N23	+ 1.0	
DSDP Sites	366[1]	Lower Miocene	+ 0.62 to + 0.84	
	329[2]	(pre-N8)		
DSDP Sites	366	Middel – Upper Miocene	+ 0.55	+ 0.70
	366	(N8-N17)	+ 0.95	
	397[3]		+ 0.58	
	116[1]		+ 0.93	
	329		+ 0.53	
DSDP Sites	366	Messinian	+ 0.54	+ 0.30
	397	(N17)	+ 0.36	
	116		+ 0.23	
	329		+ 0.10	
DSDP Sites	366	Pliocene	+ 0.65	+ 0.50
	397	(N18-N22)	+ 0.27	
	116		+ 0.57	
DSDP Sites	549A[4]	Isotopic stage 2	+ 0.30	

Table 3 Carbon isotopic composition of Atlantic benthic foraminifera (adjusted to *Planulina*) for some Late Cenozoic intervals. 1) after Rabussier-Lointier, 1980; 2) after Bender and Graham, 1981; 3) after Shackleton and Cita, 1979; 4) after Vergnaud-Grazzini and Saliège, in press.

interglacial cycles. The latter variations are thought to have been caused by the CO_2 transfer from one reservoir (shelf carbonates that were formed during transgressive periods) to another, i.e., to deep water carbonates (Broecker, 1982; Berger, 1982). CO_2 transfer from one reservoir to another may also have been the main cause underlying global variations in $\delta^{13}C$ values during the Neogene, although, in fact, our knowledge on the actual processes is very poor. Perhaps a link can be made with the effects of sea-level fluctuations, as proposed by Cavelier et al. (1980), who concluded that the general pattern of $\delta^{13}C_{\Sigma CO_2}$ values through time parallels the curve of global sea-level changes of Vail et al. (1977).

MEDITERRANEAN LATE CENOZOIC CARBON ISOTOPE PATTERNS

The pre-Messinian Mediterranean

Data are available only from the Balearic Basin in the western Mediterranean (DSDP Site 372, table 4). Mixed meso-bathyal associations were used for the isotope analyses. These associations are dominated by *Planulina wuelerstorfi*, next to some species of *Uvigerina* and *Melonis*.

Since the carbon isotope composition of *Uvigerina* deviates most from *Planulina*, all benthic foraminiferal data of site 372 are to be adjusted with maximally + 0.77‰. For the analysis of planktonic foraminifera we used the group of *Globigerinoides trilobus* (table 4). Modern *G. trilobus* $\delta^{13}C$ values are higher then those of *G. ruber*; the difference is approximately 0.7‰ (Williams et al., 1977). Assuming that this difference in disequilibrium effects remained constant through time, the Miocene $\delta^{13}C$ values of *G. trilobus* were adjusted to *G. ruber* values by substracting 0.77‰.

The data of the pre-Messinian Miocene of site 372 can be subdivided into two groups. The first group involves data from the Early to early Middle Miocene set of samples (up to the Langhian/Serravallian boundary interval, planktonic foraminiferal Zon N10). These data suggest that the $\delta^{13}C$ values in the surface waters of the Mediterranean were fairly similar to the Recent ones, whereas deep $\delta^{13}C$ values for the Mediterranean were lower than those of today. The deep water values, however, were not different from values obtained for the late Early to Middle Miocene Atlantic. In pre-Late Langhian/Early Serravallian time the $\delta^{13}C$ depth-gradient in the Mediterranean was steeper than the present one.

The second group of data was derived from the Late Langhian/Early Serravallian to Tortonian set of samples. From these data it can be inferred that since the Langhian/Serravallian boundary interval Mediterranean $\delta^{13}C$

values of the deep ΣCO_2 decreased strongly and that they became significantly lower than in the "contemporaneous" Atlantic (fig. 5). Mediterranean surface $\delta^{13}C_{\Sigma CO_2}$ values started to decrease as well. Except for two time-slices (corresponding to sampling intervals 13-5-100 and 11-2-130) the surface to bottom $\delta^{13}C$ gradient was much steeper than they are in the present-day Mediterranean Sea and in the Atlantic Ocean.

Our data suggest that up to Serravallian time deep Mediterranean waters may have been of Atlantic origin; if so, this could mean that the circulation pattern was of the estuarine type. From the Serravallian up to the Late Tortonian/Early Messinian (N 10 – N 16/17 zonal interval) the deep circulation became more sluggish and the residence time of deep Mediterranean waters increased. Auffret et al. (1981) reported a marked decrease of the sedimentation rate at a level corresponding to the Langhian/Serravallian boundary interval (i.e., around the N10/N11 zonal boundary), which conclusion they

	Core level (in cm)	*G. trilobus* $\delta^{13}C$ values	$\delta^{13}C$ values adjusted to *G. ruber*	Mixed benthic $\delta^{13}C$ values (not adjusted)	$\Delta\delta^{13}C_{Pl.\text{-}Benth.}$
Tortonian Messinian	9-2-130*	– 1.03	– 1.73	– 0.17	– 1.56
	9-3-95	+ 0.74	+ 0.04	– 0.92	+ 0.96
	10-2-100	+ 1.74	+ 1.04	– 0.51	+ 1.55
Serravallian	11-2-130	+ 0.79	+ 0.09	– 0.34	+ 0.43
	11-3-130	+ 1.28	+ 0.58	– 1.31	+ 1.89
	12-3-20	+ 1.62	+ 0.92	– 0.13	+ 1.05
	12-4-120	+ 1.24	+ 0.54	– 0.63	+ 1.17
	13-1-120	– 0.02	– 0.72	– 1.73	+ 1.01
	13-5-100	+ 1.35	+ 0.65	– 0.13	+ 0.78
	13-6-100	+ 2.03	+ 1.33	+ 0.21	+ 1.12
	14-2-20	+ 1.94	+ 1.24	– 0.27	+ 1.51
	15-4-120	+ 2.31	+ 1.61	– 0.44	+ 2.05
	18-1-100	+ 1.51	+ 0.81	– 1.27	+ 2.08
Langhian	23-5-40	+ 2.50	+ 1.81	+ 0.58	+ 1.23
	25-1-130	+ 2.36	+ 1.66	+ 0.24	+ 1.42
	27-5-40	+ 2.25	+ 1.55	+ 0.19	+ 1.36
	28-5-100	+ 1.83	+ 1.13	+ 0.59	+ 0.54
	30-4-70	+ 0.75	– 0.02		
	30-6-40*	+ 0.54	– 0.23	+ 1.45	– 1.68
	32-1-125*	+ 1.91	+ 1.21	+ 1.47	– 0.26

Table 4 Carbon isotopic composition of planktonic and benthic foraminifera from DSDP Site 372 (western Mediterranean) and surface to bottom $\delta^{13}C$ gradient values. *: Values from contaminated samples or from samples affected by diagenesis.

based on the study of the textural properties of the sediment silt fraction of site 372. At the same level they noticed a decrease of traces of benthic activity (e.g. of burrowing), which may be attributed to a lowering of the oxygen content at or near the bottom. Decrease of oxygen content would be in line with the postulated slowing-down of the deep circulation, caused either by decreasing bottom water production in the Mediterranean, or by a deterioration of the connections with the Atlantic.

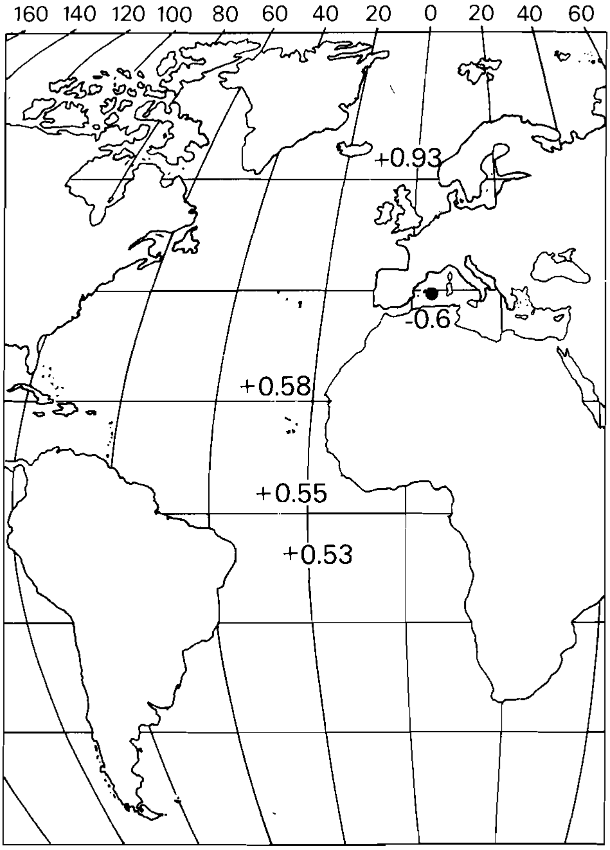

Fig. 5 Middle to Late Miocene $\delta^{13}C_{\Sigma CO_2}$ values of Mediterranean and Atlantic deep water.

The Early Messinian

Carbon isotopic data were collected from four sections in the Mediterranean proper and adjacent parts of the Atlantic. The sections of the Mediter-

Locality	Range of $\delta^{13}C$ values of *G. obliquus*	Range of $\delta^{13}C_{\Sigma CO_2}$ values of bottom waters (*Planulina*-adjusted)	Minimum and maximum values of $\Delta\delta^{13}C_{Pl.-Benth.}$
Guadalquivir Basin (Spain)	+ 0.6 to + 2.2	+ 0.27 to − 0.73	+ 1.53 to + 1.93
Core KS09 (West of Gibraltar)	+ 1.6 to + 1.5	+ 0.47 to − 0.73	0 to + 2.0
Morocco	− 1.2 to −3.0	− 2.8 to − 0.4	0 to + 2.0
Crete	− 3.0 to + 0.5	− 2.25 to − 0.25	0 to + 2.0

Table 5 Carbon isotopic composition of planktonic and benthic foraminifera in four Early Messinian sections. For references: see text.

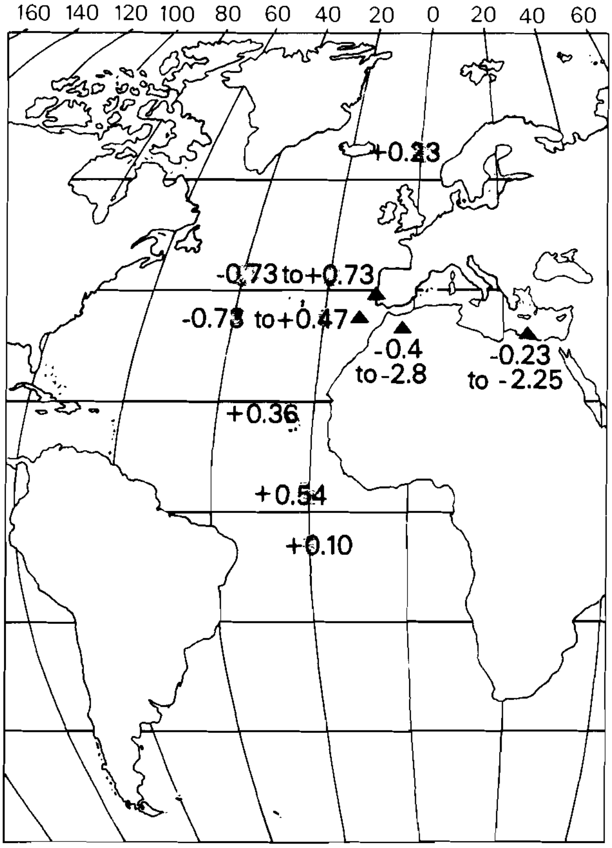

Fig. 6 Early Messinian $\delta^{13}C_{\Sigma CO_2}$ values of Atlantic and Mediterranean bottom water.

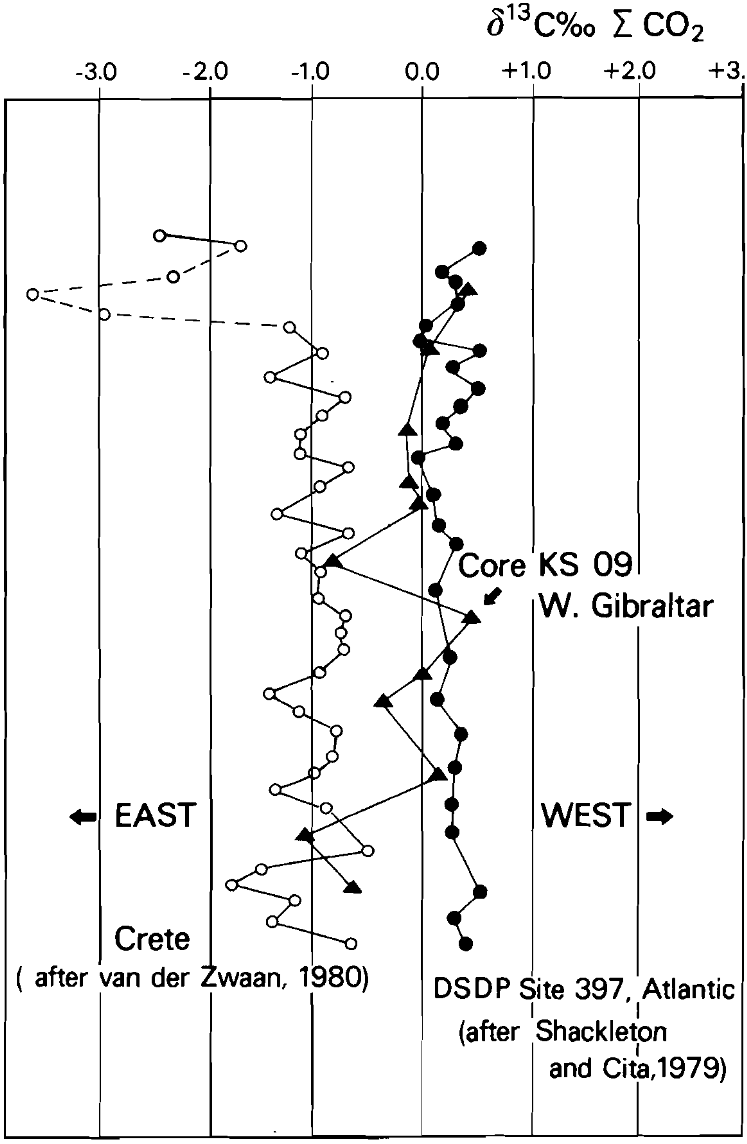

Fig. 7 Variations in $\delta^{13}C$ values in the Atlantic DSDP Site 397 (●), in a core west of Gibraltar (▲), and in a composite section on Crete (○).

ranean proper are located in Morocco (section Boudinar, Bizon et al., 1979; Vergnaud-Grazzini, unpublished data) and on Crete (Vrysses/Khaeretiana composite section, Van der Zwaan, 1982); the other two sections are the Carmona – Dos Hermanos section in the Guadalquivir Basin, Spain (Loutit and Keigwin, 1982) and the core profile of section KS09, west of Gibraltar (Vergnaud-Grazzini and Pastouret, 1980).

The data, summarized in table 5 and in figure 6, show that the $\delta^{13}C_{\Sigma CO_2}$ values of both surface and bottom waters in the Mediterranean proper and neighbouring areas were much lower than those of today. Furthermore, Messnian $^{13}\delta C_{\Sigma CO_2}$ bottom water values are generally distinctly lower than the values known from the Atlantic Ocean (see fig. 7). Occasionally, however, the Mediterranean values were within the range of the values of the "contemporaneous" Atlantic Ocean.

From our data it may be concluded that the bottom waters of the Mediterranean differed considerably from true Atlantic deep waters during most of (Early) Messinian time. This may have been brought about by the increasing isolation of the Mediterranean from the open ocean, which, in its turn, caused a reduction of the thermohaline circulation resulting in an increase of the residence time of bottom waters and in a lowering of the oxygen content.

It should be realized that the conclusions on the Mediterranean hydrography during the Early Messinian should be handled with care, since we compared data from, at least in part, shallow marine sections with those obtained from the deep Atlantic Ocean. One might even argue that true deep water circulation in the Mediterranean proper was confined to a narrow trench along the coast of North-Africa.

The Early Pliocene

Only a few samples have been analyzed thus far; their carbon isotopic data are presented in table 6. The data suggest that Mediterranean Early Pliocene $\delta^{13}C$ values were lower than the values of the present-day Mediterranean; occasionally they were within the range of values of the Early Pliocene Atlantic (fig. 8). Probably the $\delta^{13}C$ depth-gradient in the Early Pliocene Mediterranean was steeper than it is today.

Our scanty data might imply that no bottom water production took place in the Mediterranean during Early Pliocene time; it may be hypothesized that Mediterranean Early Pliocene waters were of Atlantic origin, since the connection with the Atlantic had been re-established by the opening of the Straits of Gibraltar at the beginning of the Pliocene.

Locality	δ^{13}C values of *G. obliquus*	bottom water $\delta^{13}C_{\Sigma CO_2}$	$\Delta\delta^{13}C_{Pl.-Benth.}$
Crete	+ 1.0	– 0.73	
Italy	+ 0.9	– 0.5 to + 0.4	– 0.5 to + 1.7
DSDP Site 374	+ 0.65		

Table 6 Carbon isotopic composition of planktonic and benthic foraminifera in Mediterranean Pliocene sections.

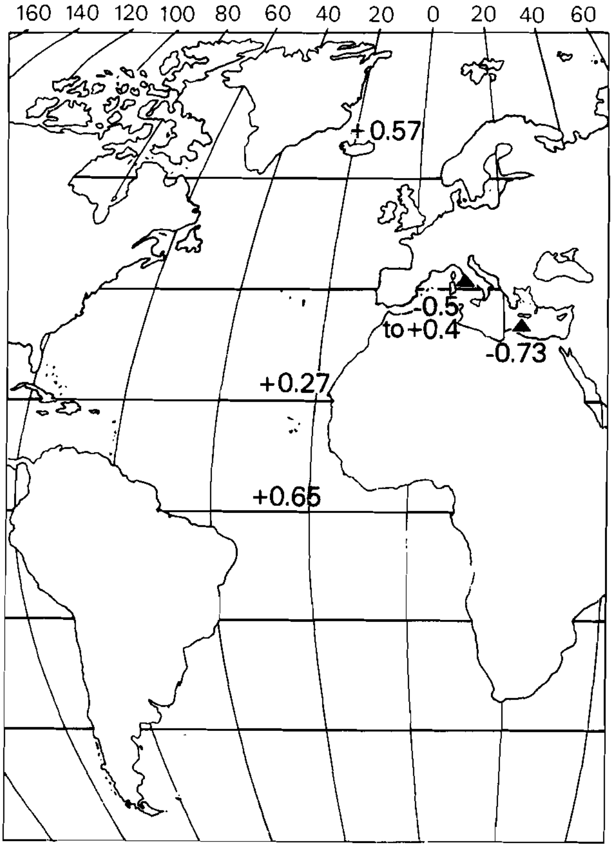

Fig. 8 Pliocene $\delta^{13}C_{\Sigma CO_2}$ values of Mediterranean and Atlantic bottom water.

The Late Quaternary

Reconstructions of the glacial and post-glacial evolution of the deep Mediterranean watermasses are based on data obtained from core 82KS31 (Alboran Sea, unpublished data) in the western Mediterranean and from cores 75KS26 (Aegean Sea, Znaidi, 1982) and GA32 (Levantine Basin, Luz, 1979) in the eastern Mediterranean (see fig. 4). Intercore correlations are based on ^{14}C data and on oxygen isotope stratigraphy. Our data on the bottom water $^{13}C_{\Sigma CO_2}$ patterns are given in figure 9.

The δ^{13}C values of the eastern Mediterranean appear to be consistently higher than those obtained for the Atlantic. This difference is of importance, since it suggests 1) bottom water formation in the eastern Mediterranean and thus 2) the existence of an anti-estuarine circulation in the eastern Mediterranean during the last glacial/post-glacial time-span.

The difference between glacial and post-glacial δ^{13}C values in the eastern Mediterranean amounts to about + 0.7$^0/_{00}$ (cores 75KS26 and GA32), which

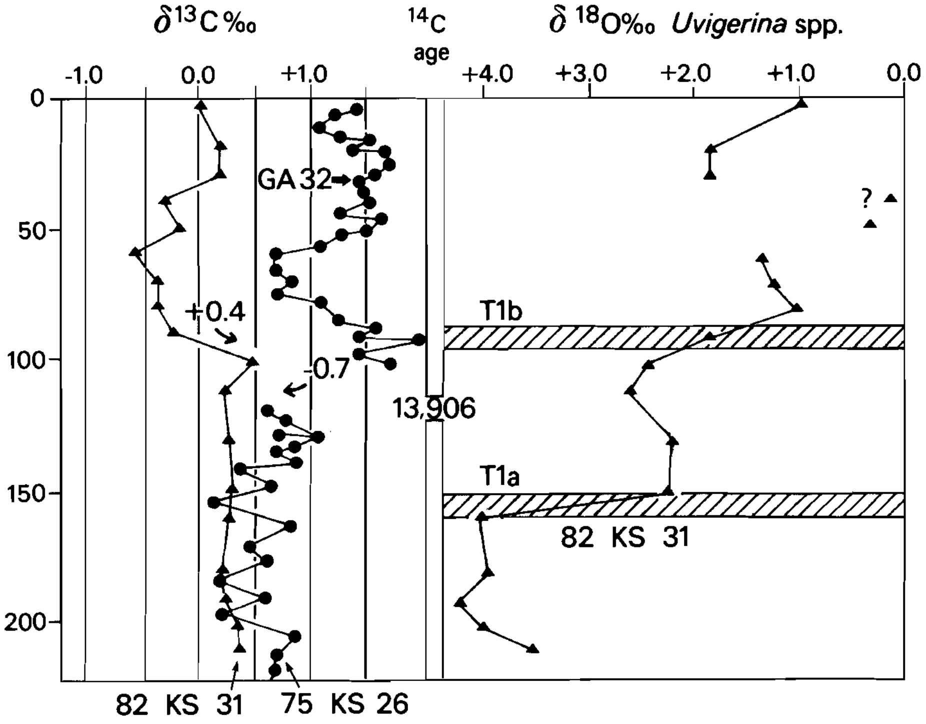

Fig. 9 Glacial to post-glacial δ^{13}C variations in core KS31 from the Alboran Sea, western Mediterranean, and in the eastern Mediterranean cores KS26 and GA32. For explanation: see text.

difference corresponds to the global increase of 0.7‰ reported by e.g. Berger (1982) and Broecker (1982).

A remarkable difference exists between the deep water $\delta^{13}C$ pattern in the eastern Mediterranean and that in the western Mediterranean (Alboran Sea, core 82KS31). Just as in the eastern Mediterranean, glacial values (+ 0.44‰) are higher than in the Atlantic, indicating that a strong thermo-haline convection existed in the Alboran Sea as well. Post-glacial values in the Alboran Sea, however, are lower (about 0‰ on the average) than glacial ones, which is in sharp contrast to the increase of 0.7‰ in the eastern Mediterranean across the glacial/post-glacial transition.

The drop of 0.44‰ in the Alboran Sea across the last glacial/post-glacial transition can be ascribed to local conditions that suppressed and even completely obliterated the global signal. To explain these local conditions one may think in terms of a significant increase in residence time of the deep waters in the Alboran Sea since post-glacial time. Possibly the sea-level rise at the beginning of the post-glacial and the increased inflow of Atlantic surface water generated a deep-sited eddie east of Gibraltar, thus trapping Alboran waters.

DISCUSSION AND CONCLUSIONS

In late Early Miocene (Late Burdigalian) time a major tectonic event caused a complete reorganisation of the paleogeographic configurations in the Mediterranean realm; most probably the marine connections towards the east (i.e. the Indo-Pacific) became definitely interrupted at the time (see also Adams et al., this volume). There seems to be little doubt that these Late Burdigalian processes, which clustered around 18 Ma ago, resulted in a drastic change of the hydrography of the Mediterranean realm.

Figure 10 summarizes the general trends in the carbon isotope record of the Mediterranean and the Atlantic since the Late Burdigalian.

Reviewing all data that could be obtained thus far we may postulate that several major changes in Mediterranean circulation patterns occurred since the Late Burdigalian, changes which, apart from the impact of climatic fluctuations, were closely related to tectonic processes shaping the geometry of the basin.

Until the Langhian/Serravallian boundary interval, Mediterranean deep waters closely resembled those in the Atlantic and circulation patterns were of the estuarine type. At about the transition from the Langhian to the Serravallian the circulation patterns changed fundamentally: the deep circulation became more sluggish and the residence time of Mediterranean deep

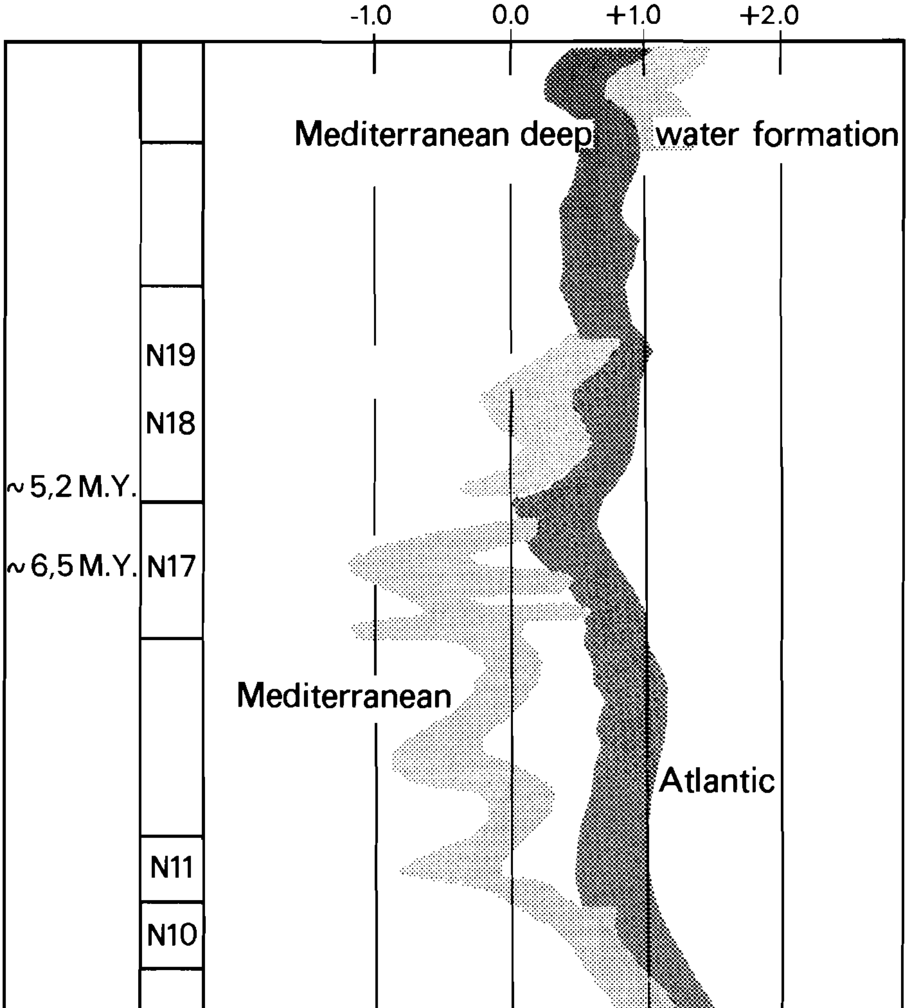

Fig. 10 General trends in the Late Cenozoic carbon isotope record of the Mediterranean and the Atlantic.

waters increased considerably. The corresponding decrease of the oxygen content of the deep waters would be in line with the slowing-down of the bottom water circulation. It seems reasonable to assume that the increased residence times of deep waters were connected with the deteriorating connections with the Atlantic Ocean and with an increase of the intra-Mediterranean fragmentation from the Serravallian onward.

The Early Messinian record is more difficult to explain, but it seems likely that bottom waters of the Mediterranean proper differed strongly from those in the deep Atlantic during most of (Early) Messinian time. Moreover, the carbon isotopic values of both surface and bottom waters were distinctly lower than they are in the present-day Mediterranean.

Our data on the Pliocene are too scanty to arrive at a sound reconstruction of Mediterranean hydrography for the whole Epoch. Data for the Early Pliocene may suggest that no bottom water formation took place and that deep waters at the time were of Atlantic origin. If we look at the general patterns for the Late Cenozoic, as represented in figure 10, it appears that the (Early) Pliocene was characterized by $\delta^{13}C_{\Sigma CO_2}$ values intermediate between those inferred for the Middle to Late Miocene and for the Late Quaternary, respectively.

The Late Quaternary record indicates that deep water formation within the Mediterranean caused high $\delta^{13}C_{\Sigma CO_2}$ values in the deep waters. The comparison between the eastern Mediterranean and the Atlantic records indicates that the eastern Mediterranean was subject to a strong thermohaline convection and that an anti-estuarine circulation existed already in last glacial/post-glacial time. The Alboran Sea underwent a specific development: its record suggests that there has been a remarkable increase of the residence time of deep water since the glacial/post-glacial transition, probably caused by the trapping of deep water immediately east of Gibraltar.

In conclusion it may postulated that the modern hydrography of the Mediterranean, characterized by in situ deep water formation, is of a very young origin. It did certainly not originate before the Late Pliocene, but our knowledge of the Late Pliocene and Early Quaternary is insufficient to fix the date of origin of the present-day hydrographic setting more precisely.

Investigation of the fluxes of watermasses contributing to the formation of North Atlantic Deep Water (NADW) demonstrates that the contribution of the Mediterranean outflow to the NADW is very small (Worthington, 1976). In fact, the Mediterranean waters contribute only a few percent to the NADW: a flux of about 0.6×10^6 m^3/s^{-1} on a total flux of NADW of 10×10^6 m^3/s^{-1}. If we consider these Recent fluxes it seems to be unlikely that the flux of outflowing Mediterranean water was sufficiently high during the Late Cenozoic to have been of influence on the formation of NADW. Likewise, it may be concluded that during the Late Miocene the Mediterranean could not have had a profound effect on the deep circulation in the North-Atlantic, as suggested by Keigwin (1979), Vincent et al. (1980) and Bender and Graham (1981).

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QUANTITATIVE ANALYSES AND THE RECONSTRUCTION OF BENTHIC FORAMINIFERAL COMMUNITIES

G. J. VAN DER ZWAAN

ABSTRACT

Qualitative and quantitative analyses of Eastern and Central Mediterranean benthic foraminiferal associations showed that the Messinian salinity crisis was a relatively minor event in the sense that it had profound, but very temporal effects on the benthic foraminifera. The most important change of the past 10 m.y. took place during the Late Pliocene and was connected with the entrance of cool surface-waters into the Mediterranean. During that time the modern Mediterranean faunal patterns started to develop.

The ecological patterns of Miocene and Pliocene benthic species were determined to a great extent by one parameter: oxygen content. Occasionally an increase in the bottom salinity played a role as well. During the Late Pliocene the ecological patterns of a number of species probably changed. Coinciding with a number of (local) extinctions and the entry of temperate species, a number of indigenous species started to proliferate in the oxygen-deficient environment which they had avoided before.

INTRODUCTION

For over 150 years benthic foraminifera have been the subject of active interest. At the beginning research was mainly devoted to the classification and the development of a comprehensive taxonomy. With the increasing demand for suitable paleontological dating tools, research ceased being purely taxonomical and became concerned with the biostratigraphic application of microfossils to the geological record. In the course of this research benthic foraminifera became a comparatively well-known group of fossils. Gradually, however, planktonic foraminifera and later on calcareous nannofossils proved to be better tools to perform biostratigraphic correlations with, and consequently interest in the smaller benthic foraminifera diminished.

From the 1950's onwards, Phleger and Bandy pioneered the environmental interpretation based on foraminiferal associations, and the interest in the smaller benthic foraminifera increased. However, up to now, the paleoecology of this group of fossils has proved to be such a complex puzzle that it seems that we are only just starting to see the beginning of a pattern. It is therefore not surprising that Boltovskoy (1965) concluded that "the near future of this science is rather bleak".

Recent developments in the mathematical treatment of data in geochemistry (application of stable isotope analysis and clay-mineral analysis) and the application of oceanographic models suggest that the future of paleoecology is not necessarily bleak. On the contrary, paleoecology seems to be very promising if these different disciplines are combined. A hindrance, however, to the further development of paleoecology is that generally the interpretation of the physical/chemical aspects of ancient environments is regarded as the main purpose of paleoecological research. It is important to realize that a great number of non-physical processes play a role as well. These processes should be taken into consideration if one is to evaluate species-environment interactions correctly.

In this paper an attempt is made to summarize the Miocene to Pleistocene paleoecological history of the Eastern and Central Mediterranean benthic foraminifera. As our story proceeds, we shall try to touch upon some of the above-mentioned points.

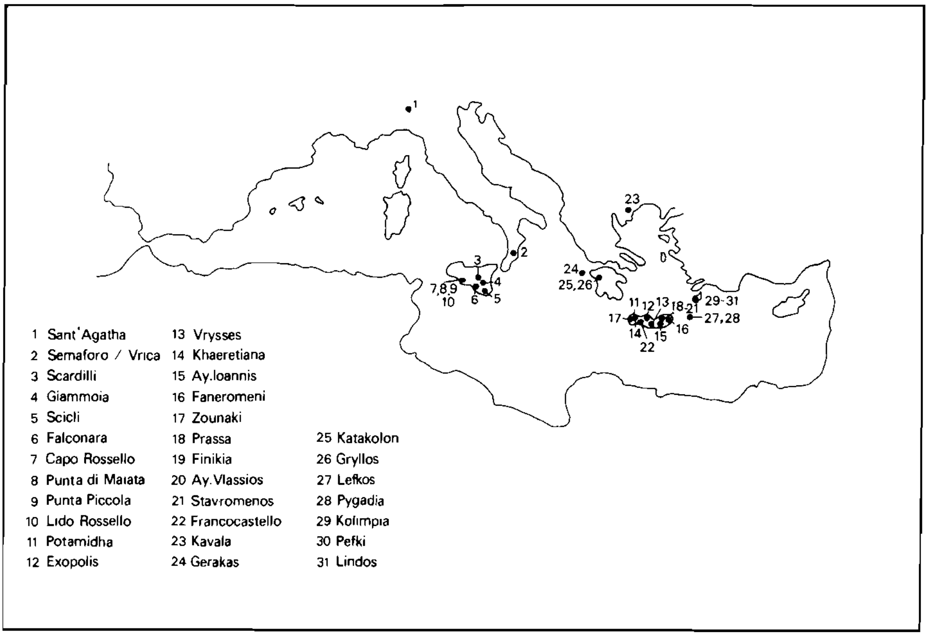


Fig. 1 Location of the sections mentioned in the text.

DEFINITION OF THE PROBLEM

This paper is based on a compilation of data gathered over the past five years by members of the Department of Stratigraphy and Paleontology of Utrecht State University. On the basis of these internal reports, data published earlier and an additional inventory of many samples by the author, a range-chart was constructed with presence/absence data for the smaller benthic foraminifera. The 31 sections used for this study are located in the Eastern and Central Mediterranean and range in age from Tortonian to Pleistocene (see figs. 1 and 2).

The crude range-chart which resulted is depicted in figure 3. Lagenids and miliolids were excluded from this compilation because of the great taxonomic heterogeneity which meant that the compilation would be unreliable. There is a concentration of first and last occurrences of benthic foraminifera at two biostratigraphic levels. A relatively minor concentration occurs around the Messinian event, during which huge amounts of evaporites were deposited

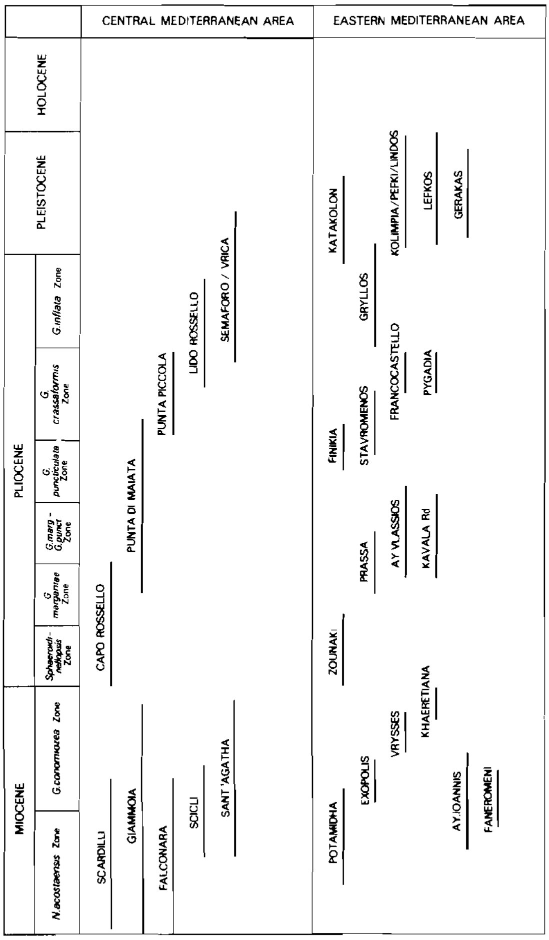


Fig. 2 Relative age relations of the sections mentioned in the text, based on planktonic foraminiferal datumlevels.

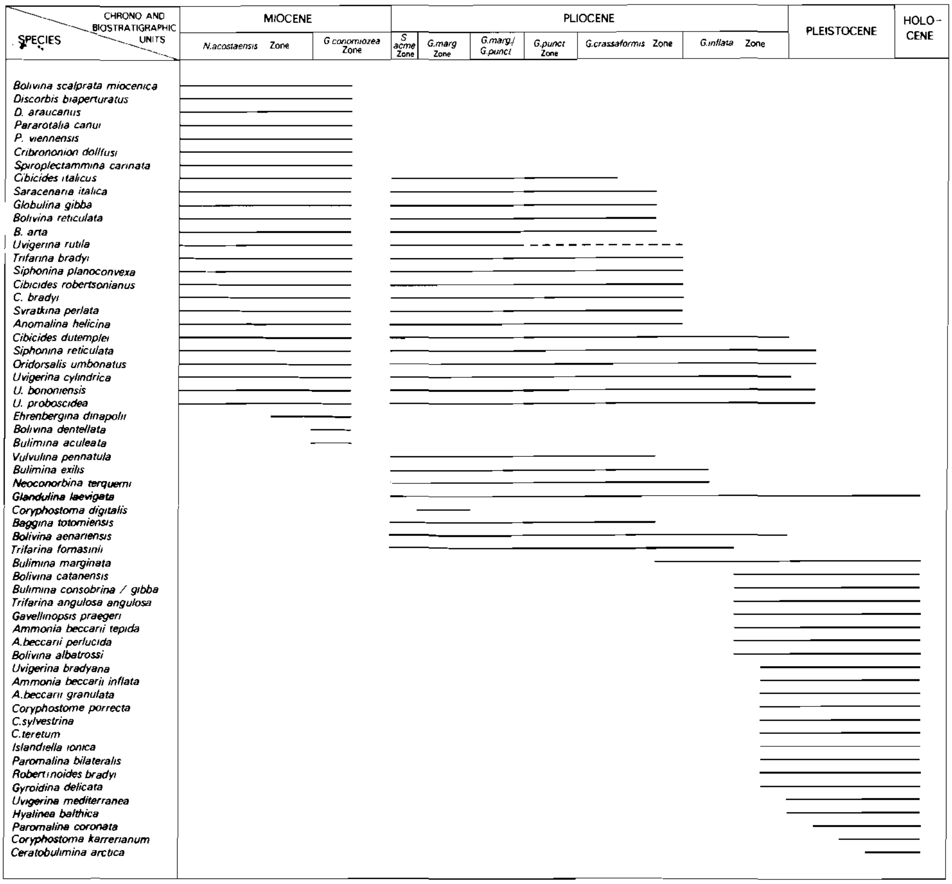


Fig. 3 Simplified range-chart of benthic foraminifera, based on the first and last occurrences in the 31 sections. Miliolids and lagenids were disregarded.

in the Mediterranean. The most important turn-over in species composition, however, evidently took place during the Late Pliocene, more precisely during the *Globorotalia crassaformis* Zone and the *Globorotalia inflata* Zone (sensu Spaak, 1983). This pattern is summarized in figure 4. In this figure the number of first and last occurrences per biostratigraphic zone is plotted. The two faunal changes mentioned before are more or less prominent. The change which coincides with the Messinian and the lowermost Pliocene indeed turns out to be a minor one, whereas the Late Pliocene change seems to be the most important one of the past 10 m.y. of the Eastern and Central Mediterranean history. An interesting detail is that on the two occasions an increased number of last occurrences precedes the increased number of first occurrences.

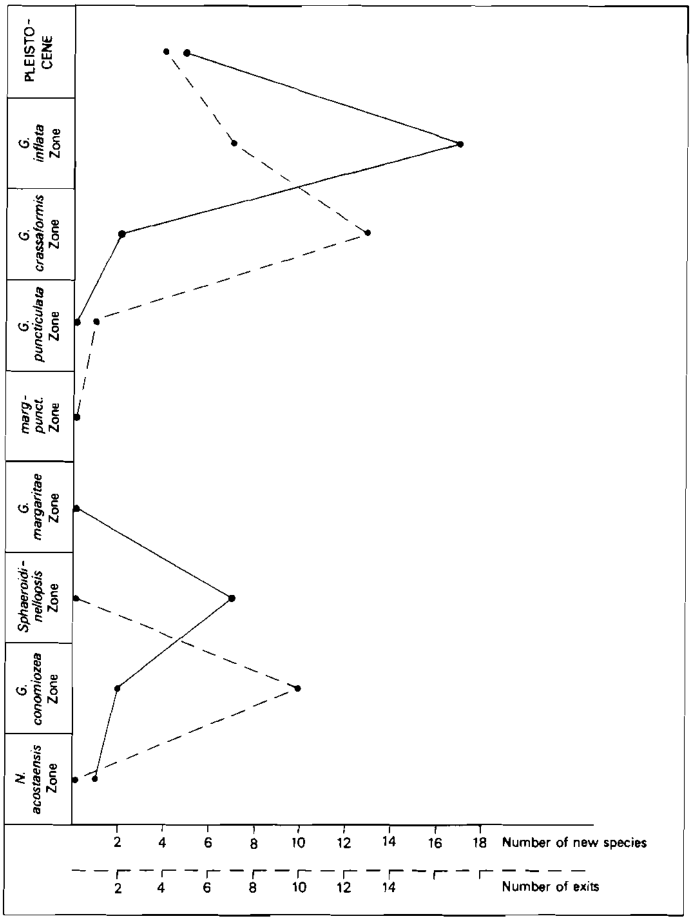


Fig. 4 Number of first and last occurrences per biostratigraphic zone, based on the range chart of figure 3.

This qualitative analysis was followed by a number of quantitative analyses. The first step in the analyses consisted of a Q-mode principal component analysis (program PCA, Davis, 1973). This was performed on 425 samples; the samples were chosen in such a way that each biostratigraphic zone, from the *Neogloboquadrina acostaensis* Zone upwards, was covered as completely as possible (fig. 5). Moreover, care was taken that the number of samples from the Eastern Mediterranean more or less balanced the number of samples from the Central Mediterranean. For each sample the frequencies of 40 taxa or groups of taxa (listed in table 1) were entered. These relative frequencies are all based on 200-counts in the > 125 μ size fraction.

1. *Ammonia beccarii* (Linnaeus)
2. *Asterigerina planorbis* d'Orbigny
3. *Bolivina alata* (Seguenza)
4. *Bolivina antiqua* d'Orbigny
5. *Bolivina plicatella* Cushman
6. *Bolivina reticulata* Hantken
7. *Bolivina scalprata* Schwager var. *miocenica* Macfadyen
8. *Bolivina spathulata* (Williamson) including *Bolivina dilatata* Reuss and *Bolivina dentellata* Tavani
9. *Bulimina costata* d'Orbigny including *Bulimina inflata* Seguenza and *Bulimina striata* d'Orbigny.
10. *Bulimina elongata* d'Orbigny including *Bulimina aculeata* d'Orbigny
11. *Bulimina exilis* Brady
12. *Bulimina marginata* d'Orbigny
13. *Bulimina subulata* Cushman and Parker including *Bulimina lappa* Cushman and Parker
14. *Cancris auricula* (Fichtel and Moll) including *Cancris oblonga* Brady
15. *Cassidulina carinata* Silvestri
16. *Cassidulina laevigata* d'Orbigny
17. *Chilostomella ovoidea* Reuss
18. *Cibicides bradyi* (Trauth) together with *Cibicides robertsonianus* (Brady)
19. *Cibicides italicus* Di Napoli Alliata
20. *Cibicides lobatulus* (Walker and Jacob) including *Cibicides refulgens* (De Montfort)
21. *Cibicides ungerianus* (d'Orbigny) including *Cibicides dutemplei* (d'Orbigny)
22. *Discorbis* species including *Rosalina globularis* d'Orbigny
23. *Elphidium* species
24. *Globobulimina* species
25. *Globocassidulina* species
26. *Gyroidina* species
27. *Hanzawaia boueana* (d'Orbigny)
28. *Nonion barleeanum* (Williamson) including *Nonion soldanii* (d'Orbigny) and *Nonion pompilioides* (Fichtel and Moll)
29. *Nonion scaphum* (Fichtel and Moll)
30. *Oridorsalis umbonatus* (Reuss)
31. *Reusella spinulosa* (Reuss)
32. *Siphonina bradyana* Cushman
33. *Sphaeroidina bulloides* d'Orbigny
34. *Trifarina angulosa* (Williamson)
35. *Uvigerina bononiensis* Fornasini
36. *Uvigerina cylindrica* (d'Orbigny) subsp. *gaudryinoides* Lipparini
37. *Uvigerina peregrina* Cushman
38. *Uvigerina proboscidea* Schwager
39. *Uvigerina rutila* Cushman and Todd
40. *Valvulineria complanata* (d'Orbigny)

Table 1 List of taxa or groups of taxa used for the Q-mode principal component analysis.

In table 2 the eigenvalues of the first five principal components are given. According to criteria set by M. M. Drooger (1982) only the first two principal components are significant. A plot of all samples along these first two components is given in figure 6. The general picture is that a dense cluster of Miocene and Pilocene samples forms the centre of the plot, whereas three

	Eigenvalue	Total variance (%)	Total variance (cumulative %)
C_I	1087	35	35
C_{II}	362	12	47
C_{III}	262	8	53
C_{IV}	213	7	60
C_V	166	5	65

Table 2 Eigenvalues, percentages of the total variance and the cumulative percentages of the total variance of the five most important components found in the principal component analysis of 425 samples using the frequencies of 40 species.

		NUMBER OF SAMPLES USED FOR PRINCIPAL COMPONENT ANALYSIS	
		CENTRAL MEDITERRANEAN	EASTERN MEDITERRANEAN
PLEISTOCENE			Gerakas 10 Katakolon 16 Gryllos · 17
PLIOCENE	*G. inflata* Zone	Vrica·29	
	G. crassaformis Zone	P Piccola 46	Francocastello 22 Stavromenos 23
	G. puncticulata Zone		
	marg. - punct Zone		Ay Vlassios 30
	G. margaritae Zone	Capo Rossello 28	Prassa 24
	Sphaeroidi - nellopsis Zone	Capo Rossello 8	Zounaki 21
MIOCENE	*G conomiozea* Zone	Sant'Agatha 45	Khaeretiana 23 Vrysses 15 Ay.Ioannis.12
	N acostaensis Zone	Scardilli 23	Ay.Ioannis.10 Potamidha.23

Fig. 5 Number of samples per section used for the Q-mode principal component analysis.

groups of samples deviate from this central one. Along the first principal component (positively correlated with *Bolivina spathulata*) a great number of samples are separated from the central cluster; closer inspection proves that the majority of them are derived from Miocene and Pliocene laminated sediments, which were deposited during oxygen-deficient bottom-water con-

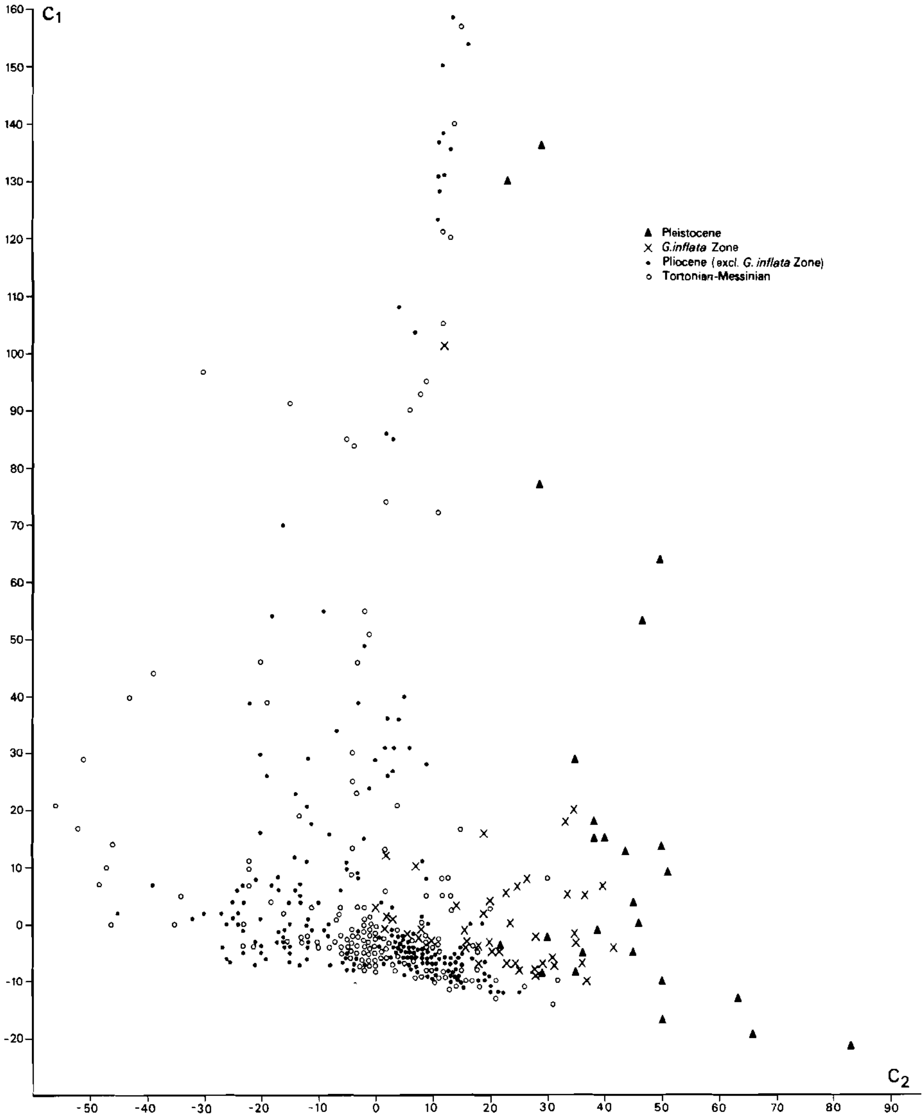


Fig. 6 Plot of samples along the first and second principal component.

ditions. A second group of samples plots out of the central cluster and reaches strongly negative values along the second principal component (positively correlated with *Cassidulina carinata* and *Bulimina marginata* and negatively with *Bolivina plicatella*); the majority of these samples prove to be of Messinian Age. A third group of samples reaches positive values along the second principal component. These samples are of Pleistocene age, whereas the samples derived from the youngest Pliocene zone, the *Globorotalia inflata* Zone, plot more or less in between the central cluster and the Pleistocene one.

This preliminary qualitative and quantitative analysis described above clearly indicates the major changes in the benthic foraminiferal composition and allows us to reduce our confusing amount of data to three main issues:

1. How were the stable marine and oxygen-deficient biotopes populated through time?
2. How did the associations react to the Messinian salinity crisis and what was the neteffect of this event?
3. What was the cause and netresult of the Late Pliocene change of the benthic foraminiferal distribution patterns?

THE STRUCTURE OF MUD-DWELLING COMMUNITIES

In order to understand the nature of the changes in the benthic foraminiferal composition, we first have to consider the structure of the Miocene-Pliocene shallow and deep dwelling mud-communities. In order to be able to do this, R-mode analyses were carried out on several suites of samples. This was done by using the computer-program BALANC, which calculates correlations between proportions eliminating the closed-sum effect. On the basis of these correlations a cluster diagram was constructed using the program DENDRO. Both computer-programs are based on the free open covariances model of M. M. Drooger (1982).

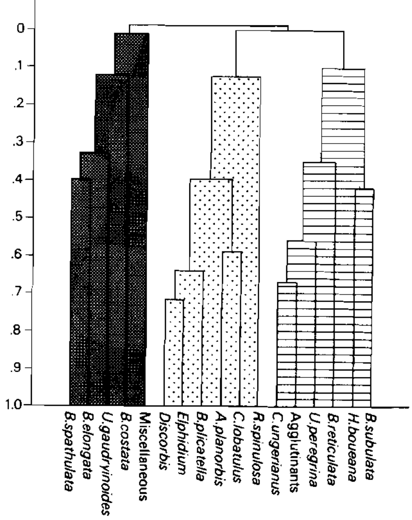
The paleoecological tolerance patterns of the species mentioned in the following sections, were determined as described by Van der Zwaan (1982a). Stable isotope analyses were performed on suites of samples from some sections; this enabled us to make paleosalinity estimates. In almost all sections laminated sediments do occur; from detailed faunal analyses of these laminated sediments an order of peaks in relative abundance of the species could be established; this order was taken as being indicative of the varying tolerances of oxygen-deficiency. Detailed stratigraphic mapping in many of the sampled areas gave additional information e.g. on the relative depth of deposition of the sediments.

The general structure of shallow mud-communities can be illustrated using the dendrogram of an Upper Miocene composite section, consisting of the Exopolis, Vrysses and Khaeretiana sections from Crete (data given by Van der Zwaan, 1982a). The maximum depth of deposition of the sediments was estimated to be about 200–300 metres. The dendrogram of figure 7 was constructed on basis of the proportions of 17 taxa or groups of taxa in 176 samples. An arrangement of the species as in this dendrogram can be recognized in analyses of almost all Miocene shallow water mud-associations at present available. It is characterized by the occurrence of three groups. One group consists of epiphytes or vegetation-bound species like *Cibicides lobatulus*, *Asterigerina planorbis*, *Discorbis* species, and *Elphidium* species. If present, two species are always added to this group: *Bolivina plicatella* and *Reussella spinulosa*. Very probably these species too were epiphytes or vegetation-bound. The most probable interpretation is that these shallow living species were all transported basin-inwards by plant-rafting and should therefore be considered as allochthonous in the deeper mud-environment.

The other species constitute two clusters which in most of the analyses are interrelated by some positive correlations. One group is always dominated by species like *Cibicides ungerianus*, *Uvigerina peregrina*, *Bolivina reticulata* and the agglutinants. From their distribution in the various sections it is evident that these species are not tolerant to environmental stress of any nature, more particularly high salinities and oxygen-deficiency. The other group is dominated by species like *Bulimina costata*, *B. elongata*, *Bolivina spathulata* and *Uvigerina cylindrica gaudryinoides*. In contrast with the previous group, this one consists of species tolerant to environmental stress, which is mostly represented by oxygen-deficiency at the bottom. There is, however, some differentiation within this group if high bottom salinities start to play a role, as they did during the Messinian. It then appears that only *Bolivina spathulata* and *Bulimina elongata* tolerate oxygen-deficiency in conjunction with high salinities.

Since the dendrogram of figure 7 gives a picture which is fairly typical for all Miocene and Pliocene shallow water associations, it can be concluded that during that time span the species were arranged mainly along one stress-gradient, which was determined by the amount of oxygen available at the bottom. Oxygen in its turn is highly decisive for the amount of nutrients available at the bottom. Therefore, one often sees a strong similarity between associations from oxygen-deficient and nutrient-rich environments (Van der Zwaan, 1982a). Only in those environments where the bottom salinities were strongly increased were the species arranged along two interacting stress-gradients.

Deeper water mud-communities are more or less similarly constructed. In



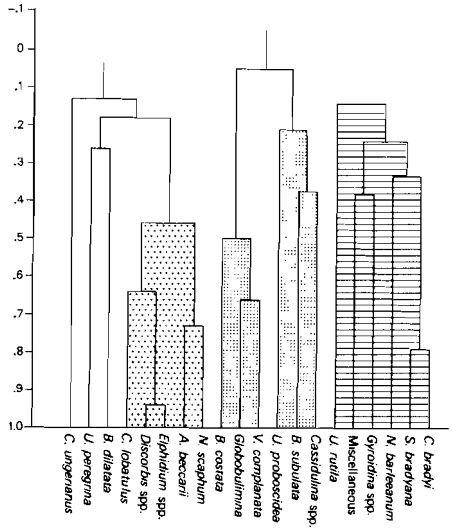


Fig. 7 Dendrogram based on the proportions of 17 taxa in 176 samples from the Late Miocene Cretan sections Exopolis, Vrysses and Khaeretiana.

Fig. 8 Dendrogram based on the proportions of 17 taxa in 46 samples from the Messinian Sant' Agatha section.

figures 9 and 8 the dendrograms of the Tortonian Scardilli section (20 taxa, 37 samples; maximum depth of deposition estimated to be about 700 metres; data by Van der Zwaan and Den Hartog Jager, 1983) and of the Messinian Sant' Agatha section (17 taxa, 46 samples; maximum depth of deposition estimated to be about 300—500 metres; data by Voogt, internal report) are depicted. In these deeper water environments the species arrangement in the dendrogram is similar to the one of the shallow water associations; the species composition, however, may be somewhat different. The group of (allochthonous) vegetation-bound species may be enlarged with displaced *Ammonia beccarii* and *Nonion scaphum* (e.g. Scardilli), whereas in these deeper water associations species like *Siphonina bradyana, Cibicides bradyi, Nonion barleeanum, Gyroidina* species and *Uvigerina rutila* gradually replace the group of *Cibicides ungerianus* c.s. A difference between the deep and the shallow water associations is the sharper differentiation of the stress-tolerant group. It is subdivided into a group which only proliferates during moderate oxygen-deficiency or nutrient-rich conditions (*Valvulineria complanata, Globobulimina* species, *Bulimina costata, Chilostomella ovoidea*) and a group which is tolerant to the interaction of oxygen-deficiency and increased salinities (slightly raised salinities: *Cassidulina* species, *Bulimina subulata* and

Uvigerina proboscidea; strongly raised salinities: *Bolivina spathulata, Uvigerina cylindrica gaudryinoides* and *Bulimina elongata*).

Analyses of the Late Miocene sections mentioned and some additional ones (Potamidha: Wonders and Van der Zwaan, 1979; Faneromeni: Wildenborg, internal report; Ay. Ioannis: Stam, internal report) resulted in a preliminary diagram (fig. 10) which indicates the occurrence of the highest abundances of the species of the stress-tolerant group with decreasing oxygen-content and increasing salinities.

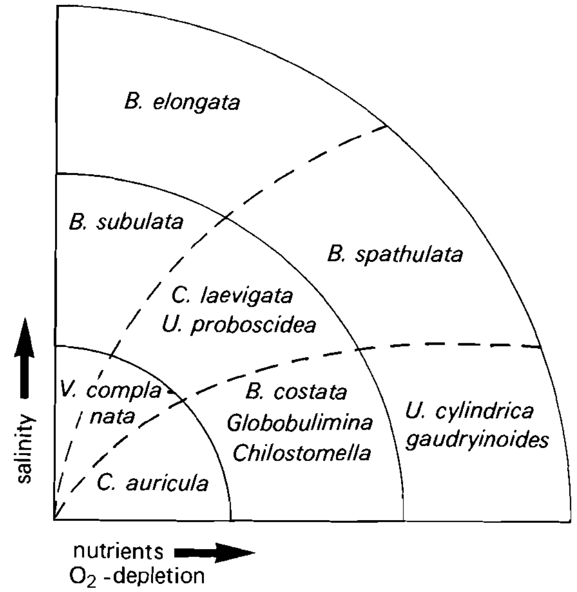
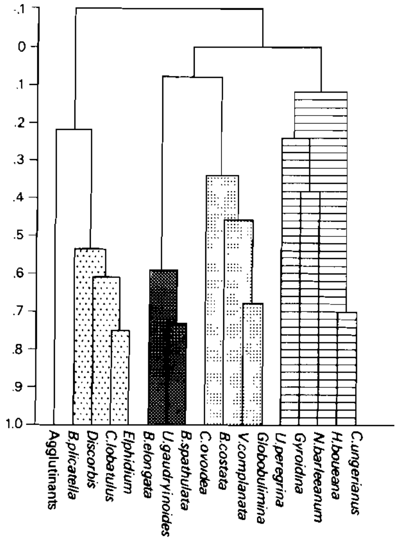


Fig. 10 Tentative diagram of maximum abundances of some Late Miocene benthic foraminiferal species with increasing salinity and/or decreasing oxygen-content.

THE LATE PLIOCENE EVENT

The principal component analysis (fig. 6) shows that the Miocene and Pliocene benthic foraminiferal associations are remarkably similar. This implies that the neteffect of the salinity crisis on the distribution patterns of benthic foraminifera was negligible. The effects consisted of a temporal interaction of the oxygen and salinity stress-gradients, followed by the eventual reduction of the bottom life nearing the evaporation phase.

A much more fundamental change occurred during the Late Pliocene-Pleistocene. During the Miocene and the greater part of the Pliocene the species arrangement along the stress-gradients was rather constant, but the



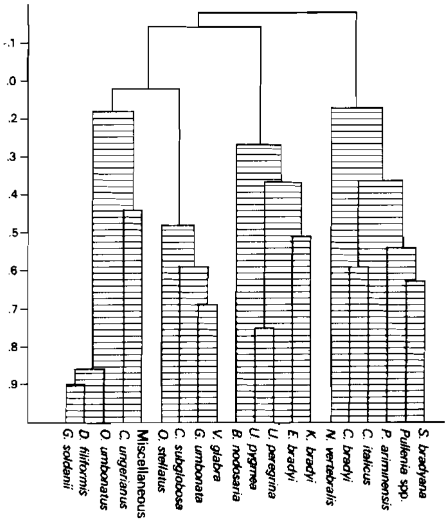


Fig. 9 Dendrogram based on the proportions of 20 taxa in 37 samples from the Tortonian Scardilli section, Sicily.

Fig. 11 Dendrogram based on the proportions of 20 taxa in 35 samples from the Pliocene Capo Rossello section, Sicily (based on data by Brolsma, 1978).

Late Pliocene event changed these patterns. This is illustrated in figures 11, 13 and 14. In these figures the dendrograms of the deeper water associations from three Italian sections are shown. From the Capo Rossello section (fig. 11) 35 samples were analyzed, using the proportions of the 20 quantitatively most important taxa. The original data matrix was published by Brolsma (1978). The dendrogram shows a peculiar arrangement of four groups, which differ widely in their composition from the other analyses available. In fact, most of the species present can be regarded as being not tolerant to stress of any kind. If the cumulative frequencies of the groups are plotted along the stratigraphic column (fig. 12), the picture becomes clearer. The shape of the dendrogram is caused by the rapid succession of the four groups in the lowermost Pliocene zone (MPL-1) and the lower part of the MPL-2. During the MPL-2 a balanced, diverse association was re-established. This pattern is clearly attributable to the re-immigration of benthic species into the Mediterranean after the salinity crisis (compare Wright, 1980) or more probably to the gradual environmental differentiation during the Early Pliocene after the initial homogeneity. During this time-slice stress-tolerant species are quantitatively poorly represented. This indicates that we are dealing with environ-

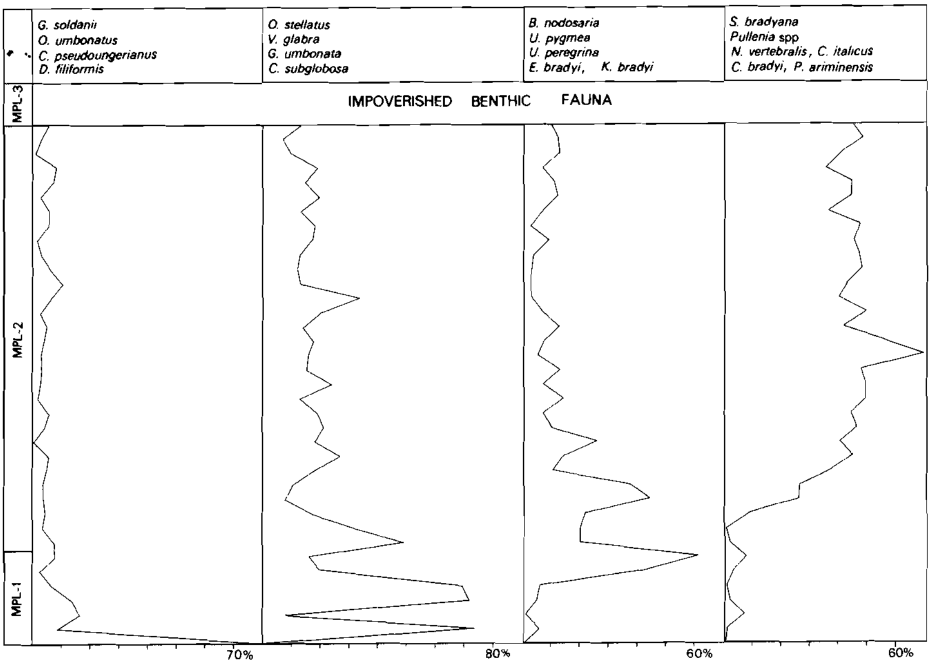
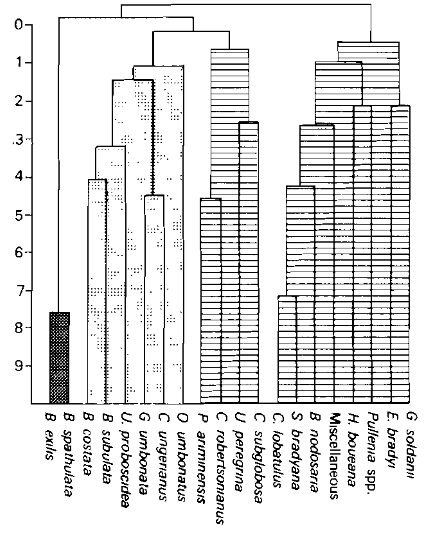


Fig. 12 Cumulative frequencies of the species in the four clusters of figure 11.

ments which were characterized by a minimum of stress, stable salinities and relatively high oxygen-contents of the bottomwater.

The next available analysis is the one of the Punte Piccola section (20 taxa from 46 samples), which is also based on an original data matrix by Brolsma (1978). The Punte Piccola associations belong to the lowermost part of the *Globorotalia crassaformis* Zone (sensu Spaak, 1983). As can be seen in figure 13, the picture of the benthic foraminiferal composition has changed drastically. Four clusters are recognizable, which are arranged again along one stress-gradient, i.e. oxygen-deficiency. Two species, *Bolivina spathulata* and *Bulimina exilis* are extremely frequent in one of the dark-coloured, laminated layers; these sediments indicate clearly deposition under oxygen-deficient conditions. Species of the second cluster, with *Bulimina costata, B. subulata* and others, proliferate less in the laminated intervals, but are still most frequent there. The other two clusters consist of species which are increasingly less tolerant to stress and are inhabitants of stable marine waters.

There are two striking differences between this dendrogram of a Late Pliocene association and dendrograms of the Miocene and Early Pliocene associations. Firstly, the rather homogeneous groups of stress-tolerant and stable marine species are now each divided into two sub-groups. This might indicate that the associations started to adapt to some sort of increased environmental variability, i.e. an arrangement along two (or more) stress-gradients. A second important observation is the fact that new species gradually started to proliferate in the oxygen-deficient biotope (e.g. *B. exilis*) and that the species which were formerly restricted to the group of stable marine species moved to the stress-tolerant group (*Gyroidina umbonata*, the *Cibicides ungerianus* group and *Oridorsalis umbonatus*).



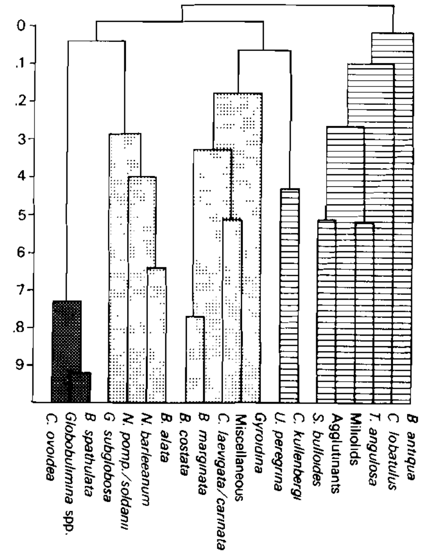


Fig. 13 Dendrogram based on the proportions of 20 taxa in 46 samples from the Pliocene Punte Piccola section, Sicily (based on data by Brolsma, 1978).

Fig. 14 Dendrogram based on the proportions of 20 taxa in 36 samples from the Late Pliocene/Pleistocene Vrica section, Calabria.

An analysis of the associations from the Pliocene part of the Vrica section (Ausems, internal report) proves that the trend of increasing changes in the community structure continues in time. The studied part of the Vrica section belongs to the *Globorotalia inflata* Zone (cf. Spaak, 1983); the frequencies of 20 taxa from 36 samples were analyzed. In figure 14 it can be seen that the group of stress-tolerant species did increase. Now, in addition to the species *Bolivina spathulata*, *Chilostomella ovoidea* and *Globobulimina* species, which are all extremely abundant in but mainly above the laminated intervals, there are two other groups which are occasionally abundant in and above the laminated marls. These groups are composed of *Bulimina costata*, *Bulimina marginata*, *Cassidulina laevigata/C. carinata*, *Gyroidina* species, *Globocassidulina subglobosa*, *Nonion barleeanum*, *Nonion soldanii/pompilioides*, and *Bolivina alata*. Thus again new species entered (*B. marginata*) and species previously present in the stable marine cluster moved to the stress-tolerant cluster (*C. laevigata/carinata*, *G. subglobosa*, *N. soldanii/pompilioides* and *B. alata*). To the stable marine group the following species were added: *Sphaeroidina bulloides*, *Trifarina angulosa* and *Bolivina antiqua;* these species were until then subordinate elements in the associations.

On the basis of the data presented so far, one has to conclude that a major event took place during the Late Pliocene. This event affected the species abundances, as is evident from the principal component analysis (fig. 6). Many new species entered and old ones became extinct in the Mediterranean (fig. 3). Most importantly, however, it seems likely that the community structure of the mud-dwelling associations changed as well.

THE NATURE OF THE LATE PLIOCENE EVENT

The timing and the nature of the effects of the northern hemisphere glaciation on the Mediterranean are poorly known. Thunell (1979a, b) and Keigwin and Thunell (1979) suggested the occurrence of a cooling some time after the exit of *Globorotalia margaritae.* They observed a significant change in the surface-water isotope composition. This interval of changes in the properties of the Mediterranean water-masses probably corresponds to the top of the *Globorotalia puncticulata* Zone or the base of the *Globorotalia crassaformis* Zone (cf. Spaak, 1983). Spaak (op. cit.) infers too that there were smaller-scale climatic changes which are expressed by the entries and exits of index-species (compare Zachariasse and Spaak, this volume). Zachariasse and Spaak suggest that a larger scale and more permanent change must have taken place during the later part of the *Globorotalia crassaformis* Zone and that it would have coincided with a major cooling. Also the results of Thunell and Williams (this volume) show convincingly that a major event did indeed take place during that time. Apparently, cool-temperate surface-waters from the Atlantic entered the Mediterranean. Recently, Zagwijn and Suc (1983) also demonstrated this cooling and dated it at 2.3 m.y. They stated that that "level marks the onset of a cyclic climatic development in the style of the Quaternary climate".

These data show that the entry of cool-temperate surface-waters probably caused the changes in the Eastern and Central Mediterranean benthic foraminiferal associations. There is a short time-lag between the changes in surface-water properties and the bottom-water change; the benthic associations started to react clearly only from the *Globorotalia inflata* Zone upwards.

The nature of the changes in the bottom-water properties might be indicated by the principal component plot of figure 6. The Late Pliocene-Pleistocene cluster is separated from the Miocene-Pliocene one along the second principal component. This second component is positively correlated with *Cassidulina carinata* and to a lesser extent with *Bulimina marginata*. Both species are known to be particularly frequent in high productive bottom-waters, especially *B. marginata* (Bandy et al., 1964a, b, 1965). One can argue, therefore, that the neteffect of the Late Pliocene event was an increase in the bottom productivity. This might imply that the entrance into the Mediterranean of cool surface-waters and possible lowering of the surface-water temperature resulted in a better vertical mixing of the water and, as far as the benthic foraminifera were concerned, ultimately higher productive systems. In reality, matters were probably far more complex than that. An important additional factor was possibly a decrease in the environmental stability. The planktonic foraminifera (Zachariasse and Spaak, this volume), the stable isotope data (Thunell and Williams, this volume) and the data of Zagwijn and Suc (1983) indicate that cooler and warmer periods succeeded each other with increasing vigour. This could have resulted in an alternation of cooler, well ventilated (productive) periods and warmer, less ventilated (less productive) periods. Another complication is the fact that the deeper basins were affected periodically by stagnation events, which resulted in the deposition of organic-rich sapropelic sediments.

If we consider all the data available, the Late Pliocene event gives an impression of considerable complexity. Not only did the oceanographic patterns change during that time, but probably the biological patterns were reorganised considerably as well. It is without doubt during that time that the modern Mediterranean foraminiferal patterns were shaped.

ECOLOGICAL PATTERNS THROUGH TIME

Figures 3 and 4 give an impression of the changes in the distribution of benthic foraminifera during the Late Pliocene. From figure 4 it can be deduced that the total number of local extinctions during the Late Pliocene time-slice is more or less balanced by the number of immigrating (temperate?) species, although the peak of exits precedes that of the entries. In other words, the Mediterranean became temporily an ecologically undersaturated area in which immigrating species could establish themselves successfully next to the indigenous population. The most likely explanation for the local extinctions of a number of species is that the physical/chemical conditions at the bottom changed considerably in conjunction with the changes in oceanography.

Although the total number of species probably did not change very drastically, a considerable modification of the ecological patterns took place. The successive dendrograms, presented before, suggest a rather systematic change of the species arrangement. This is summarized in figure 15.

One could argue that these patterns are caused by the clustering technique used or by other statistical artefacts. There is, however, no indication that this is the case. Statistical effects, like the closed-sum effect, are thought to have been successfully eliminated by the BALANC procedure. The dendrograms should be ipso facto free from this. Of course, the relative position of the clusters in the dendrograms is a matter which can be manipulated, but in the case of every analysis these clusters were arranged according to the highest frequencies of the species relative to the laminated intervals. It should be noted further that in the dendrograms only a selection of species out of the total association is given. However, since the most frequent taxa in each section were used for the quantitative analyses (cumulative frequencies of these taxa are between 65–90%) the dendrograms are considered to be representative for the association and mutually comparable. The pattern in figure 15 is far from complete, as it is based only on the information contained in the dendrograms presented in this paper. The picture can be modified in the future if for instance analyses of Pliocene shallow water associations are incorporated. For instance, *B. exilis* and *B. alata* appear earlier in the Pliocene in the Cretan than in the Sicilian sections. Nevertheless, it is considered to be representative enough for some conclusions to be drawn.

From the dendrograms and figure 15 it is evident that a number of species shift from clusters indicative of stable marine conditions to clusters indicative of moderate oxygen-deficiency or from the latter clusters to those indicative of strong oxygen-deficiency. These shifts coincided with and were probably related to the Late Pliocene event. An important observation is that all the shifts are in one direction, i.e. from relatively stable biotopes to more stressed ones. Further, it is important to note that the shifts occurred mainly in the group of indigenous species; from all the species which enter the record in the course of the time, only *Bulimina exilis* and *Bulimina marginata* were able to populate stressed biotopes successfully. This suggests that the shifts were rather unrelated to the ecological effects of the newly entered species. On the contrary, it seems that the shifts are connected to a large extent with the extinction or drastic decrease in abundance of species typical of the oxygen-deficient habitats (e.g. *U. gaudryinoides*, *B. exilis*, *U. proboscidea*, *B. subulata*) which in turn may have been due to the changed physical/chemical conditions. This could have created an ecological "vacuum" on which some species reacted by populating these biotopes. What in fact could have hap-

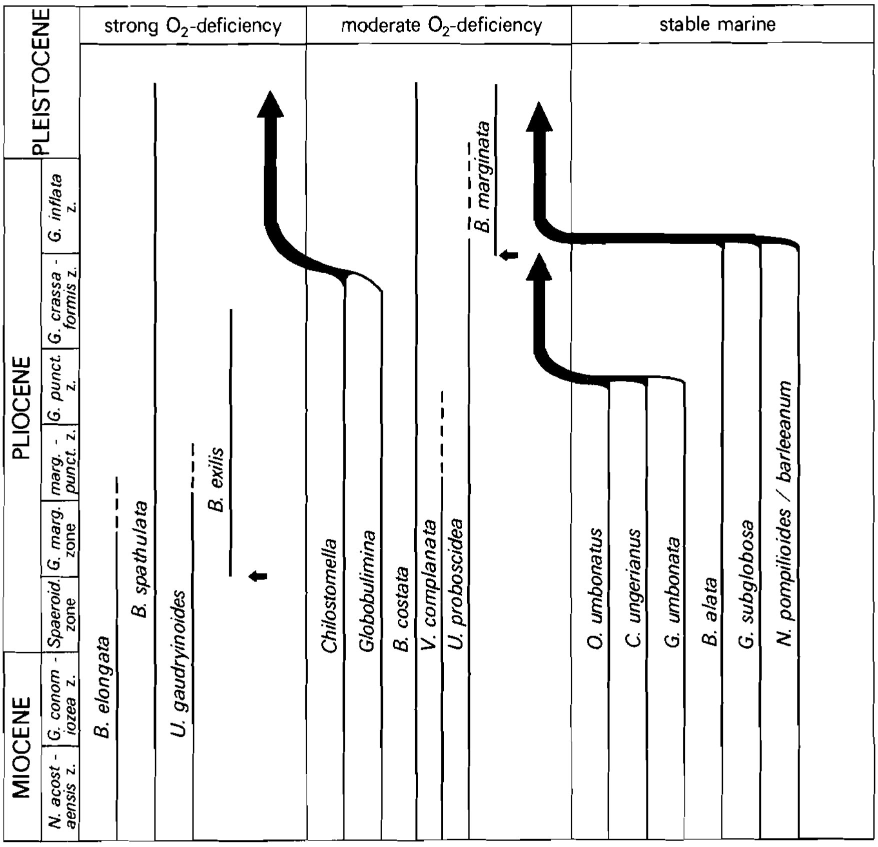


Fig. 15 Synthesis of ecological patterns through time of the species mentioned in the text and the dendrograms. For discussion see text.

pened is known in the literature as niche expansion or niche compression (compare e.g. Pianka, 1978) and is shown to occur in many types of populations, from plants to higher vertebrates. In this concept, species can expand their habitat if there is an ecological vacuum or, in other words, if there is no resisting competition pressure from other species. It is useful to emphasize that it is not implied that species change their niche, as this impression may have been given in earlier publications by using the term "changing niche pattern" (Van der Zwaan, 1982a, b). The only implication is that within its fixed physical/chemical/biotic tolerance limits a species can be maximally abundant in different environments depending on competition. In an environment with many competing species it will inhabit a small environmental range; with a few species it has "room" to expand over a wider environmental range.

The phenomenon of reorganisation of the ecological patterns is probably intrinsic in large scale physical/chemical changes in the marine environment which result in faunal turn-overs. Such events, resulting in (local) extinctions and the occurrence of new species, are numerous in geological history. Therefore, such phenomena are in our opinion of extreme importance to our evaluation of past ecological patterns and consequently to our reconstructions of ancient environments.

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MARINE AND CONTINENTAL ANTAGONISTIC INFLUENCES IN MEDITERRANEAN LATE NEOGENE TO RECENT CLAY SEDIMENTATION

HERVÉ CHAMLEY

ABSTRACT

The clay mineralogy of Mediterranean Late Miocene to Quaternary marine sediment successions mainly reflects the terrigenous source material; diagenetic and sedimentary processes within the basin apparently played a subordinate role only. Sorting effects, such as differential settling, occur especially on the shelf, but may be observed also in some re-deposited sediment types. Diagenetic effects can be easily recognized; they are generally restricted to specific facies, areas and time-slices. These effects include degradation in organic-rich sediments and neoformations in deposits of volcanic origin.

Terrigenous influences extended throughout the Mediterranean since the Tortonian. These influences were related to tectonic activity in different areas during limited intervals of time, and to climatic changes that occurred without interruption. They continued even during the Messinian, which was marked by a specific peri-Mediterranean climatic crisis.

The clay mineral associations within the Mediterranean basins are a measure for the average stage of weathering of the adjacent continental soil and rock formations.

INTRODUCTION

Large amounts of clays have been deposited in the Mediterranean realm since Late Tortonian time, even during the Messinian, when argillaceous interbeds were deposited during the accumulation of evaporite sequences (e.g., Drooger, 1973; Ryan, Hsü et al., 1973; Hsü, Montadert et al., 1978). Clay minerals are also nearly always found in relatively coarser sediments.

During the last twenty years numerous studies have been performed on the occurrence, the nature and the meaning of Mediterranean clay minerals. The purpose of this paper is to illustrate by means of succinct examples the way in which clay mineral associations from marine sediments can be used to reconstruct marine and continental environments that existed since the Late Neogene. The sections investigated include various DSDP profiles, piston cores and outcrops on land (fig. 1); different techniques were applied: inorganic geochemistry, X-ray diffraction, and electron microscopy. In many cases comparisons have been made with lithological, micropaleontological and/or isotopic data.

MARINE INFLUENCES ON CLAY SEDIMENTATION

In marine environments diagenetic processes occur mainly in organic and volcanic sediments.

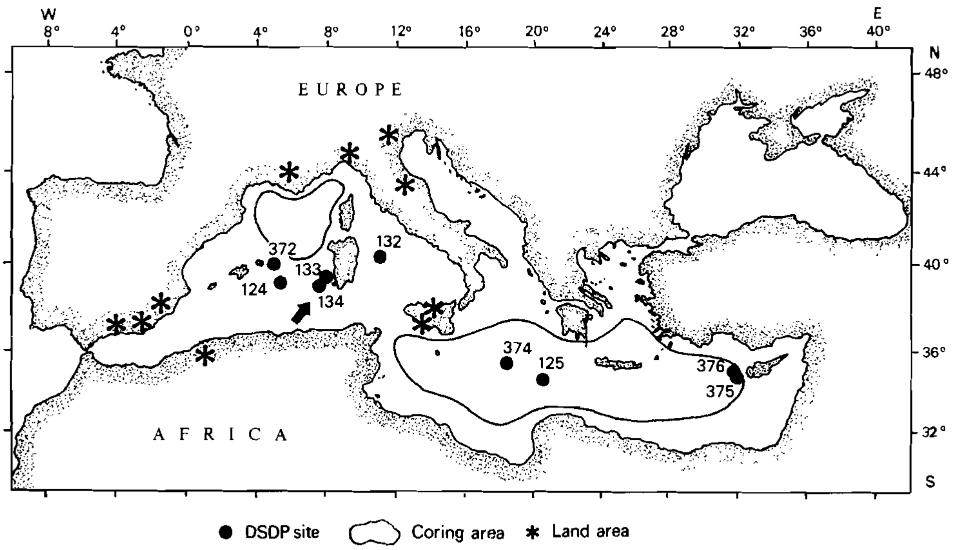

Fig. 1 Position of sections and major areas studied.

Organic environments

Sapropelic and sapropelitic layers are frequently found in Quaternary successions of the Eastern Mediterranean. Such layers were formed in particular in the deepest and most confined areas (Hellenic Trench, Levantine Basin, Ionian Basin); often they can be correlated from one core to the other. Sapropelic and sapropelitic layers have also been described from the Pliocene and from the Tortonian (Cita et al., 1977; Cita and Grignani, 1982; Kidd et al., 1978; Rossignol-Strick et al., 1982; Sigl et al., 1978).

The Quaternary sapropels generally display sharp lower and less distinct upper boundaries. Most probably their formation was related to the effects of a density stratification of Eastern Mediterranean water masses during the humid (often the interglacial) periods. The density stratification was probably mainly caused by the input of fresh waters from the Black Sea/Aegean Sea and/or from the Nile river, which resulted in stagnation of dense and saline intermediate and deep marine waters (e.g., Ryan, 1969; Cita and Grignani, 1982). The decrease of the vertical circulation favoured a reducing environment and, consequently, the preservation of organic matter of continental and marine origin. Hence, plant remains and siliceous debris can now easily be studied (Chamley, 1971; Rossignol-Strick, 1973). The periodical renewal of the normal vertical circulation, in general during the dryer and colder stages, permitted the progressive re-oxygenation of the basin and the reappearance of benthic life.

Sapropels often display morphological, mineralogical and geochemical changes, which were not observed in the under and overlying normal sediments. The latter sediments contain classical "cloudy" and flaky clay particles, similar to those formed on peri-Mediterranean landmasses. The sapropels proper tend to be devoid of the smaller clay particles; they only include large flakes displaying corrosion at their periphery (Chamley, 1971, 1972; Cita et al., 1977). The amount of smectite decreases frequently; the ratios of other clay minerals often change, complexes of organic matter with silica and various trace elements are formed. The measure of change appears to increase towards the central part of the sapropel area, in the deepest part of

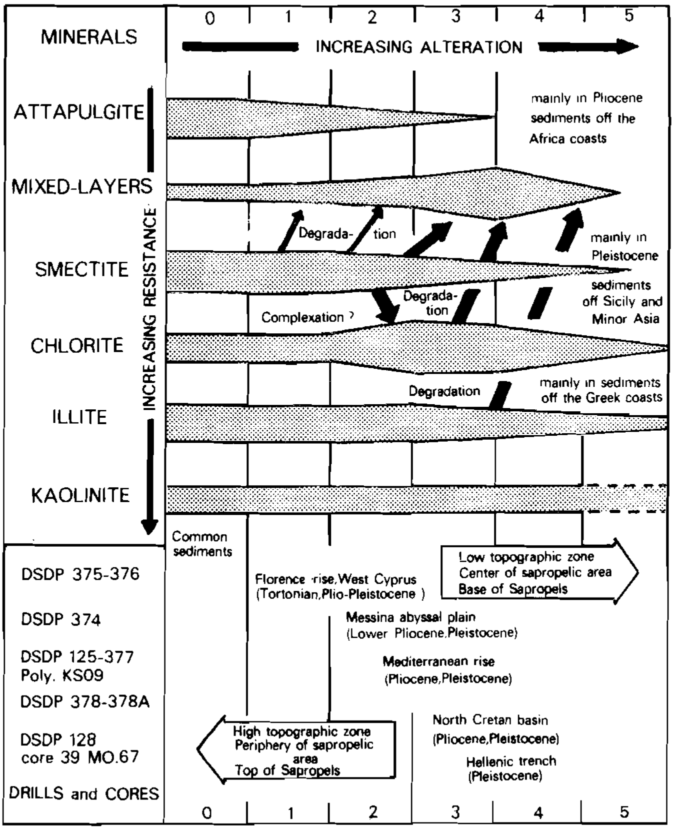

Fig. 2 Clay mineral diagenesis in Plio-Pleistocene sapropels of the Eastern Mediterranean (after Sigl et al., 1978).

the basin, at the basis of the organic layers. Clay minerals and other components from sapropelitic sediments from the margins of the basins appear to be only slightly or not at all modified (Robert and Chamley, 1974; Dominik and Stoffers, 1979).

Clay minerals from Eastern Mediterranean sapropels are thought to have been dissolved to a variable extent by organic acids. Clay destruction was related to the position of the sapropels in the basin, the degree of accumulation of organic material, and the original composition of the clay fraction (Sigl et al., 1978). Five steps have been recognized in the clay alteration processes (fig. 2). The implications are:

- an increased susceptibility to weathering by organic compounds from kaolinite to palygorskite. The susceptibility range is kaolinite < illite < chlorite < irregular mixed layers < smectite < palygorskite.
- the existence of mineralogical "barriers" to the clay mineral alteration, e.g., smectite is only attacked when palygorskite fibres are nearly destroyed, the degradation of chlorite depends on the stage of the smectite alteration, etc.
- the development of new composite minerals, such as organo-mineral complexes (pseudo-chlorites) and irregular mixed layers.

It may be concluded that Eastern Mediterranean sediments were subject to diagenetic processes acting in various ways during restricted periods in the Late Cenozoic, but sediments deposited during such periods are easily recognizable because of the characteristic lithology of the organic-rich layers.

Volcanic environments

In the Mediterranean sediments of volcanic origin occur often close to volcanic islands (e.g., southern Tyrrhenian Sea, Straits of Sicily, the eastern basins); tephra layers are widely distributed (Keller et al., 1978; Ninkovich and Heezen, 1965). These deposits are, as a rule, hardly influenced by clay diagenesis, because of restricted specific surfaces and low susceptibility to weathering of many glassy particles (Chamley and Giroud d'Argoud, 1978). The most important changes are identified close to volcanic sources, where various alteration processes occur (e.g. Chamley, 1971; Honnorez, 1970; Monaco et al., 1979; Valette, 1972).

The pumiceous sediments from the collapsed caldeira of Santorini (Aegean Sea) represent a good example of marine clay diagenesis in such volcanic environments (Chamley and Millot, 1972). The (sub)recent sediments at the top of the piston cores show an abundance of pumice and of various ashes from the eruption of Thera (Santorini) island, and of siliceous debris, mainly diatoms. Clay minerals are scarce; the composition is similar to that of normal, land-derived clays found outside the caldeira (illite, chlorite, smectite). Lower in the cores the abundance and the crystallinity of smectite increase rapidly. The clay minerals develop at the outside of the pumiceous particles, not on glassy fragments. Simultaneously the diatom fragments are progressively dissolved, but the total amount of silica remains constant. At about 180 cm below the sediment surface, all biogenic silica is dissolved. The increase of smectite continues more slowly below this level (fig. 3).

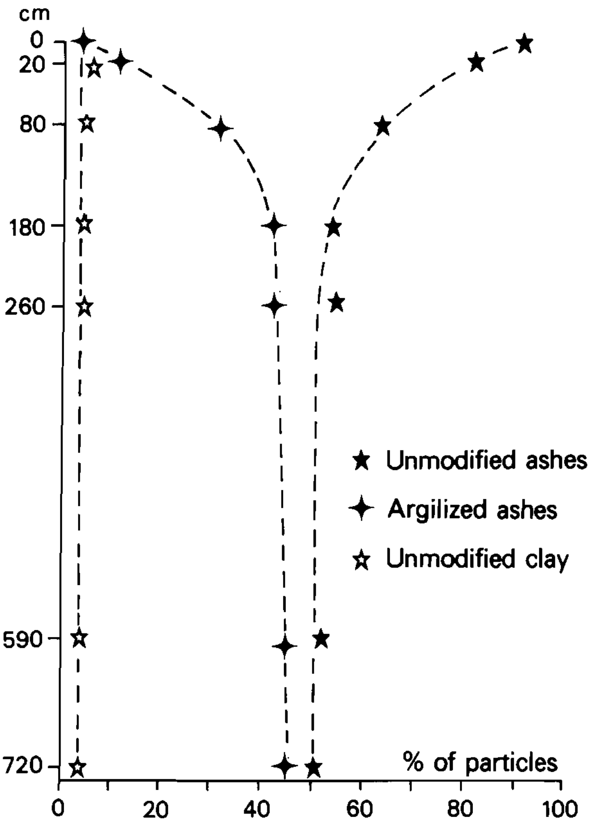

Fig. 3 Diagenetic evolution of pumice particles into smectite in a diatom-rich piston core recovered from the Santorini caldeira, Aegean Sea (after Chamley, 1971).

These observations may be explained as follows: Very fine and porous pumice is geochemically very unstable because of its large specific surface and its amorphous structure. The pumice particles are rapidly transformed into smectite from the surface inwards, making use of the available silica derived from diatom debris. After all diatoms have been dissolved, the smectite growth continues more slowly, using the less easily available silica of the volcanic debris. Such examples of clay diagenesis are recorded in restricted areas of the Mediterranean Sea, and can easily be recognized by lithological, mineralogical and geochemical studies.

Hydrodynamic processes

Most of the hydrodynamic processes that strongly influenced the clay mineralogy are observed on the continental shelves and slopes; they evidence differential settling mechanisms (e.g. Aloisi et al., 1975; Arnoux and Chamley, 1974; Chamley, 1971; Monaco, 1971; Orsolini and Chamley, 1980). In the deeper environments differential settling processes are not so common and often of secondary importance only. Here processes occur in reworked sediments, like turbidites (Maldonado and Stanley, 1981; Monaco et al., 1982; Rupke, 1975). Thus the clay mineralogy of marine sediments is mainly influenced by the transport and the distribution of mineral particles in suspen-

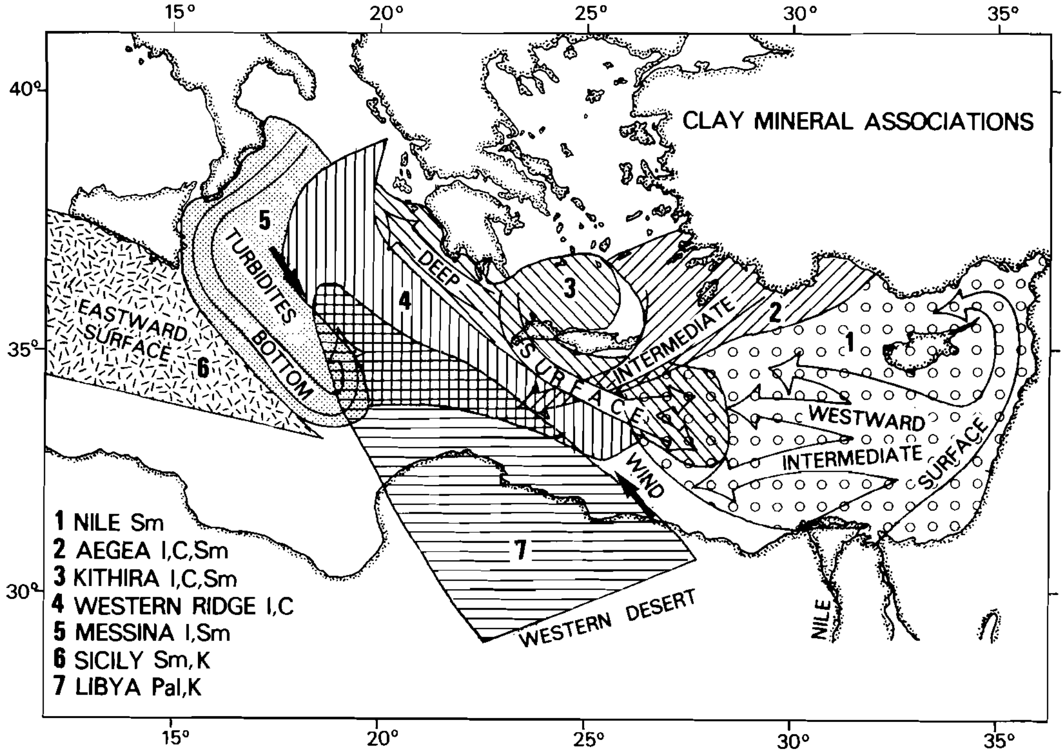

Fig. 4 Distribution of clay minerals in the Eastern Mediterranean by different water masses (after Venkatarathnam and Ryan, 1971).

sion in different water masses, which implies that different water masses are characterized by a typical clay mineral association.

Only a few examples of such general processes have been described for various basins in the Mediterranean (e.g. Tomadin, 1974; Venkatarathnam and Ryan, 1971). For instance, Venkatarathnam and Ryan (1971) published theoretical dispersion patterns of clay minerals derived from seven areas around the southeastern Mediterranean (fig. 4): the Nile basin, the area North-East of the Aegean Sea, the Kithira area, the area north of the Ionian Sea, southern Italy, southern Sicily and northern Libya. These authors proposed a tentative model in which six different water masses account for the distribution of clays in surface sediments: Nile-derived surface waters and inferred intermediate waters more westward, Aegean surface and intermediate waters, deep water off the Peloponnesus moving to the North-West, bottom water and turbidity currents in the Messina cone and abyssal plain, water bodies characterized by eastward-directed surface currents from the Atlantic and the western Mediterranean, and water bodies characterized by the influence of North-African, northward-directed winds.

Such models are scarce for the Mediterranean, and they are difficult to prove, because of the strong mixing and the wide dispersal of clay minerals from different sources. Changes in the composition of clay mineral associations from one area to another, however, are usually very progressive; they reflect differences in the average supply of detritus from different sources (Chamley, 1971; Emelyanov, 1972; Stanley, 1972). This may be explained in terms of the narrowness of the Mediterranean and the proximity of landmasses favouring the mixing of detrital minerals, the latitudinal extension of the basin which prevents important North-South exchanges, and the semi-enclosed character of the Mediterranean, which limits exchanges of water masses with the world ocean. As a consequence it seems justified to interpret changes in Mediterranean clay mineral associations in terms of environmental changes that occurred on the neighbouring landmasses through time.

CONTINENTAL INFLUENCES ON CLAY SEDIMENTATION

Tectonics

Tectonic movements defining the uplift of landmasses are clearly reflected in the clay mineral record of the adjacent basins; the renewal of the reliefs will often result in great changes in the processes of erosion and transport. For instance, the Pliocene of Capo Rossello (Caltanisetta Basin, southern Sicily, Cita and Decima, 1975) is characterized by two successive intervals with distinct lithological and mineralogical properties (Chamley, 1976). The Lower Pliocene comprises hemipelagic, marly limestones (Trubi) with significant amounts of palygorskite, which is frequent in Paleogene sediments of North-Africa (e.g. Millot, 1964; Sassi, 1974). The transition from Trubi limestones to the overlying terrigenous, clayey marls of the Monte Narbone Formation, which took place in early Late Pliocene time, corresponds to a sudden increase of smectite and kaolinite. The latter minerals are abundant in older Sicilian rock sequences (e.g. Mascle, 1973). The Upper Pliocene shows a progressive increase of the amount of smectite and kaolinite.

It is not difficult to understand these observations if we consider the Plio-

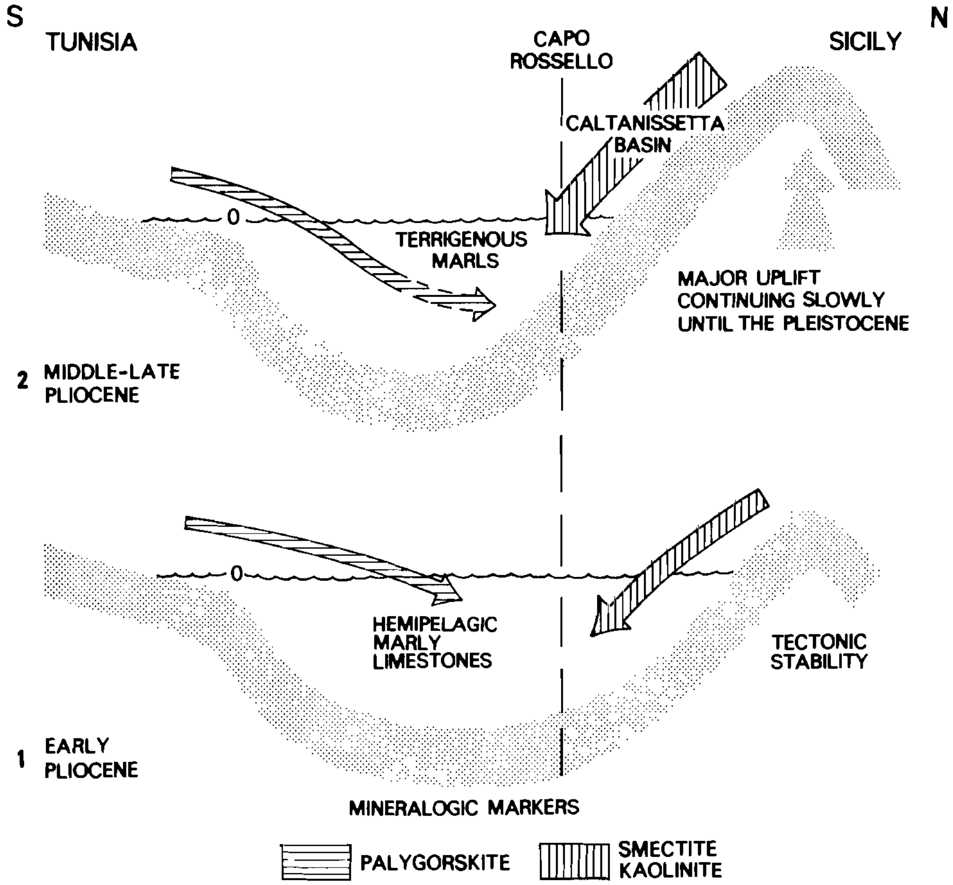

Fig. 5 Tectonic interpretation of lithological and mineralogical changes in the Pliocene of Capo Rossello, Caltanisetta Basin, southern Sicily (after Chamley, 1976).

cene geotectonic history of the Caltanisetta Basin (fig. 5). In the Early Pliocene Capo Rossello was situated in an open marine, large basin where mainly pelagic, calcareous oozes were deposited. The admixture of terrigenous components was controlled by the influence of African as well as European sources, which supplied, besides more common minerals like illite, chlorite and mixed layers, minerals like palygorskite, smectite and kaolinite. During the early Late Pliocene a major tectonic event caused the uplift of northern Sicily (Mascle, 1973). At the time the Capo Rossello area became subject to a rapidly increasing supply of clastics of local, i.e., Sicilian provenance, which is reflected in the clay mineral record by the increase of clay minerals like smectite and kaolinite. The uplift of Sicily continued progressively in the course of the Late Pliocene, which led to the increase of clastic supply from Sicilian sources, and, ultimately, resulted in the emersion of the Caltanisetta Basin.

The Capo Rossello example can easily be understood, since the mineralogical changes correspond to changes in lithology, and because the literature provides reliable data supporting the clay mineralogical interpretation. In many cases, however, clay mineral stratigraphy is the only tool that can be used to recognize the effects of tectonic movements in marine sediment successions. This especially applies to sequences deposited far away from land, in a setting where only fine-grained material in suspension reaches the bottom of the basin. For instance, several mineralogical breaks have been observed in Late Miocene and younger deep sea sediments of the Central and Eastern Mediterranean (Chamley et al., 1977), which breaks can be related to tectonic events affecting Italy, Sicily, the Hellenides, the Taurides, or the deep basins proper.

Climate

Changes in the composition of clay mineral associations in marine sediments that can be translated in terms of environmental changes on adjacent landmasses are mostly climate-controlled. Soil formation under stable tectonic conditions progressively leads to an equilibrium between the continental climate and the clay mineralogy. Fluctuations in the climate through time cause changes in the nature of soils and, consequently, in the composition of clay mineral associations.

Since clays accumulating in marine basins mainly originate from the erosion of superficial, unconsolidated, widely distributed soils, their mineralogy often reflects the climatic conditions that underlie pedogenesis and continental weathering. Hence, many tentative paleoclimatic reconstructions based on clay mineral analyses of marine sequences have been made for the

Mediterranean. A few examples will be discussed here; they concern the Late Quaternary, the Plio-Pleistocene, and the Late Miocene.

Late Quaternary

The clay mineralogy of Upper Quaternary successions reflects in various ways the alternation of glacial and interglacial periods. In general particles transported to the sea during cold and rather dry periods are well-shaped, they show a fairly high SiO_2/Al_2O_3 ratio, and they contain relatively abundant, well-crystallized illite, chlorite and feldspars. Particles deposited during warm – humid periods, on the other hand, are often smaller, and they display flaky outlines; an increased amount of mixed layers, kaolinite, and poorly crystallized smectite can be observed. There is a decrease of SiO_2 and of oxidized facies.

Measurements performed on X-ray diagrams make it possible to estimate the intensity of continental weathering, and to reconstruct climatic conditions. In paleoclimate curves obtained from mineralogical data it appears sometimes possible to discriminate between the relative importance of temperature and humidity factors, by incorporating radiometric ages and data on sedimentation rates (Chamley, 1971). The comparison of mineralogical

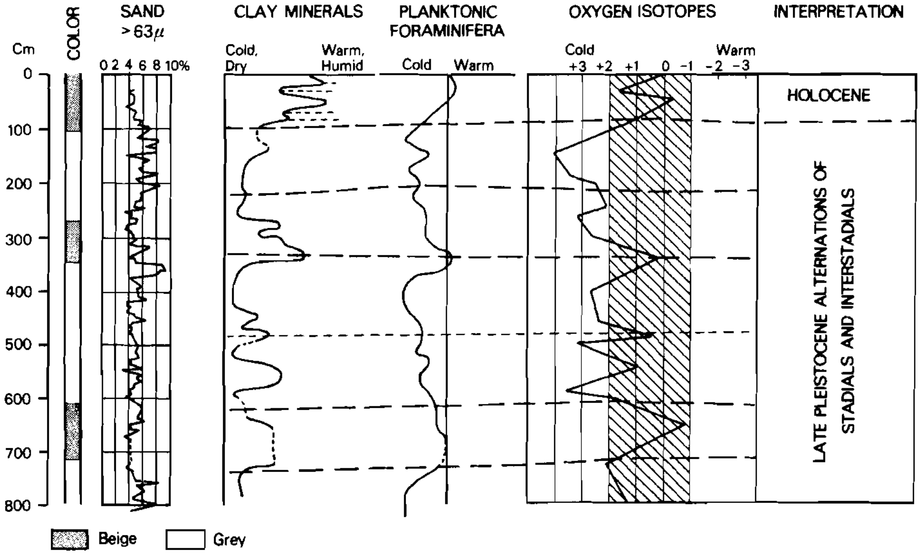

Fig. 6 Climatic curves for the Late Quaternary of a core in the Western Mediterranean, inferred from clay minerals, planktonic foraminifera and oxygen isotopes (after Rotschy et al., 1972).

data with those obtained from e.g. planktonic foraminifera, calcareous nannoplankton, pteropods or stable isotopes (fig. 6) offers a promising tool to distinguish various climatic signals for a certain time-slice (e.g. Blanc-Vernet et al., 1969, 1975; Cita et al., 1977; Müller et al., 1974; Rotschy et al., 1972). One of the main problems and, consequently, one of the main topics of current research, however, is to separate climatic from other environmental signals that can be inferred from the clay mineral record of marine cores.

Plio-Pleistocene

Data on the general evolution of Mediterranean Plio-Pleistocene climates are still scarce. One of the most complete sections to study the climatic evolution is formed by the sediments of DSDP Site 132 in the Tyrrhenian Sea. In principle, the whole Pleistocene can be studied in a similar way as described for the Late Quaternary, because the climatic factors influencing the clay mineralogy were the same.

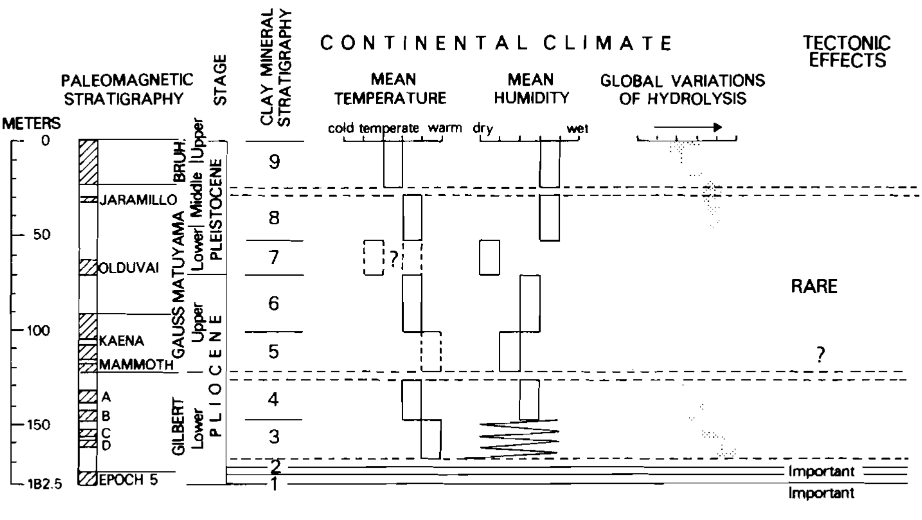

Fig. 7 Tentative reconstruction of the Plio-Pleistocene climatic evolution, based on the clay mineralogy of DSDP Site 132, Tyrrhenian Sea (after Chamley, 1975).

The paleoclimate curve inferred from clay mineral data of Site 132 (fig. 7) roughly corresponds to that based on planktonic foraminifera (Cita, 1973; Chamley, 1975). Three time-successive climatic intervals have been proposed for the Quaternary; these intervals are characterized by:

- rather dry and temperate conditions, from about 2 to 1.5 MY

– temperate to temperate-warm and humid conditions, from about 1.5 to 0.7 MY
– temperate-humid conditions with great fluctuations in the intensity of weathering processes, related to the alternation of glacial and interglacial stages, from about 0.7 MY to Present.

It is far more difficult to reconstruct the development of the Pliocene climate by means of clay mineral analysis, because it is more difficult to discriminate between various influences, such as cold and humid, or warm and dry, than it is for the Pleistocene. Moreover, the effects of tectonic movements may have interfered with climate-induced changes. The comparison of clay mineral data with those derived from e.g. foraminifera (Cita, 1973), however, makes it possible to arrive at a tentative, generalized climatic reconstruction (fig. 7; see also Chamley, 1975). Apart from two short episodes marked by tectonically-controlled reworking of palygorskite, smectite, kaolinite and iron oxides, the Pliocene can tentatively be subdivided into four climatic intervals, which are characterized by:
– arid, warm conditions with fluctuations in continental humidity, from about 5 to 4.1 MY
– transitional, temperate-warm and fairly humid conditions, from about 4.1 to 3.4 MY
– fairly dry, probably temperate-warm conditions with increased hydrolysis, from about 3.4 to 2.7 MY
– transitional, temperate-warm, fairly humid conditions with a decrease of hydrolysis, from about 2.7 to 2.0 MY.

This working hypothesis has to be checked and improved by more detailed comparisons of clay mineral and other data, such as can be obtained from marine microfossils and from continental markers (e.g. pollen, Suc and Cravatte, 1982).

Messinian

Uppermost Tortonian to lowermost Pliocene clay mineral associations have been studied from sediments of Mediterranean D.S.D.P. sites (legs 13 and 42) as well as from sequences exposed on land (Spain, Algeria, Sicily, southern France, northern Italy; see also fig. 1).

One of the most important results implies the almost systematic increase of the smectite group in Messinian successions, which increase is accompanied by a lower diversity of the clay mineral associations (Chamley et al., 1978; Chamley and Robert, 1980; Rouchy, 1981). Various data indicate that the clay mineralogy of Messinian sediments is hardly influenced by diagenetic processes; it mainly reflects terrigenous supply (Chamley et al., 1977).

Since smectites are generally less frequent in pre-Messinian (in particular Tortonian) deposits than they are in Messinian sediments, it seems most probable that the smectites represent the erosion products of soils that developed, and weathering processes that occurred, during the Messinian itself. This would require the existence of well-developed smectite soils along the margins of the marine basins during most of Messinian time. Such smectite soils are known to extend mainly in poorly-drained areas with a temperate to warm climate and with a high contrast between dry and humid periods (Paquet, 1969). The alternation of dry and wet episodes during the Messinian could have contributed to a cyclicity in pedogenesis and sedimentation patterns, which ultimately led to the great lithological changes observed in many areas of the Mediterranean basin. This may be summarized as follows (fig. 8):

– the arid parts of a cycle would have corresponded to ionic trapping in

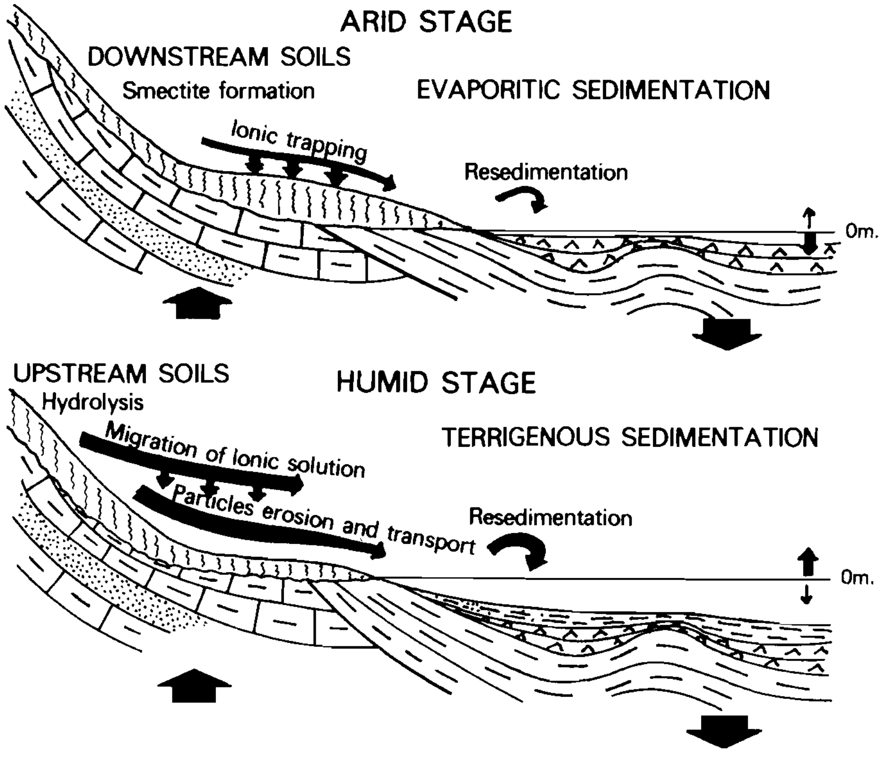

Fig. 8 Interpretation of Messinian pedologic and sedimentary cycles, based on the study of Sicilian clays (after Chamley et al., 1977; note that the duration of arid and humid stages may have changed considerably through time).

downstream areas of the presumedly desiccated basin, and to the formation of major evaporites in the basin proper.

– the humid parts of a cycle would have determined hydrolysis and reworking of soils on land and, as a result, the deposition of smectite-rich terrigenous sediments on top of evaporites.

It is of importance to note that the conspicuous mineralogical changes typical for the Messinian, have not been found outside the Mediterranean. For instance, sediments of Site 397 (off Cape Bojador, eastern North-Atlantic) do not show any important change in the clay mineralogy from the Upper Tortonian to the Pleistocene (fig. 9, Chamley and Giroud d'Argoud, 1979). Only small variations in clay mineralogy were observed, which implies the existence of a fairly stable climatic regime since Late Miocene time. Such fairly stable conditions governed large parts of the world; they developed after a world-wide cooling event (e.g., Shackleton and Kennett, 1975).

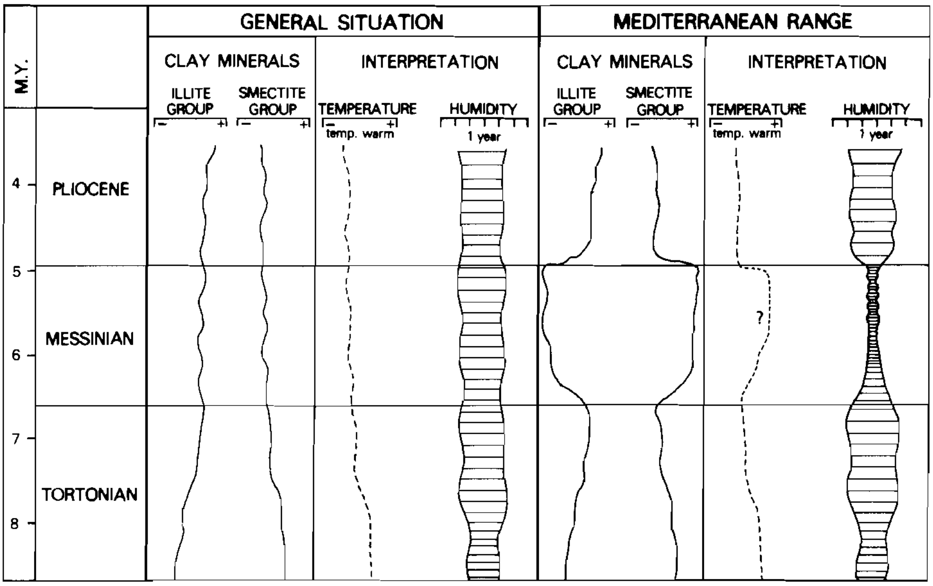

Fig. 9 Outline of Late Neogene climatic development within and outside the Mediterranean area, inferred from clay mineral data.

The great mineralogical differences between Mediterranean and extra-Mediterranean areas are confined to the Messinian; in Tortonian time and during the Pliocene the Mediterranean climatic patterns were comparable to those of adjacent parts of the world's oceans. Therefore, the Mediterranean Messinian climate was probably strongly influenced by specific conditions in the Mediterranean itself. Probably the Messinian salinity crisis was associated with a peri-Mediterranean climatic crisis, which was related to a number of specific environmental conditions (fig. 9) that were confined to the Mediterranean and did not occur outside (Chamley and Robert, 1980). These conditions include the semi-enclosed character of the Mediterranean, the increased desequilibrium of the water budget, the strong evaporation and formation of evaporites, the subsequent atmospheric "desiccation", the relative aridification of Mediterranean borderlands, the more pronounced alternations of dry and humid periods, the development of smectite-rich soils in coastal areas and, perhaps, a slight increase of the average temperature.

It may be concluded that the clay mineralogy of Mediterranean pre- and post-Messinian sequences mainly reflects the development of the world's climate, whereas the clay mineralogy of Messinian deposits was determined by the influence of specific peri-Mediterranean climatic conditions. Other influences were apparently only of local and/or ephemeral character, tectonic activity, for instance, being mainly restricted to the Tortonian/Messinian and Messinian/Pliocene boundary intervals. Locally, the geomorphological configuration permitted the development of large amounts of fibrous clays, including palygorskite and sepiolite, as in the Cucuron Basin, southeastern France (Chamley et al., 1980). Differential settling played a subordinate part in some areas; the influence of petrographic provinces on the composition of Messinian clay mineral associations was generally masked by the development of specific soils.

CONCLUSIONS

The clay mineral record of Mediterranean Late Tortonian to Recent sediments reflects the combined effects of marine and continental processes. As a rule, however, marine influences seem to have been restricted in space and time; they mainly affected three easily recognizable sediment types: 1) Sapropels and sapropelitic sediments, which display various stages of mineralogical degradation, depending on, among other things, the degree of organic accumulation. 2) Sediments of volcanic origin, which bear evidence of neoformation of smectite in restricted areas, mainly in sediments with abundant fine, porous ashes and biogenic, siliceous debris. 3) Sediments from deep sea fans and from the continental shelf which may show differential settling and other sorting effects, caused by synsedimentary processes or reworking phenomena. The relation between the clay mineral associations and the overlying water masses is often masked by mixing processes, the absence of North–South exchanges of any importance, and by the overprint of supply from neighbouring landmasses.

Continental influences had a large impact on the composition of the clay mineral associations throughout the Late Cenozoic. The effects of tectonic events influenced the clay mineralogy of the marine sequences less often and on a more local scale than did changes in climate, but such tectonic effects were more vigorous and could mask the climatic signal. The tectonic instability often caused a rejuvenation of reliefs. As a consequence, the clay mineral associations transported into the marine basins during periods of tectonic instability reflect erosion products of rock formations rather than reworked soils. Clay minerals allow to recognize tectonic events that occurred since the Late Miocene, both from studies of land sections and of deep sea cores, the latter generally being devoid of any other lithological changes that can be related to tectonic activity.

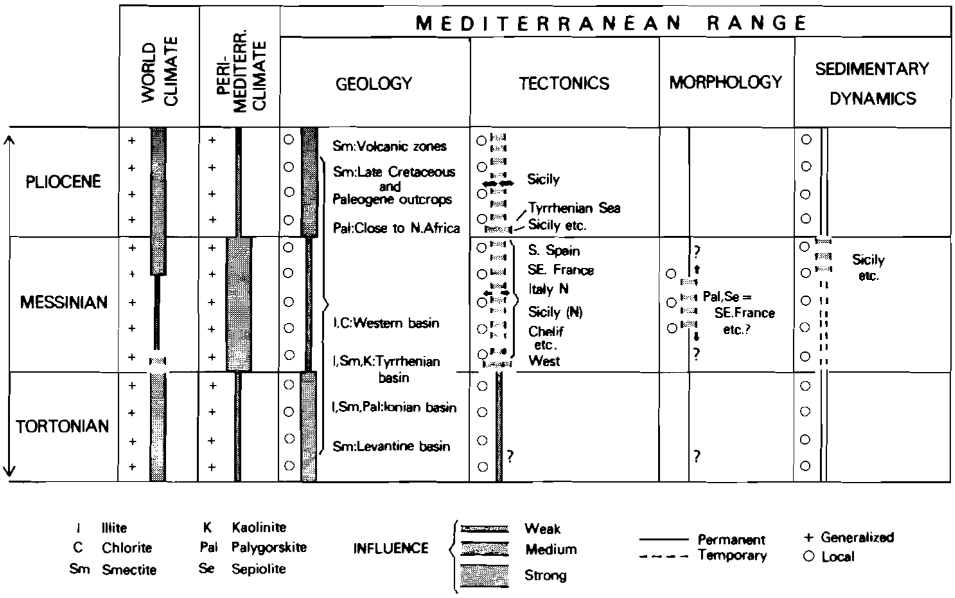

Fig. 10 Influence of various environmental parameters on Late Neogene clay sedimentation in the Mediterranean (after Chamley and Robert, 1980).

The early Late Miocene world-wide cooling initiated an increased supply of slightly altered continental products; for some time afterwards a fairly constant climatic regime characterized the open oceans. In Messinian time, however, specific climatic conditions developed in the Mediterranean, probably caused by a peri-Mediterranean crisis in the rainfall regime. These conditions were marked by the abundant supply of smectite in Messinian time; they ended at the beginning of the Pliocene in response to the Early Pliocene flooding.

A summary of the influence of various environmental parameters on Mediterranean Late Neogene clay sedimentation is visualized in figure 10.

The clay mineralogy of Plio-Pleistocene successions reflects in various ways, and with a variable degree of precision, weathering processes on neighbouring landmasses which were in particular related to the alternation of glacial and interglacial periods. In combination with other paleoclimatic data the clay mineral curves are therefore of great use to unravel the complex pattern of the effects of climatic signals and those of other environmental changes.

ACKNOWLEDGEMENTS

This paper is dedicated to all colleagues working on Mediterranean Late Cenozoic clay mineralogy, and to those who accepted to collaborate with me in order to elucidate Mediterranean paleoenvironments. I am very grateful to J. E. Meulenkamp, F. Moormann and G. J. Van der Zwaan for their reading of the manuscript and for their valuable suggestions. The drawings were made by A. van Doorn.

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MIDDLE MIOCENE TO PLIOCENE PALEOENVIRONMENTAL RECONSTRUCTION OF THE MEDITERRANEAN AND ADJACENT ATLANTIC OCEAN: PLANKTONIC FORAMINIFERAL RECORD OF SOUTHERN ITALY

W. J. ZACHARIASSE and P. SPAAK

ABSTRACT

A quantitative planktonic foraminiferal record is presented for the Middle Miocene to Pliocene of Southern Italy. Statistical analysis of 339 samples indicates that the total data set contains three different associations which are interpreted as tropical, subtropical and temperate. The transition from the tropical to subtropical association takes place in the Late Serravallian and reflects the southward displacement of the areal distribution of low-latitude faunas in the Mediterranean and adjacent Atlantic induced by a pronounced cooling.

The relatively stable, subtropical fauna pattern of the Tortonian – Early Pliocene is interrupted during the Late Messinian. The replacement of the subtropical fauna by a temperate one takes place in the Late Pliocene and corresponds with a significant cooling trend and an intensification of climatic contrasts, possibly of a glacial/interglacial mode. Small-scale migratory events occur throughout the Middle Miocene to Pliocene and are especially frequent in periods of rapidly declining temperature.

INTRODUCTION

An important tool in unravelling the paleoceanographic and climatic record is the analysis of planktonic foraminiferal distribution patterns in space and time. Modern biogeographic patterns closely reflect the partitioning of the oceans into a number of specific water-masses the boundaries of which correspond with oceanic discontinuities. The geographic position and intensity of these discontinuities are controlled by oceanic circulation patterns and correspond with areas of steep gradients in physical-chemical parameters and food conditions. A simplified illustration of the interrelationship between oceanic circulation, distribution of physical-chemical parameters and distribution of planktonic foraminifera is given in figure 1. Space-time changes in biogeographic patterns reflect changes in paleocirculation patterns and are brought about by changes in global climate and/or geometry of the ocean basins.

Analyses of faunal/floral patterns, stable isotopes, carbonate preservation profiles and erosional patterns indicate that present-day oceanic circulation patterns and climatic regime originate in the Neogene and became established in response to changing basin configuration (e.g. Berggren and Phillips, 1971; Berggren and Hollister, 1977; Kennett, 1977; Keigwin, 1978; Keller, 1981a; Berggren and Schnitker, 1981). Although the cause, mode and timing of the successive stages in the evolution of Neogene climate and circulation patterns are partly conflicting there is ample evidence for a progressive climatic deterioration and a steepening of latitudinal temperature gradients (e.g. Cifelli, 1976; Haq, 1980; Woodruff et al., 1981; Keller, 1981b; Berggren and Schnitker, 1981; Berggren, 1982; Thunell and Belyea, 1982).

In the present study a composite quantitative planktonic foraminiferal record is presented for the Middle Miocene to Pliocene of Southern Italy. An attempt is made to specify the planktonic foraminiferal record in terms of paleoceanographic conditions in the Mediterranean and adjacent Atlantic and climatic evolution.

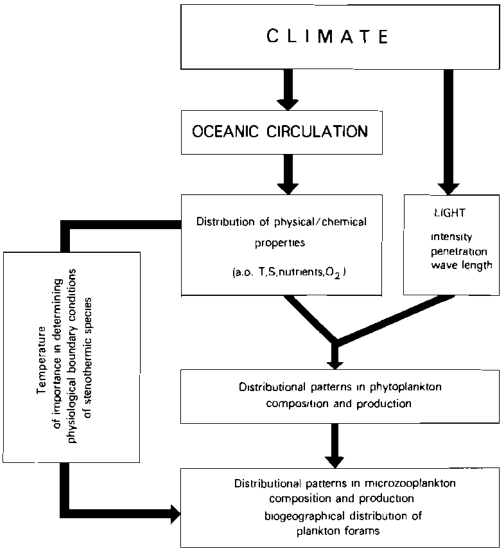


Fig. 1 Simplified flow-chart of factors important for the distribution of planktonic foraminifera.

MATERIAL AND METHODS

The composite planktonic foraminiferal record is based on the quantitative analysis of 339 samples distributed over various sections in Sicily and Calabria (Southern Italy). The Miocene record is based on the Sicilian sections Giammoia and Falconara (for location: see Van der Zwaan, this volume); the Pliocene record is based on sections described by Spaak (1983). Per sample 200–400 specimens of the greater than 125 micron fraction were determined and quantified.

The data set for the pre-Messinian interval is new and will be elaborated on elsewhere. The data set for the Messinian diatomaceous interval is taken from Van der Zwaan (1982), whereas the Pliocene data set has been recently published by Spaak (1983).

A reliable quantification depends on the stability in the operational definitions of the taxonomic units. To meet this prerequisite lump-categories were made for strongly overlapping taxa. Lump-categories include the groups of *G. druryi-nepenthes*, *G. apertura-obliquus*, *G. inflata* (including *G. puncticulata*, *G. bononiensis*, and *G. inflata*). The *G. bulloides* group includes several variants of which *G. bulloides* is separately counted.

MIOCENE RECORD

The Miocene record spans the interval from the Lower Serravallian (*G. peripheroronda* Zone) up into the Messinian (*G. conomiozea* Zone). As shown in figure 2 a number of distinct frequency changes are concentrated in the Lower Serravallian and include the disappearance of *G. peripheroronda*, the massive increase of the group of *G. apertura-obliquus* and the rapid decline in abundance of *Globoquadrina*. The latter taxon shows a very discontinuous and low frequency pattern up to a level in the Tortonian where it vanishes from the Mediterranean record. At the same level the group of *G. nepenthes-druryi* drops to lower frequencies and disappears in the Lower Messinian. The frequency pattern of *G. trilobus* shows an overall upward decrease. Neogloboquadrinids display a remarkably high morphological diversity in the Upper Serravallian. Rapidly shifting dominances of individual taxa are recorded in the Messinian diatomaceous interval. The major frequency changes are schematically summarized in figure 3.

The R-mode program BALANC (M. M. Drooger, 1982) was used to analyze the total set of data for trends and correlations. To prevent the results from being biased by a strong overprint of the specific Messinian environmental conditions no data were used from the diatomaceous interval. Negative overall trends were found in *G. trilobus*, *G. peripheroronda*, *Globoquadrina* and the group of *G. druryi-nepenthes*. Positive overall trends were recorded for the frequency patterns of *G. scitula*, *Orbulina*, and the group of *G. apertura-obliquus* (fig. 3).

Amongst the taxa displaying a negative overall trend *Globoquadrina*, *G. peripheroronda*, and the group of *G. druryi-nepenthes* are extinct. However, in conformity with the literature (e.g. Cita and Colombo, 1979; Berggren, 1982; Thunell and Belyea, 1982) these taxa are considered here as stenothermic with relatively high minimum temperature requirements. The same ecological characteristic applies to the extant *G. trilobus*.

Amongst the taxa showing an overall positive trend the recent *G. scitula*

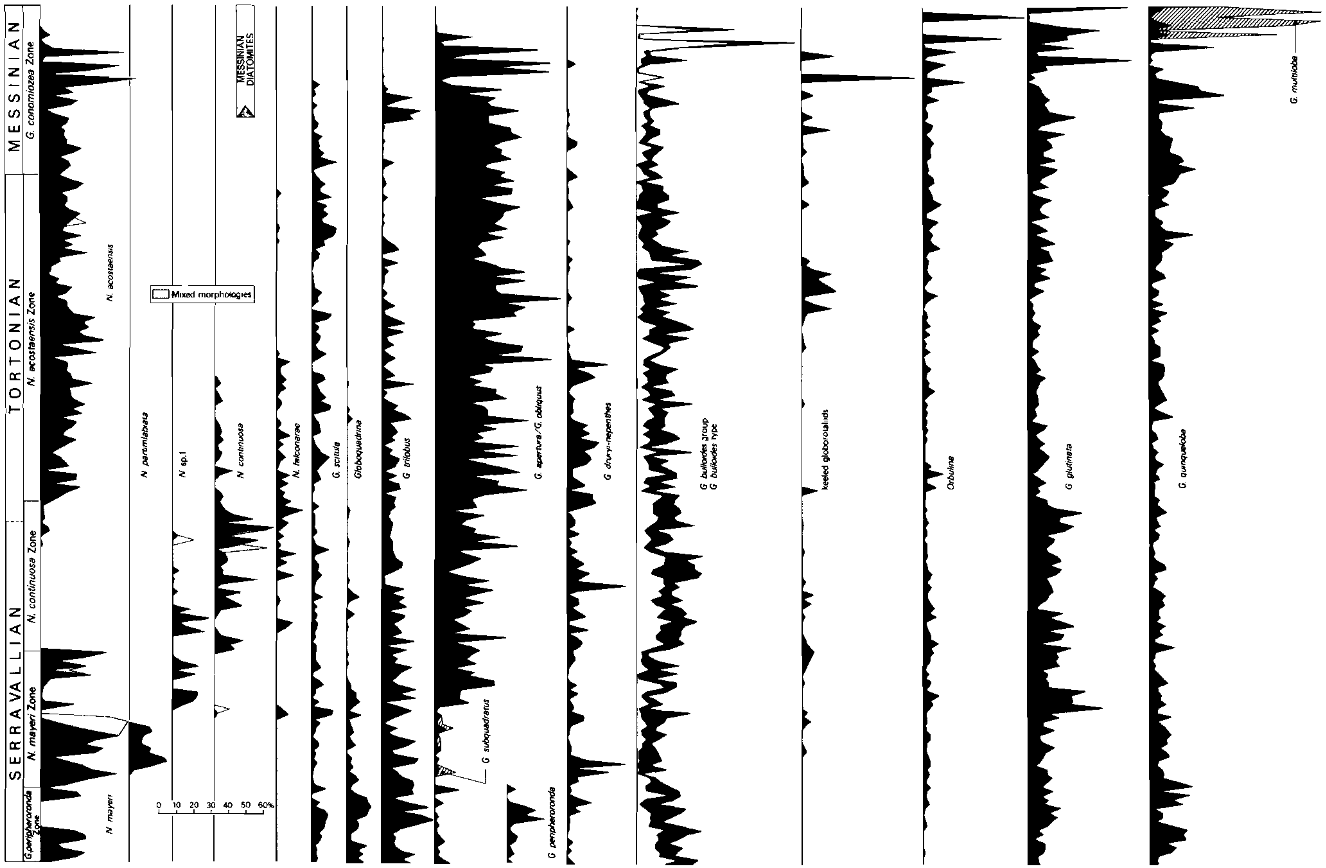


Fig. 2 Frequency distribution of planktonic foraminifera in the Miocene composite section from Sicily (Southern Italy).

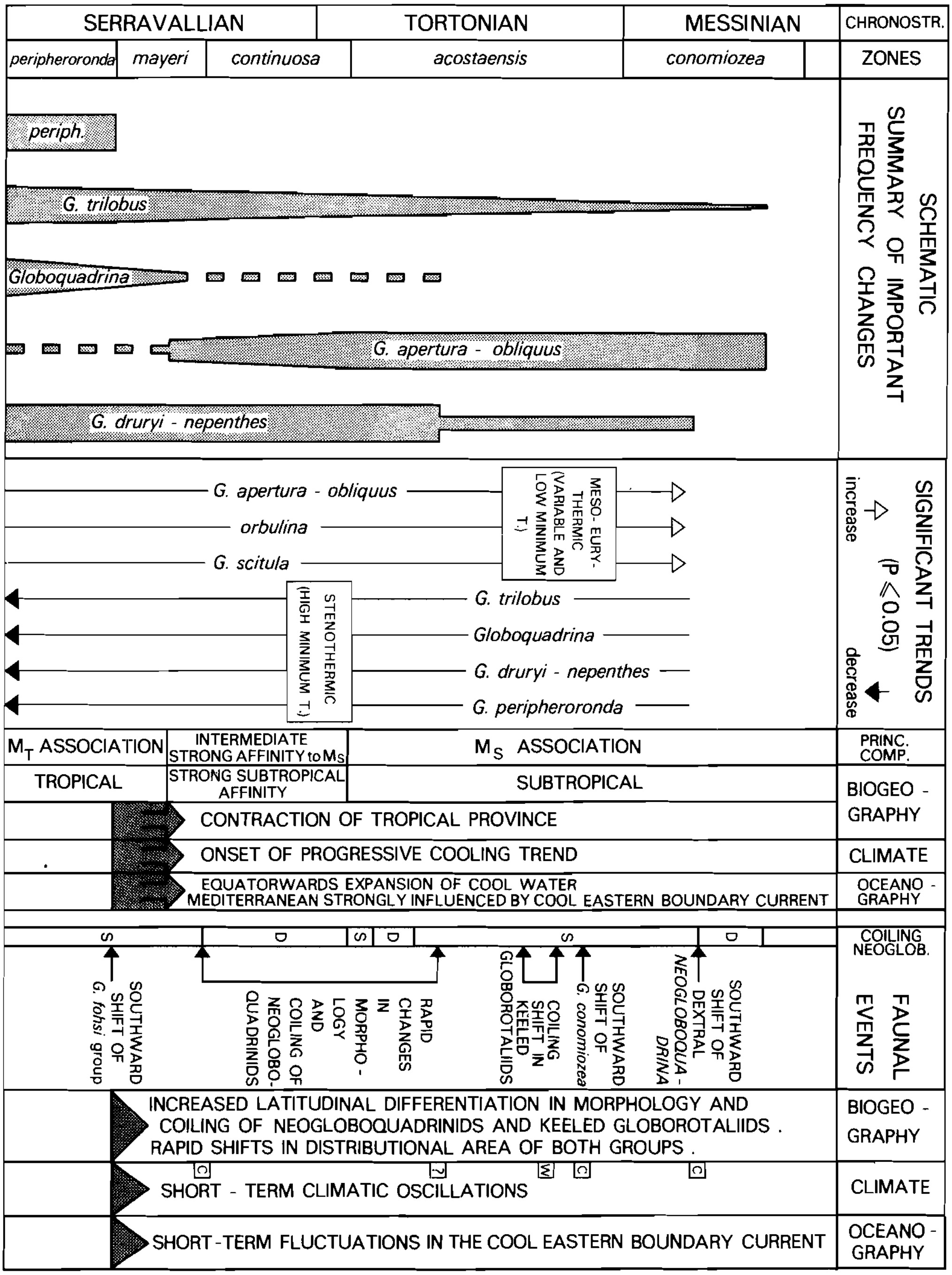


Fig. 3 Miocene fauna characteristics and paleoenvironmental conditions in the Mediterranean and adjacent Atlantic Ocean.

and *Orbulina* are distinctly meso-eurythermic with variable to low minimum temperature limits. The ecological characteristic of the extinct group of *G. apertura-obliquus* can be compared best with that of the recent group of *G. ruber-rubescens* (Spaak, 1983). Therefore, the group of *G. apertura-obliquus* may have had its optimum distribution in subtropical waters.

The above enumeration of faunal changes indicates that the Mediterranean fauna changed from dominantly tropical to subtropical in the course of the Miocene.

To visualize the overall Miocene faunistic change and to verify where the transition takes place, the total Mio-Pliocene data set (including the data from the Messinian diatomaceous interval) was subjected to a Q-mode principal components analysis (PCA-program of Davis, 1973). This analysis reduces the total matrix to three significant components which together constitute 71% of the total variance (see table 1).

A plot of loadings of the first two components clearly indicates the presence of two different Miocene associations: a Lower Serravallian association and a Tortonian-Lower Messinian one. Both associations are bracketed in the Upper Serravallian (fig. 4).

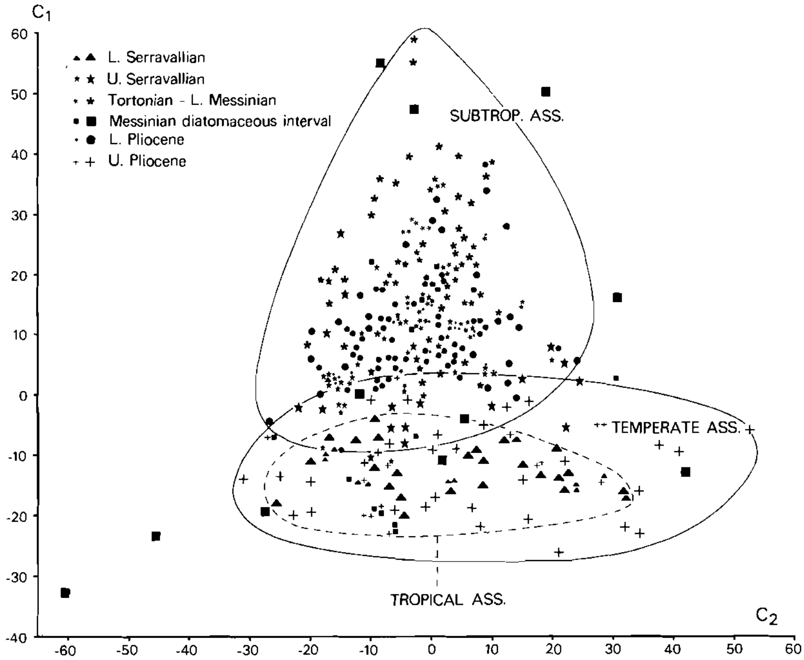


Fig. 4 Loadings of the first two components for 339 samples from the Middle Miocene to Pliocene of Southern Italy.

species	1	2	3	4	5
G. apertura-obliquus	.9	–.0	–.1	157.1	29.7
G. subquadratus-elongatus	–.1	.0	–.1	189.6	51.7
G. bulloides group	–.3	–.5	–.5	168.4	71.1
G. bulloides type	–.2	–.2	–.2	80.9	80.5
Neogloboquadrina	–.2	.8	–.3	54.5	86.8
G. trilobus	–.0	–.0	–.0	29.6	90.2
G. scitula	.0	–.0	.0	28.1	93.5
G. druryi-nepenthes	.0	–.0	–.0	22.3	96.0
G. quinqueloba-multiloba	–.2	–.1	.8	18.5	98.2
G. glutinata	–.1	–.2	.1	8.3	99.1
Globoquadrina	–.0	–.0	.0	5.1	99.7
Orbulina	.0	.0	.1	2.2	100.0
Sphaeroidinellopsis	.0	–.0	–.0	.1	100.0

a

species	1	2	3	4	5
G. apertura-obliquus	–.5	.5	–.1	227.7	30.7
G. elongatus	.0	–.0	–.0	188.7	56.1
G. bulloides group	–.1	–.7	–.3	106.8	70.4
G. bulloides type	.2	–.4	–.0	88.2	82.3
Neogloboquadrina	.8	.3	–.3	42.6	88.0
G. trilobus	–.1	.1	–.0	34.2	92.6
G. scitula	.0	–.0	–.0	29.0	96.5
G. nepenthes	–.0	.0	–.0	6.8	97.5
G. quinqueloba	.1	–.2	–.0	6.3	98.3
G. glutinata	–.2	.0	–.1	5.8	99.1
Globoquadrina	–.0	.0	–.0	3.6	99.6
Orbulina	.0	.0	–.0	2.2	99.9
Sphaeroidinellopsis	–.0	.0	.0	.5	99.9
G. margaritae	–.0	.0	–.0	.3	100.0
G. inflata group	.1	–.0	.9	.1	100.0
G. crassaformis	–.0	.0	–.0	.1	100.0

b

species	1	2	3	4	5
G. bulloides group	–.0	.7	.2	238.5	49.8
G. bulloides type	.1	.7	–.1	158.4	82.8
Neogloboquadrina	1.0	–.1	.2	35.3	90.2
G. trilobus	–.1	–.1	–.2	16.5	93.7
G. scitula	–.0	–.1	–.1	14.1	96.6
G. quinqueloba	–.0	.0	–.2	7.2	98.1
G. glutinata	–.2	–.1	.9	4.9	99.1
Orbulina	.0	.0	–.1	4.1	100.0

c

Table 1 Composition of the first three components (1, 2, 3), eigenvalues (4) and total variance in cumulative % (5) for : a) 339 samples from the Middle Miocene – Pliocene, b) 141 samples from the Pliocene and c) 67 laminated samples from the Middle Miocene – Pliocene.

The differentiation of the Miocene data set in two associations is almost entirely determined by the loadings of the first component which is dominated by the group of G. *apertura-obliquus* (table 1). The loadings of the second component, dominated by neogloboquadrinids, do not contribute significantly to the discrimination of the Miocene data set. The Tortonian-Lower Messinian association, therefore, is characterized by high abundances of the group of G. *apertura-obliquus*, whereas the Lower Serravallian one shows an inverse relationship.

The results of the principal components analysis, in combination with the evidence obtained from the frequency changes and trends summarized in figure 3, clearly indicate that the Mediterranean fauna changed from dominantly tropical to subtropical in the Late Serravallian (fig. 3). This major fauna turn-over reflects the rapid contraction of the tropical province in the Mediterranean and Atlantic Ocean brought about by the sudden onset of a climatic deterioration. The climatic inflection-point is placed at the disappearance level of the G. *fohsi* group in the Mediterranean. The expansion of cool water of the eastern boundary current displaces the areal distribution of the G. *fohsi* group southwards (maximum as far south as 27°N, DSDP Site 397) which results in its extermination in the Mediterranean.

Superimposed on the large-scale change in planktonic foraminiferal biogeography and climatic conditions, small-scale, migratory events are registered by abrupt coiling changes and morphological discontinuities in neogloboquadrinids and globorotaliids (fig. 3). Migrational events are especially frequent in the Late Serravallian-Early Tortonian. Here six different neogloboquadrinid taxa show rapidly fluctuating and alternating frequencies (fig. 2) and portray the high degree of morphological diversity of neogloboquadrinids during the Late Serravallian-Early Tortonian time-span. These migrational events signal short-term, low-amplitude oscillations along a long-term climatic deteriorating trend which starts with the extermination of the G. *fohsi* group and culminates in the Late Miocene with the successive introduction of G. *conomiozea* and dextrally coiled neogloboquadrinids (fig. 3).

The maximum cooling in the latest Miocene combined with geodynamic processes, may have played a role in the isolation and subsequent desiccation of the Mediterranean (e.g. Hsü et al., 1977; Van der Zwaan, 1982) The response of an increasingly deteriorating connection between the Mediterranean and Atlantic Ocean to the composition of the Mediterranean fauna is heralded by an increase in the frequency of the eurytopic species G. *quinqueloba* and G. *glutinata* (fig. 2). In the subsequent diatomaceous interval eutrophic and eurytopic species show highly fluctuating and alternating frequencies (fig. 2), which finds expression in the wide scatter of vector loadings in figure 4.

The repeated occurrence of diatomites and associated changes in fertility are attributed by Van der Zwaan (1982) to the complex interaction of glacial-eustatically controlled inflow/outflow patterns through a shallow Atlantic-Mediterranean gateway and local recycling of nutrients along intra-Mediterranean sills. At an early stage of the diatomaceous interval the eutrophic species *N. acostaensis* and *G. conomiozea* attain extremely high frequencies in the diatomites. At a later stage, immediately antedating the level of extermination of planktonic foraminiferal faunas, the more eurytopic species *G. bulloides*, *G. glutinata*, and *Orbulina universa* are associated with the diatomites, whereas *G. quinqueloba* and *G. multiloba* dominate the homogeneous (nutrient-depleted) intervals. The five last-mentioned species are thought to tolerate extreme physical-chemical and trophic conditions and their fluctuating dominances reflect the rapidly varying conditions in a highly-saline and restricted environment.

PLIOCENE RECORD

The Pliocene record extends from the lowermost Pliocene up to the level of the first occurrence of *H. balthica* and shows a number of important frequency changes (fig. 5) which are schematically summarized in figure 6.

Approximately at the level of first occurrence of *G. puncticulata*, *G. nepenthes* becomes extinct, while *G. elongatus* starts to become a characteristic Pliocene fauna element. Other distinct changes are concentrated higher up into the Pliocene and include a drop in the frequency of the group of *G. apertura-obliquus* and a strong increase in the abundances of *G. quinqueloba* and *G. bulloides.*

A computer analysis of the total Pliocene data set, using the BALANC program, shows significant overall trends in the frequency distribution of several taxa (fig. 6). Positive overall trends were found in *G. elongatus*, *G. bulloides*, *G. quinqueloba*, *Orbulina*, and the *G. inflata* group, whereas the group of *G. apertura-obliquus*, *G. trilobus*, and *G. nepenthes* display negative overall trends. The ecological significance of these trends can be explained best in terms of surface water temperature. Taxa showing a negative overall trend are considered to have narrower temperature tolerance ranges than the group of taxa displaying a positive overall trend. In this sense, the warm-water aspect of the Lower Pliocene fauna diminishes upwards.

The disappearance of the subtropical faunal aspect in the course of the Pliocene is clearly reflected in the plot of loadings of the first two components for the total Mio-Pliocene data set (fig. 4). The Lower Pliocene association correlates with high loadings of the first component (dominated

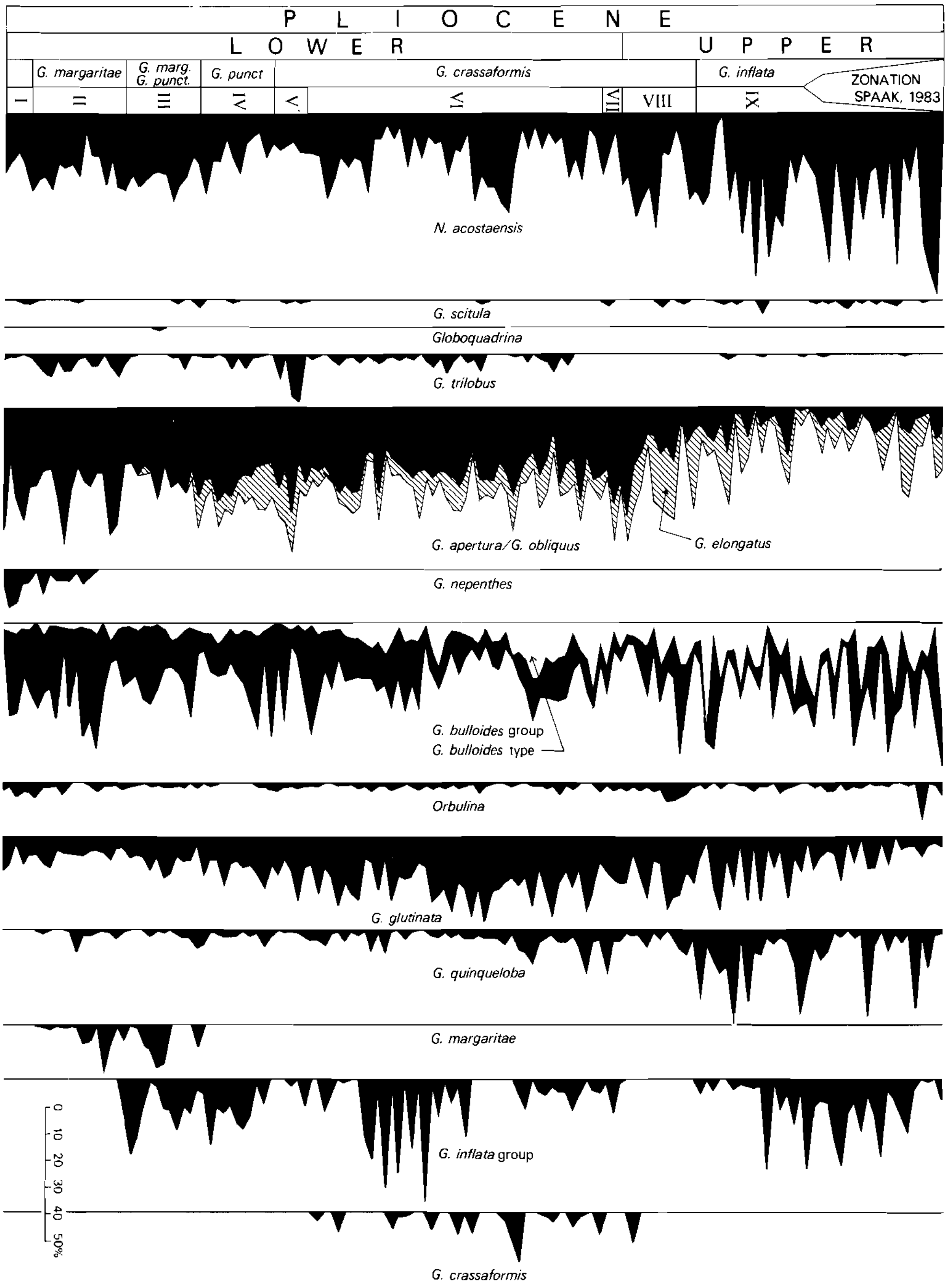


Fig. 5 Frequency distribution of planktonic foraminifera in the Pliocene composite section from Sicily and Calabria (Southern Italy).

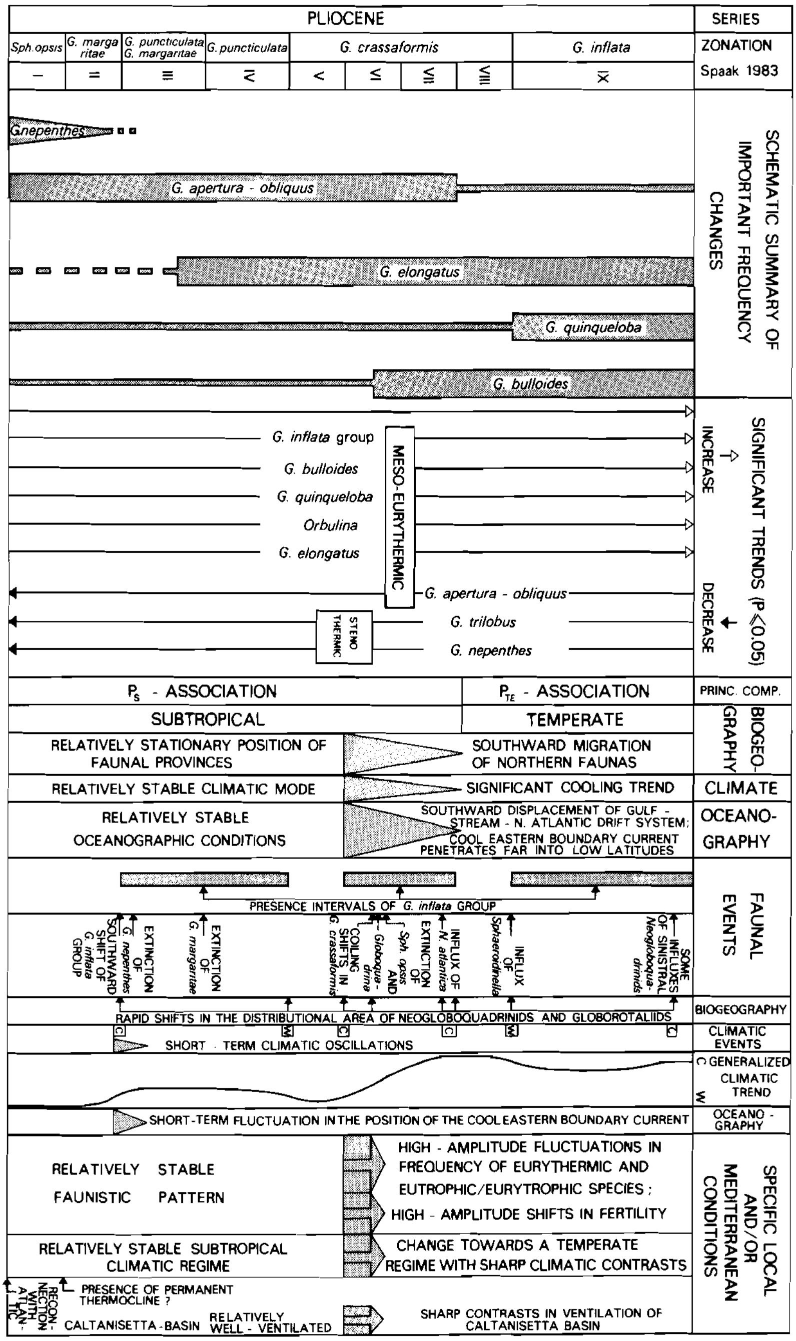


Fig. 6 Pliocene fauna characteristics and paleoenvironmental conditions in the Mediterranean and adjacent Atlantic Ocean.

by the subtropical group of G. *apertura-obliquus*), whereas the Upper Pliocene one is characterized by low loadings of the first component in combination with highly variable loadings of the second component (dominated by *Neogloboquadrina*).

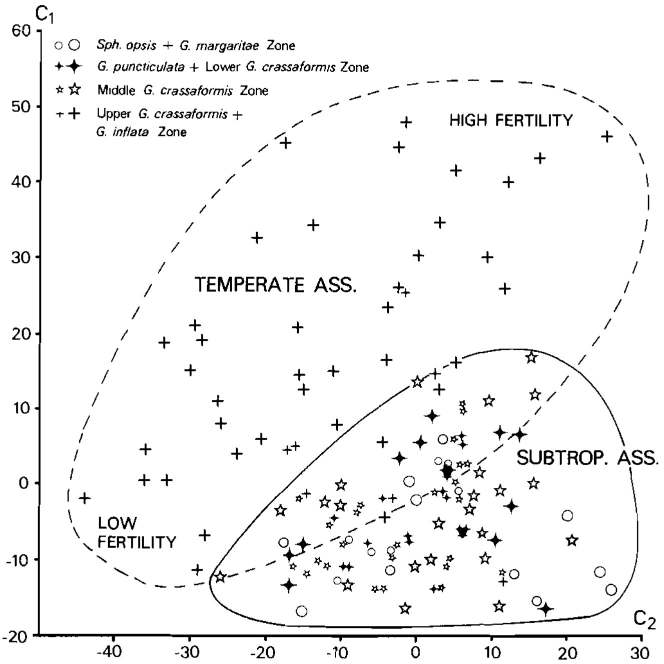


Fig. 7 Loadings of the first two components for 141 samples from the Pliocene of Southern Italy.

The ecological significance and stratigraphic position of the Pliocene fauna turn-over becomes more evident if solely the Pliocene data set is analyzed. Figure 7 gives the loadings of the first two components for 141 Pliocene samples plotted for four biostratigraphic intervals. Although not sharply delimited, the allocation of the Pliocene fauna turn-over fits in best with the level which corresponds with the base of Interval VIII of Spaak (1983). Inspection of the composition of the components (table 1) shows that the loadings of the Lower Pliocene association are essentially characterized by high frequencies of the subtropical group of G. *apertura-obliquus* and low frequencies of G. *bulloides* and neogloboquadrinids, whereas the loadings of the Upper Pliocene association show an inverse relationship. The wide scatter of loadings of the Upper Pliocene association results from the highly fluctuating frequencies of neogloboquadrinids, G. *bulloides*, and (to a lesser extent) of G. *quinqueloba*.

The difference in the overall fauna composition of the Lower and the Upper Pliocene, in combination with the frequency changes and trends summarized in figure 5, indicates that the Lower Pliocene association has a dominant subtropical aspect, whereas the Upper Pliocene fauna displays a strong temperate affinity. The recurrent peak frequencies of neogloboquadrinids in the Upper Pliocene are ascribed to periodical highly-fertile conditions. In the modern ocean neogloboquadrinids show an extremely wide latitudinal range in which the frequency distribution is primarily determined by the degree of eutrophication (e.g. Reiss et al., 1974; Reiss et al., 1980; Coulbourn et al., 1980). The high abundances of *G. quinqueloba* and *G. bulloides*, associated with low frequencies of neogloboquadrinids, characterize the cool-water, low fertility conditions in the Late Pliocene. *G. quinqueloba* and *G. bulloides* are eurytopic species thriving both at high (e.g. Zobel, 1971; Thiede, 1975; Halicz and Reiss, 1981; Prell and Curry, 1981) and low nutrient levels (e.g. Eckert, 1965; Reiss et al., 1974) and often occupy unstable (i.e. cold-water and upwelling regions) or stressed environments (i.e. local inshore areas and semi-enclosed seas).

The Tortonian-Early Messinian and Early Pliocene associations are statistically indiscriminate regardless of whether the total set (fig. 4) or the specific subset (not shown) is analyzed and portray the uniform overall composition of the planktonic foraminiferal faunas in both time-slices. This conclusion is in line with the uniform overall composition of the benthonic foraminiferal communities for the same time-slices (Van der Zwaan, this volume).

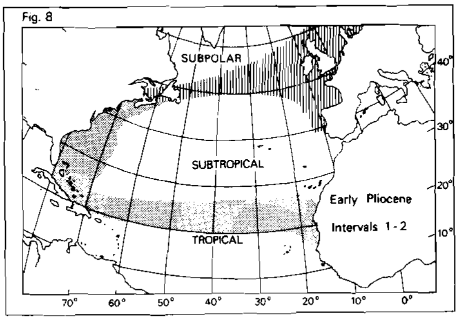
Loadings for the Lower Serravallian and Upper Pliocene samples strongly overlap when the total set is analyzed (fig. 4) but cluster separately when each specific subset is used (not shown). In the latter case the Lower Serravallian samples correlate with high frequencies of *G. trilobus* and low frequencies of *G. bulloides*, whereas the inverse relationship holds for the Upper Pliocene samples. This reflects the difference between the tropical Early Serravallian fauna and the temperate Late Pliocene one.

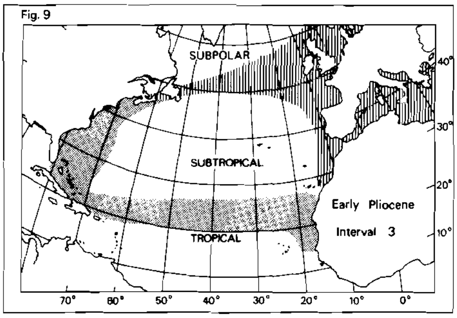
Summarizing, the quantitative record indicates a significant climatic cooling phase in the Late Pliocene (upper part of the *G. crassaformis* Zone). The significant admixture of northern fauna elements in the Mediterranean since the Late Pliocene marks the time when the Mediterranean became permanently influenced by the cool eastern boundary current.

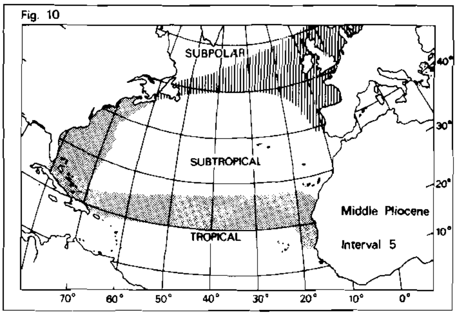
Superimposed on the large-scale fauna change several instantaneous and small-scale faunistic changes took place, which seem to be related to short-term climatic oscillations and concomitant fluctuations in the transport of cool water by the eastern boundary current (fig. 6).

One of the most prominent small-scale events is the sudden spreading of the *G. inflata* group (i.e. *G. puncticulata*) in the Mediterranean (fig. 6). Since the recent *G. inflata* in the NE Atlantic Ocean is bound to the cool eastern boundary current (e.g. Bé and Tolderlund, 1971), the sudden spreading of the *G. inflata* group in the Mediterranean and waters off Africa, as far south as 27°N (DSDP Site 397), documents a significant expansion of the cool eastern boundary current. Figures 8 and 9 illustrate the generalized gyral circulation and biogeographic pattern of the North Atlantic shortly before and after the introduction of *G. puncticulata* into the Mediterranean.

At the base of the *G. crassaformis* Zone the *G. inflata* group disappears from the Mediterranean for a prolonged period (fig. 6). The corresponding







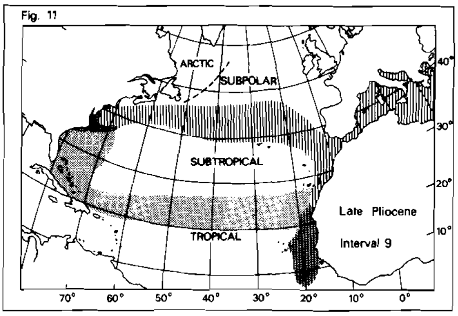


Fig. 8 Generalized gyral circulation and planktonic foraminiferal biogeography of the North Atlantic for biostratigraphic intervals I and II. Reconstruction is based on the recent situation as given by Cifelli and Beniér (1976).

Fig. 9 Generalized gyral circulation and planktonic foraminiferal biogeography of the North Atlantic for biostratigraphic interval III.

Fig. 10 Generalized gyral circulation and planktonic foraminiferal biogeography of the North Atlantic for biostratigraphic interval V.

Fig. 11 Generalized gyral circulation and planktonic foraminiferal biogeography of the North Atlantic for biostratigraphic interval IX.

high relative frequencies of *G. trilobus* (fig. 5) indicate that the *G. inflata* group shifted northwards due to a short-term climatic amelioration and associated weakened influence of the cool eastern boundary current (fig. 10).

The re-appearance of the *G. inflata* group (i.e. *G. bononiensis*) is followed by a series of faunistic events including the extinction of *Globoquadrina* and of *Sphaeroidinellopsis* and several coiling shifts in *G. crassaformis* (fig. 6). Apparently the renewed expansion of cool water transported by the eastern boundary current caused the re-introduction of the *G. inflata* group into the Mediterranean and into waters off Africa, now, as far south as 5°N (DSDP Site 366A; see Spaak, 1981). This second Pliocene cooling phase is certainly more intense and permanent than the one registered at the base of Interval III (fig. 6) and culminates in the upper part of the *G. crassaformis* Zone. Within the latter interval the Mediterranean fauna changes from subtropical to more temperate. This change coincides with the arrival of the northern Atlantic species *N. atlantica* and the renewed disappearance of the *G. inflata* group (fig. 6). The latter event has also been recorded off Africa (DSDP Sites 397, 366A; Spaak, 1981) and immediately follows the last Pliocene occurrence of *G. menardii* and *G. miocenica* in DSDP Site 397 (Spaak, 1983). The complex signal registered by the short-term presence of *N. atlantica* (Mediterranean), the short-term absence of the *G. inflata* group (Mediterranean and off Africa) and the disappearance of the *G. menardii* group (off Africa) suggests a southward intrusion of cold water, which forced the eastern boundary current to flow more westward.

The re-introduction of the *G. inflata* group (i.e. *G. inflata*) into the Mediterranean and into waters off Africa, again, as far south as 5°N, together with the introduction of *Sphaeroidinella* in the Mediterranean, may be associated with slightly warmer climatic conditions and the return to a more eastward flowing eastern boundary current (fig. 11).

The successive exterminations of *G. nepenthes*, *G. margaritae*, *G. altispira*, and of *Sphaeroidinellopsis* in the Mediterranean Pliocene are faunistic events of global significance and seem to be related to distinct Pliocene cooling phases.

FAUNISTIC PATTERN IN LAMINITES

Laminites occur throughout the Mio-Pliocene composite column. The plot of loadings of the first two components for 67 laminated samples (excluding the ones from the Messinian diatomaceous interval) clusters the samples in two associations (fig. 12). All laminated samples from the Middle Miocene to Lower Pliocene belong to one single association characterized by a rela-

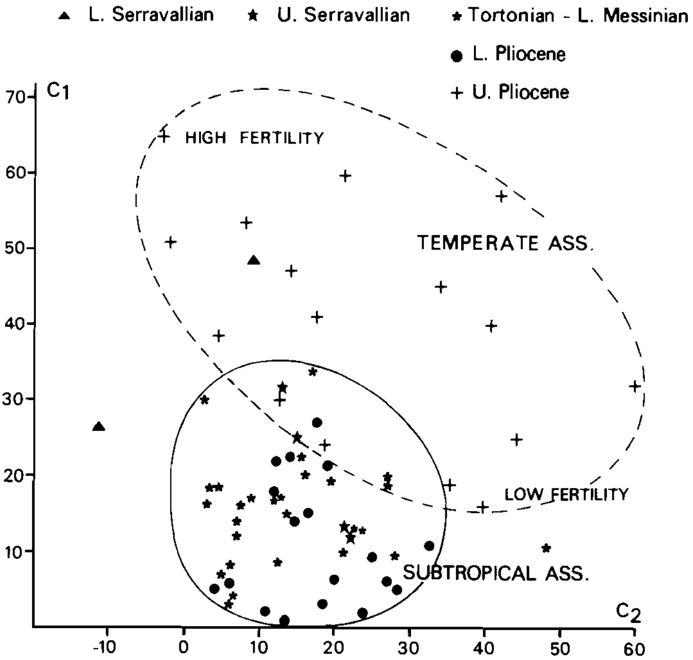


Fig. 12 Loadings of the first two components for 67 laminated samples from the Mio-Pliocene of Southern Italy.

tively uniform and low frequency pattern of neogloboquadrinids and *G. bulloides*. Laminites from the Upper Pliocene contain a contrasting association which is characterized by high frequencies of neogloboquadrinids and highly varying abundances of *G. bulloides*. The ecological significance of both laminite-bound associations is interpreted in terms of surface water fertility being uniformly low in the Middle Miocene – Early Pliocene and variably high in the Late Pliocene.

Whatever processes led to the preservation of lamination, a correlation between fertility and lamination is obvious only for the Pliocene laminites. Sharp contrasts in local basin ventilation, thus, parallel high-fertile surface water conditions in the Late Pliocene and are most probably associated with the intensification of climatic contrasts, possibly of a glacial-interglacial mode (fig. 6).

CONCLUSIONS AND DISCUSSION

The Middle Miocene - Pliocene record of Southern Italy clearly documents changing faunistic patterns in the Mediterranean and Atlantic Ocean in response to a stepwise, progressive, climatic deterioration.

A major fauna turn-over takes place in the Late Serravallian, which was marked by the replacement of a dominant tropical fauna by a subtropical one, and reflects a significant biogeographic change induced by a pronounced climatic cooling (fig. 3).

The Mediterranean signal agrees well with the southward migrations of low-latitude faunas and floras in the Atlantic during the Middle Miocene as reported by Haq (1980), Berggren and Schnitker (1981) and Thunell and Belyea (1982). Further evidence for a Middle Miocene cooling is documented by hiatuses and increased carbonate dissolution associated with low species diversity reported by Keller (1980, 1981b) from the Pacific and by a distinct drop in the oxygen isotope signal (Shackleton and Kennett, 1975; Woodruff et al., 1981). The decline in temperature during the Middle Miocene is generally attributed to the growth of the East Antarctic Ice sheet (Shackleton and Kennett, 1975; Kennett, 1977). Berggren and Schnitker (1981) suggest that the subsidence of the Iceland-Faeroe Ridge triggered the expansion of the East Antarctic Ice sheet and the onset of the Middle Miocene cooling trend. It is worth noticing that the onset of the Middle Miocene cooling, as recognized in the Mediterranean, correlates exactly with the beginning of the evaporitic phase in the Gulf of Suez region (El-Heiny and Martini, 1981), suggesting a causal relationship between both events.

The relatively stable, subtropical, fauna pattern in the Tortonian – Early Pliocene is interrupted during the Messinian. Increasingly elevated and fluctuating frequencies of eurytopic species parallel the establishment of a highly-saline and restricted environment (fig. 3). The cooling phase in the Late Miocene reported by various authors (e.g. Kennett, 1977; Loutit, 1981; Berggren and Schnitker, 1981) may be partly reflected by the successive introductions of *G. conomiozea* and dextrally coiled neogloboquadrinids in the Mediterranean and may have played a role in the final isolation of the Mediterranean towards the end of the Miocene.

Another major faunistic change is registered in the Upper Pliocene (upper part of the *G. crassaformis* Zone) and marks the replacement of a subtropical association by a temperate one. This major faunistic event is associated with a significant decline in temperature which begins in the early part of the *G. crassaformis* Zone and culminates in the later part of the nominate zone (fig. 6).

Recurrent and laminite-bound peak frequencies of neogloboquadrinids in the Upper Pliocene temperate association are considered to represent periodical highly-fertile surface water conditions and may be associated with an intensification of climatic contrasts, possibly of a glacial – interglacial mode.

The composition of the Upper Pliocene temperate association closely parallels that of the recent Mediterranean indicating that the final constraints of the recent biogeographic pattern originate in the Late Pliocene. A similar Late Pliocene biogeographic rearrangement is reported by Van der Zwaan (this volume) for the Mediterranean benthonic foraminiferal communities. Hence, the Late Pliocene cooling event changed drastically both the surface water and deep water conditions in the Mediterranean.

Interesting is the close correspondance of the Pliocene faunal events and vegetational changes identified by Zagwijn and Suc (1983) in the palynological record of the northwestern Mediterranean. The palynological pattern indicates stable, humid and warm climatic conditions in the Early Pliocene which matches nicely with the paleoenvironmental estimates summarized in figure 6. This climatic regime altered in the course of the *G. crassaformis* Zone towards a dry and contrasting climate, the onset of which corresponds with the change-over from a warm to cool planktonic foraminiferal association in the upper part of the *G. crassaformis* Zone. Zagwijn and Suc (1983) correlate the onset of dry and contrasting climatic conditions in the northwestern Mediterranean with the base of the Praetiglian cold climatic phase which represents the earliest interval of full glacial conditions (Zagwijn, 1974).

The rapid climatic cooling in the later part of the *G. crassaformis* Zone is registered as a significant and permanent $\delta^{18}O$ enrichment in the record from the western Mediterranean DSDP Site 132 (Thunell and Williams, this volume). Both authors report comparable and correlative shifts in the oxygen isotopic records from various extra-Mediterranean basins which they interpreted as representing the onset of Northern Hemisphere glaciation.

The initiation of Northern Hemisphere ice growth and associated southward displacement of the Gulf Stream-North Atlantic Drift System (Berggren and Hollister, 1977; Berggren and Schnitker, 1981) led to a significant southward incursion of high latitude Atlantic faunas (Thunell and Belyea, 1982) and resulted in the replacement of a subtropical planktonic foraminiferal association by a temperate one in the later part of the *G. crassaformis* Zone of the Mediterranean.

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THE STEPWISE DEVELOPMENT OF PLIOCENE-PLEISTOCENE PALEOCLIMATIC AND PALEOCEANOGRAPHIC CONDITIONS IN THE MEDITERRANEAN: OXYGEN ISOTOPIC STUDIES OF DSDP SITES 125 AND 132

ROBERT C. THUNELL and DOUGLAS F. WILLIAMS

ABSTRACT

Planktonic foraminiferal oxygen isotopic records from the eastern (DSDP Site 125) and western (DSDP Site 132) basins of the Mediterranean indicate the existence of a number of distinct climatic regimes during the last 4.0 million years, each of which is separated by an abrupt climatic step. The major events identified in the Mediterranean records are also evident in open ocean $\delta^{18}O$ records indicating that the isotopic steps are the result of global climatic changes.

The interval between approximately 4.0 and 2.5 MYBP is marked by relatively warm, stable conditions during which a short-term $\delta^{18}O$ enrichment occurs around 3.2 MYBP. This short-term temporary event is considered to reflect a surface water cooling rather than the build-up of continental ice. At about 2.5 MYBP, a permanent shift occurs in the $\delta^{18}O$ record for Site 132, with values becoming systematically enriched by $0.7^0/_{00}$ above this point. Based on the nature of this event, it is interpreted as representing the initial build-up of permanent Northern Hemisphere glaciation.

Within the middle Pleistocene, a second step-like shift is recorded at both sites with $\delta^{18}O$ values again becoming systematically more positive. Above this shift the climatic regime is characterized by an intensification of glacial – interglacial cycles. This transition from one climatic mode to another in the middle Pleistocene may be associated with the development of perennial sea-ice cover in the Arctic at this time.

INTRODUCTION

Evidence is accumulating that the transformation of an ice-free world in the earliest Cenozoic to the glaciated conditions of the Pleistocene was not brought on by a gradual or steady deterioration of climate, but rather through a series of distinct climatic steps (Thunell, 1981a; Berger et al., 1981; Berger, 1982). These climatic steps include: (1) the development of modern thermohaline circulation near the Eocene-Oligocene boundary (Kennett and Shackleton, 1976); (2) the establishment of unrestricted circum-Antarctic flow in the middle to late Oligocene (Kennett, 1977); (3) the development of a permanent Antarctic ice sheet in the middle Miocene (Shackleton and Kennett, 1975a; Savin et al., 1975; Woodruff et al., 1981); and (4) the onset of major Northern Hemisphere glaciation in the middle to late Pliocene (Berggren, 1972; Shackleton and Kennett, 1975b; Shackleton and Opdyke, 1977).

Recently, a number of high resolution studies of deep sea oxygen isotope records have demonstrated the occurrence of a significant change in the mode of global climatic variability in the middle Pleistocene (Shackleton and Opdyke, 1976; Prell, 1980; Pisias and Moore, 1981; Shackleton et al., 1982). Specifically, the late Pleistocene is marked by high amplitude 100,000 year glacial – interglacial cycles, in comparison to lower amplitude, higher frequency climatic changes in the early Pleistocene. The shift from one climatic regime to another, approximately 900,000 years ago, has been attributed to increased continental ice volume during late Pleistocene glaciations (Prell, 1980), and the establishment of a permanent Arctic Ocean ice sheet at this time (Herman and Hopkins, 1980; Williams et al., 1981).

This sequence of Cenozoic climatic steps is well documented in oxygen isotope records from open ocean regions. However, the deciphering of such a sequence becomes more difficult when dealing with records from marginal seas, such as the Mediterranean, due to a strong overprint of regional paleoceanographic events on the global climatic signal. This regional effect is clearly evident in late Pleistocene oxygen isotope records from the Mediterranean which are often marked by glacial – interglacial amplitudes twice that of the open ocean (Emiliani, 1955, 1974; Vergnaud-Grazzini, 1975; Cita et al., 1977; Thunell et al., 1977; Vergnaud-Grazzini et al., 1977; Thunell and Williams, 1982). These large glacial – interglacial isotopic fluctuations are attributable not only to global ice volume changes, but local temperature and salinity changes as well. If long term trends in the glacial-interglacial isotopic amplitude can be resolved, oxygen isotopic records from the Mediterranean can potentially be used to detect the development of basin-to-basin and Mediterranean-to-Atlantic paleoceanographic differences in response to changes in both global and regional paleoclimatic conditions. In general, the application of stable isotopes to pre-late Pleistocene paleoenvironmental studies in the Mediterranean region has received only limited use. Oxygen and carbon isotopic studies have been carried out on several late Miocene sections from Spain (Loutit and Keigwin, 1982), Sicily (van der Zwaan, 1979; McKenzie et al., 1979) and Crete (van der Zwaan and Thomas, 1980), but longer term records have been lacking.

With this in mind, time series oxygen isotope records were produced for the Pliocene-Pleistocene sections of DSDP Sites 125 (eastern basin) and 132 (western basin). Our objectives were to: (1) document the occurrence and timing of major climatic changes during this time period and (2) compare the Mediterranean record with those representative of the open ocean.

The Pliocene-Pleistocene record of paleoclimatic change in the Mediterranean has been previously studied in detail using the planktonic foraminiferal fauna from these two sites (Ciaranfi and Cita, 1973; Cita et al., 1973; Thunell, 1979a). In contrast, the limited geochemical studies of several

Pliocene intervals by Lawrence (1973) and Longinelli and Cita (1973) are the only previous attempts to use oxygen isotopes to reconstruct paleoceanographic and paleoclimatic changes at these sites.

MATERIALS AND METHODS

Two continuously cored sites from DSDP Leg 13 recovered marine sequences suitable for establishing detailed Pliocene-Pleistocene oxygen isotopic records for the eastern and western Mediterranean. Site 125 (34° 37′N; 20° 25′E) was drilled on the Mediterranean Ridge in the Ionian Sea at a water depth of 2782 m. The elevation of this site above the surrounding abyssal plain resulted in a pelagic sequence free of turbidites (Ryan et al., 1973). The upper 4.5 cores (40.0 m) were used in the present study, and contain a fairly complete (90% recovery) late Pliocene through Pleistocene record. Site 132 (40°15′N; 11°26′E) was drilled on the Tyrrhenian Rise in the western Mediterranean at a depth of 2835 m. The upper 15 cores (135 m) were used in this study, and represent a nearly complete (90% recovery) middle-early Pliocene through Pleistocene sequence. For the intervals studied, the average sedimentation rates are 2.5 and 3.5 cm/10^3 years for Sites 125 and 132, respectively, based on previous biostratigraphic studies (Ciaranfi and Cita, 1973; Cita et al., 1973; Thunnell, 1979a). The sediments of Site 132 were sampled at 1.5 m intervals, representing a time span of approximately 43,000 years. The sampling density was much higher at Site 125, with samples being taken every 25 cm, or one every 10,000 years.

Oxygen isotopic analyses were performed following the methods outlined in Williams and others (1977). Approximately 20–25 clean specimens of the planktonic foraminiferal species *Globigerinoides ruber* from the 150–300 μm size range were first roasted for one hour in vacuo to remove any extraneous organic matter and then reacted with purified phosphoric acid at 50°C in vacuo. The isotopic difference between the sample CO_2 and that of the PDB standard was determined with VG Micromass 602D isotope ratio mass spectrometer. All isotopic values are reported in standard δ notation as the per mil (‰) enrichment or depletion in ^{18}O relative to the PDB-1 standard (Epstein et al., 1953) after making all machine corrections. Replicate analyses of the NBS-20 carbonate standard for the 14 month analytical period represented in this data set yielded a standard deviation of the mean (1σ) ± 0.15‰ for $\delta^{18}O$ and ± 0.07‰ for $\delta^{13}C$.

BIOSTRATIGRAPHIC FRAMEWORK OF SITES 125 AND 132

A number of late Neogene planktonic foraminiferal biostratigraphic zonations have been established for early Pliocene-Pleistocene marine sequences of the Mediterranean region (Bizon and Bizon, 1972; Cita, 1975; Zachariasse, 1975; Thunell, 1979b; Spaak, 1983) and used to subdivide the Pliocene-Pleistocene sections from Sites 125 and 132 (fig. 1). The zonation of Cita (1975) has been used in the present study, primarily because it allows for the easiest correlation of Mediterranean sections with open ocean sequences. This zonal scheme utilizes a number of planktonic foraminiferal datums which are considered to be globally isochronous and have been dated using paleomagnetic polarity records in open ocean sediments (Saito et al., 1975; Berggren, 1977; Thunell, 1981b). Two datums which are particularly useful and have been calibrated to the paleomagnetic time scale (Berggren, 1977) include the last occurrence of *Globorotalia margaritae* at ∿ 3.3 MYBP (MPL3-MPL4 boundary) and the last occurrence of *Sphaeroidinellopsis* at ∿3.0 MYBP. An age of 1.6 MYBP has been used in this study for the Pliocene/Pleistocene boundary, as discussed in Haq et al. (1977). This zonation of Cita (1975) was also used as a basis for biostratigraphically subdividing

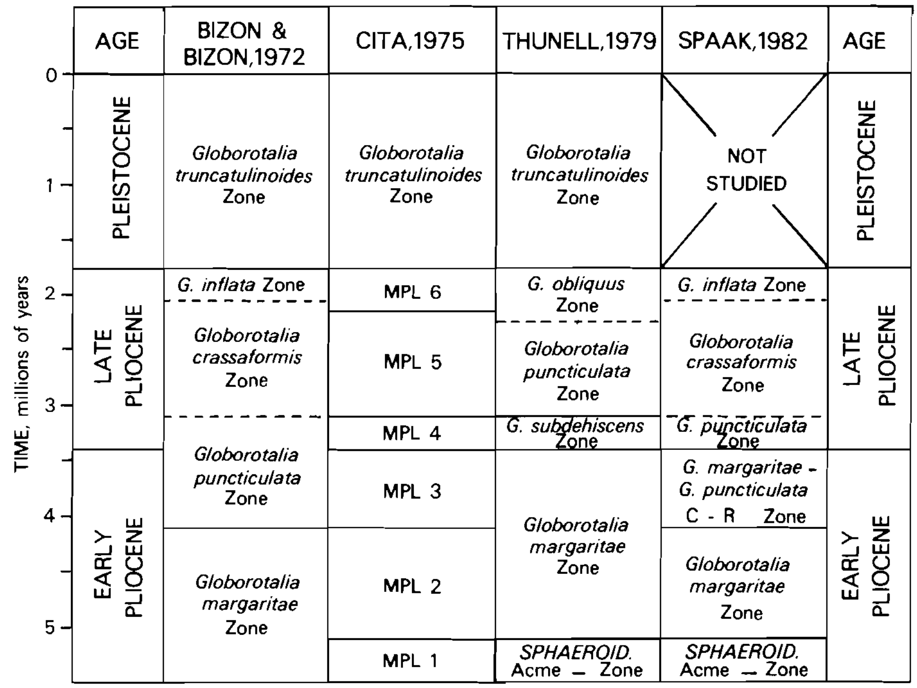

Fig. 1 Correlation of planktonic foraminiferal zonal schemes previously established for the Mediterranean region. The absolute time scale is based on the correlation of the zonation of Cita (1975) with the paleomagnetically-dated Atlantic zonation of Berggren (1977).

the Pliocene-Pleistocene section of DSDP Site 397 off Cape Bojador (Mazzei et al., 1979), and as will be discussed later, the oxygen isotopic record from Site 397 (Shackleton and Cita, 1979) provides an ideal reference for comparison with the Mediterranean isotopic records of this present study.

OXYGEN ISOTOPIC RESULTS FOR THE PLIOCENE–PLEISTOCENE

Eastern Mediterranean Site 125

The oxygen isotopic record generated for Site 125 in the eastern Mediterranean (fig. 2) extends back into the late Pliocene or zone MPL 6 of Cita (1975). In general, this record is marked by a high degree of variability throughout its length, exhibiting positive and negative $\delta^{18}O$ values in the near surface dwelling *G. ruber* suggestive of glacial–interglacial cycles. Superimposed on these rapid fluctuations is a tendency for the late Pleistocene values (above core 2–6) to be systematically heavier than those of the late Pliocene and early Pleistocene (cores 3 through 5) with a shift toward more positive $\delta^{18}O$ values occurring between cores 2 and 3. The average $\delta^{18}O$ value for samples below core 2 is $0.3^0/_{00}$, while the average value within cores 1 and 2 is $1.0^0/_{00}$. Despite this early to late Pleistocene isotopic shift, there does not appear to be a significant change in the amplitude of the isotopic cycles. Throughout the entire record, the glacial–interglacial isotopic cycles have an amplitude of approximately $1.5^0/_{00}$. Noticeable exceptions to this occur when sapropels (organic-rich layers) are encountered (denoted by S in figure 2). In all cases, specimens of *G. ruber* from the sapropel intervals yielded very light $\delta^{18}O$ values which increase the amplitudes of the isotopic cycles up to as much as $2.5^0/_{00}$ in some cases.

Western Mediterranean Site 132

The oxygen isotopic record for western Mediterranean Site 132 (fig. 3) extends back into the upper part of the early Pliocene within the MPL 3 Zone of Cita (1975). From the base of this record to the top, several enrichments in $\delta^{18}O$ values occur as distinct steps or shifts. In addition, an upward increase in the amplitude of the isotopic variability is apparent. The isotopic record in the lower part of this section (from the base of core 15 up through core 11–2) is characterized by a relatively stable isotopic signal with values averaging close to $-0.3^0/_{00}$. Within zone MPL 4 (core 13), a gradual change of nearly $1^0/_{00}$ occurs toward more positive $\delta^{18}O$ values from approximately 3.3 to 3.1 MYBP but the enrichment is not a permanent one as the $\delta^{18}O$

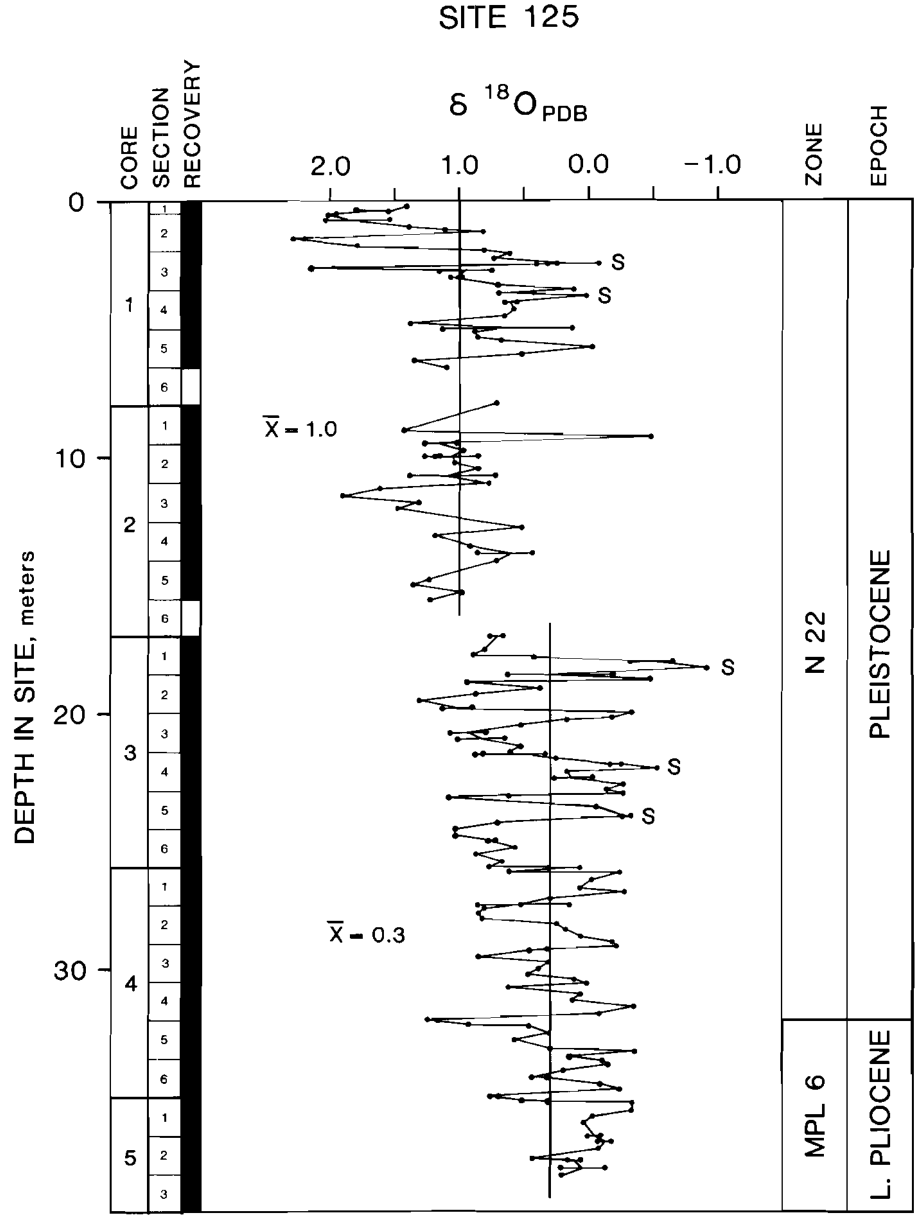

Fig. 2 Oxygen isotopic record of the planktonic foraminifer *Globigerinoides ruber* in the eastern Mediterranean DSDP Site 125. Subbottom depth and core recovery are plotted on the left. The planktonic foraminiferal zonation of Cita (1975) and the geologic epochs are indicated on the right. The symbol "S" denotes the position of organic-rich sapropel layers. Mean $\delta^{18}O$ values for different time intervals are indicated by the heavy lines.

values in core 12 return to pre-core 13 values. A permanent shift does occur, however, between cores 11-1 and 11-2 (at approximately 2.5 MYBP, within MPL 5) with $\delta^{18}O$ values above this level being enriched by an average of $0.7^0/_{00}$. From the level of this shift within MPL 5 up through the early to middle Pleistocene (core 4-2), $\delta^{18}O$ values average $0.4^0/_{00}$. This interval is not only isotopically heavier than the early to middle late Pliocene part of the section, but it is also marked by much greater variability.

A second permanent isotopic shift occurs in the middle Pleistocene between cores 4-2 and 4-1, with $\delta^{18}O$ values above this point averaging $1.7^0/_{00}$ and thus representing an average enrichment of $1.3^0/_{00}$ over the preceding late Pliocene-early Pleistocene interval (fig. 3). This upper late Pleistocene interval is also marked by a fair amount of variability (isotopic glacial–interglacial cycles with amplitudes of approximately $1.5^0/_{00}$). As observed at Site 125, analyses of *G. ruber* from within a sapropelic layer yielded anomalously light $\delta^{18}O$ values, and resulted in an enhancement of the isotopic amplitude to unusually large isotopic fluctuations (up to $2.5^0/_{00}$).

THE PLIOCENE-PLEISTOCENE SEQUENCE OF CLIMATIC CHANGE

The oxygen isotope records from DSDP Sites 125 and 132 (figs. 2, 3) allow us to identify the major climatic and oceanographic changes that have occurred in the Mediterranean during the Pliocene and Pleistocene. The sequence of climatic events recognized in these two Mediterranean sites can also be compared in detail with the $\delta^{18}O$ record established for DSDP Site 397, located off Cape Bojador, Northwest Africa (Shackleton and Cita, 1979).

Evidence from the Mediterranean isotopic record at Site 132 suggests that the early Pliocene (MPL 3) up through the middle of MPL 5, or ∿2.5 MYBP is marked by very little variability, suggestive of generally stable climatic conditions (fig. 3). Planktonic foraminiferal studies of this interval from Site 132 have previously shown that the early Pliocene was a time of generally warm conditions (Ciaranfi and Cita, 1973; Thunell, 1979a). Within this interval of overall warm, stable climates, there appears to have been a cooling trend in the early part of the late Pliocene (MPL 4) beginning around 3.2–3.3 MYBP. This cooling event has been identified in previous isotopic (Keigwin and Thunell, 1979) and faunal studies (Ciaranfi and Cita, 1973; Cita and Ryan, 1973; Thunell, 1979a) of this site, and attributed to the initiation of Northern Hemisphere ice growth. However, the isotopic record presented here in this more detailed study of Site 132 clearly demonstrates that the $1.0^0/_{00}$ ^{18}O enrichment in MPL 4 is not permanent as would be expected if

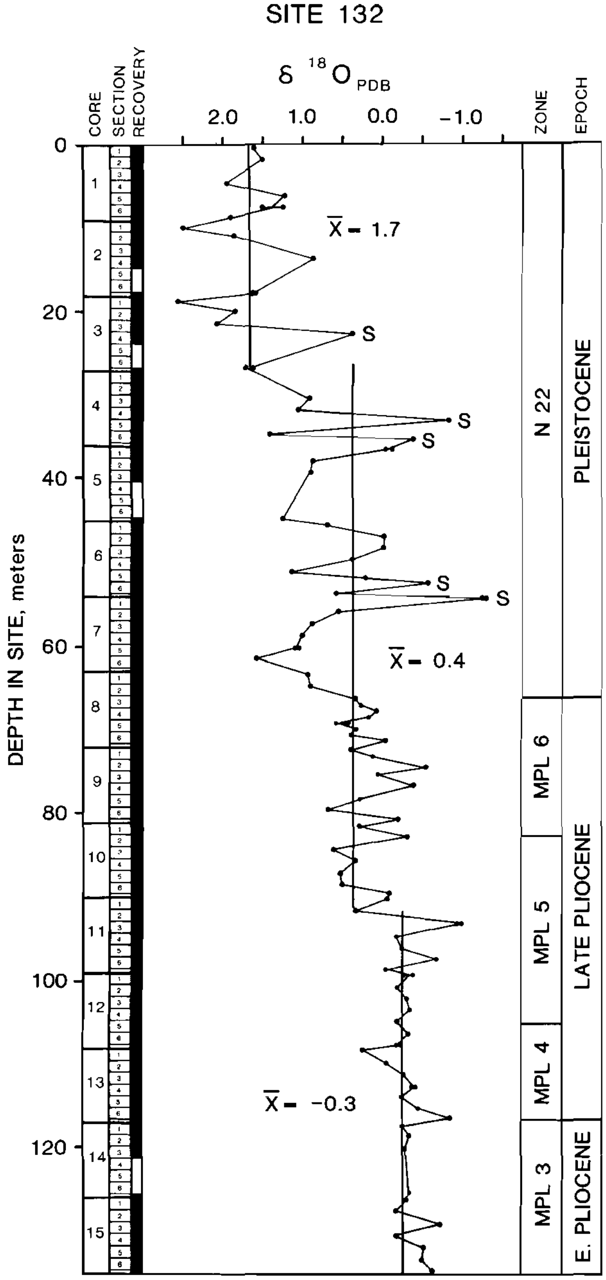

Fig. 3 Oxygen isotopic record of the planktonic foraminifer *Globigerinoides ruber* in the western Mediterranean DSDP Site 132. Subbottom depth and core recovery are plotted on the left. The planktonic foraminiferal zonation of Cita (1975) and the geologic epochs are indicated on the right. The symbol "S" denotes the position of organic-rich sapropel layers. Mean $\delta^{18}O$ values for different time intervals are indicated by the heavy lines.

it were reflecting an oceanic compositional change due to a long term accumulation of ice volume. Instead, $\delta^{18}O$ values in the upper part of MPL 4 and lower part of MPL 5 return to values typical of the early Pliocene, suggesting that the first ^{18}O enrichment during the Pliocene marks a cooling of surface waters and not the build-up of a major ice sheet.

An abrupt 1.3‰ enrichment in ^{18}O in the middle part of MPL 5, at $\sim$2.5 MYBP marks the beginning of an interval that is systematically heavier and more variable than the section below approximately 90 m (fig. 3). This enriched interval represents a long-term isotopic shift which extends up through the middle part of the Pleistocene and is at least partially due to an increase in Northern Hemisphere ice volume since there is a permanent shift to heavier $\delta^{18}O$ values. The high frequency isotopic variability which also occurs throughout this interval typifies glacio-eustatic changes in sea level as a function of glacial–interglacial cycles, and suggests that major Northern Hemisphere glaciation began at the base of this interval within the middle part of MPL 5. The global climatic cooling that should be associated with such an ice build-up is also recorded in the Mediterranean foraminiferal fauna, with a warm water planktonic foraminiferal assemblage being replaced by a cool water assemblage at this time (Zachariasse and Spaak, this volume). A major turn-over in the benthic foraminiferal fauna also accompanied the change in surface water conditions (van der Zwaan, this volume).

The character of the late Pliocene (MPL 6) to early Pleistocene record at Site 125 (fig. 2) is very similar to that found at Site 132 (fig. 3). The $\delta^{18}O$ record for this time interval is clearly dominated by cyclic glacial–interglacial fluctuations (fig. 2).

Within this late Pliocene to middle Pleistocene interval at both locations, a number of levels with very negative $\delta^{18}O$ values are clearly associated with organic-rich sapropel layers, similar to the relationship that has been well documented for the late Pleistocene in the Mediterranean (Cita et al., 1977; Vergnaud-Grazzini et al., 1977; Williams et al., 1978; Thunell and Williams, 1982; Rossignol-Strick et al., 1982). The anomalously negative $\delta^{18}O$ values have been frequently attributed to a decrease in surface water salinities, which in turn are responsible for establishing a density stratification and the development of anoxic bottom conditions. The fact that the early Pliocene sapropels are also characterized by distinct depletions in $\delta^{18}O$ may indicate that the associated anoxic bottom conditions were produced by a set of conditions similar to those responsible for the late Pleistocene anoxic events.

A second major climatic step or change occurs in the middle Pleistocene portion of the $\delta^{18}O$ records for both sites (figs. 2, 3) where another systematic enrichment in ^{18}O occurs, with the enrichment averaging 0.7‰ and

1.3‰ at Sites 125 and 132, respectively. Above this shift, both records are still dominated by cyclic glacial–interglacial fluctuations, although the glacial episodes are significantly heavier than those of the late Pliocene – early Pleistocene interval. This shift probably reflects further intensification of Northern Hemisphere glaciation and an associated cooling of surface waters. This agrees with the previous faunal work of Cita et al. (1973) and Thunell (1979a), both of which subdivided the Pleistocene into two parts, a cooler upper part marked by large temperature oscillations and a warmer lower part.

COMPARISON OF ISOTOPIC RECORDS FROM THE MEDITERRANEAN AND THE OPEN OCEAN

A comparison of the Mediterranean isotopic records presented here with records representing open ocean conditions should allow us to determine whether the events observed in the Mediterranean are regional or global in nature. First, particular emphasis will be placed on correlating the Mediterranean Sites 125 and 132 records with that for DSDP Site 397, located off the margin of Northwest Africa near Cape Bojador (fig. 4) (Shackleton and Cita, 1979). In addition, a general comparison will be made between the Mediterranean records and the major trends seen in other open ocean records (fig. 5). The relatively stable climatic conditions observed for the early Pliocene (MPL 3) at Site 132 is a feature that is typical of extra-Mediterranean records. Oxygen isotopic records from the Southern Ocean (Shackleton and Kennett, 1975a), equatorial Pacific (Shackleton and Opdyke, 1977; Keigwin, 1979, 1982), North Pacific (Keigwin, 1979), Caribbean (Keigwin, 1982) and South Atlantic (Leonard et al., in press) all indicate that the interval between approximately 5.0 and 3.0 MYBP was a time of stable ice volume and climatic conditions.

The ^{18}O enrichment in planktonic values beginning around 3.2 MYBP is another feature common to many open ocean isotopic records. However, the cause for this enrichment has been attributed to several different factors. Shackleton and Opdyke (1977) observed a similar enrichment in the benthic $\delta^{18}O$ record of an equatorial Pacific piston core and attributed it to the initial build-up of major Northern Hemisphere glaciation. This 3.0 to 3.2 MYBP event has subsequently been observed in $\delta^{18}O$ records from the North Pacific (Keigwin, 1979), Caribbean (Keigwin, 1982) and South Atlantic (Leonard et al., in press; Hodell et al., in press). In addition, the timing of this isotopic event agrees with the 3.0 MYBP age estimate for the beginning of ice rafted sedimentation in the North Atlantic (Berggren, 1970;

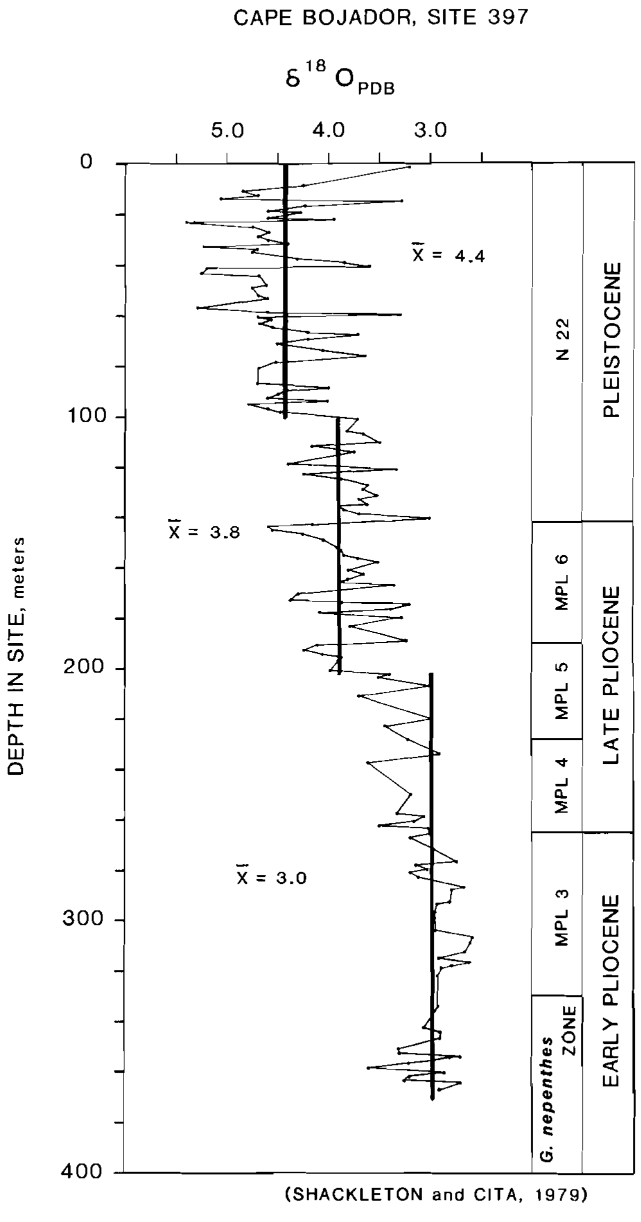

Fig. 4 Composite benthic oxygen isotopic record for DSDP Site 397, after Shackleton and Cita (1979). Subbottom depth is plotted on the left. The planktonic foraminiferal zonation of Cita (1975) and the geologic epochs are indicated on the right. Mean $\delta^{18}O$ values for different time intervals are indicated by the heavy lines.

Poore, 1981). However, the ^{18}O enrichment that is observed at approximately 3.2 MYBP at Site 132 (fig. 3) is not a permanent shift in the Mediterranean, and as discussed earlier, does not reflect a permanent build-up of ice but most probably a surface water cooling in the western basin. The planktonic $\delta^{18}O$ records of Keigwin (1982) for DSDP Sites 502 (Caribbean) and 503 (eastern equatorial Pacific) also show a temporary enrichment at 3.2 MYBP, and have been likewise interpreted by Prell (1982) to reflect a cooling event in surface waters and possibly a non-permanent growth of ice in either the Northern or Southern Hemisphere.

On the other hand, the 0.7$^0/_{00}$ shift in $\delta^{18}O$ at around 2.5 MYBP (within MPL 5) in the Site 132 record (fig. 3) is a permanent enrichment which at least partially reflects permanent ice volume growth in the Northern Hemisphere. A permanent $\delta^{18}O$ shift at this time is also quite evident in the benthic record for Site 397, off Cape Bojador (fig. 4) (Shackleton and Cita, 1979) and in both planktonic and benthic $\delta^{18}O$ records from the Northern

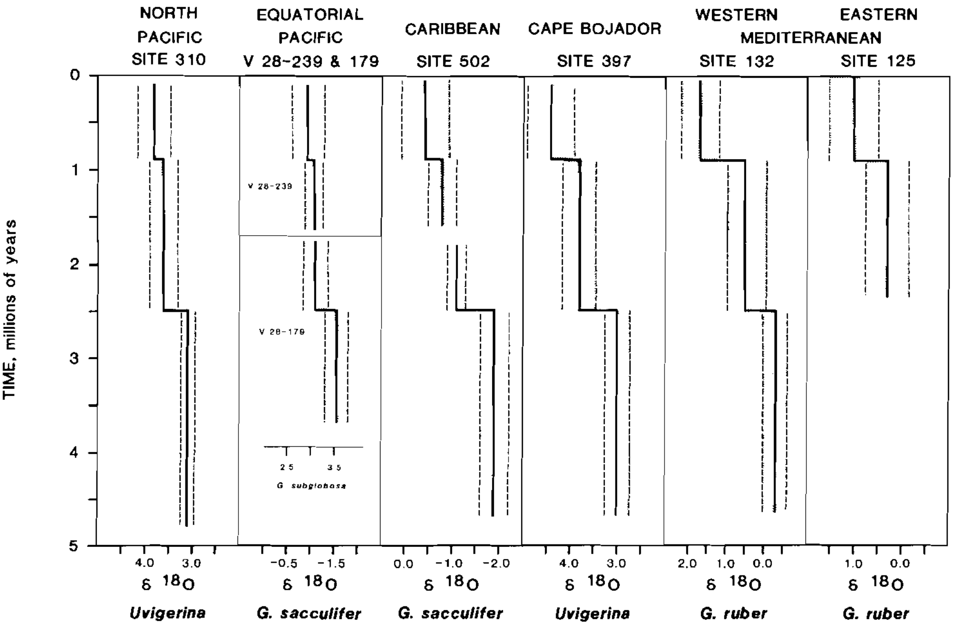

Fig. 5 Schematic diagram comparing the mean oxygen isotopic values and their variability in $\delta^{18}O$ records for DSDP Site 310 from the North Pacific (Keigwin, 1979), equatorial Pacific cores V28–239 and V28–179 (Shackleton and Opdyke, 1976, 1977), DSDP Site 502 from the Caribbean (Keigwin, 1982; Prell, 1982), DSDP Site 397 off Cape Bojador (Shackleton and Cita, 1979) and DSDP Sites 125 and 132 from the Mediterranean (this study). The vertical lines denote the mean $\delta^{18}O$ value for the time period representing significant shifts or steps in climatic conditions. The stippled area represents ± 1 standard deviation about the mean.

Pacific (Keigwin, 1979), the equatorial Pacific (Shackleton and Opdyke, 1977) and the Caribbean (Keigwin, 1982) (fig. 5). The development of permanent Northern Hemisphere ice at approximately 2.5 MYBP rather than 3.2 MYBP is also supported by sedimentological evidence. Backman (1979) has placed the beginning of ice rafting at $\sim$2.5 MYBP based on a reevaluation of the biostratigraphy of North Atlantic DSDP Sites 111 and 116. In addition, the dramatic increase in the accumulation of eolian particles in the North Pacific around 2.5 MYBP has been attributed to intensified atmospheric circulation associated with the onset of Northern Hemisphere glaciation (Rea and Janecek, 1982). We tend to favor Backman's (1979) interpretation that the ^{18}O enrichment in both planktonic and benthic records at about 3.2 MYBP is the result of a surface water cooling and the production of colder bottom waters. In addition, the 3.2 to 2.5 MYBP interval in published $\delta^{18}O$ records is typically characterized by low variability of an average amplitude not expected during Northern Hemisphere glacial–interglacial changes. Likewise, the floral record for NW Europe indicates that this interval of time was characterized by warm climates, and it was not until 2.5 MYBP that a cooling comparable to those of Pleistocene glacials occurred (Zagwijn, 1974).

The middle Pleistocene climatic shift observed in both of the Mediterranean isotopic records (figs. 2, 3) also appears related to a global paleoclimatic event (fig. 5). This change in the character of the Pleistocene oxygen isotopic record was initially observed in the Pacific by Shackleton and Opdyke (1976) and in the Atlantic by Van Donk (1976). Both of these studies demonstrated that late Pleistocene glacial $\delta^{18}O$ values are typically heavier than those of the early Pleistocene. This shift in the character of Pleistocene glacial–interglacial cycles has subsequently been observed in other faunal (Briskin and Berggren, 1975) and isotopic studies (Shackleton and Cita, 1979; Prell, 1982; Fillon and Williams, in press), and occurs at the isotopic stage 22/23 boundary, or approximately 900,000 years ago (fig. 5) (Shackleton and Opdyke, 1976; Pisias and Moore, 1981; Shackleton et al., 1982).

Within the Mediterranean region this intensification of glacial conditions during the late Pleistocene has been observed in a number of previous studies (Selli, 1967; Cita et al., 1977; Thunell, 1979), and has been attributed to an expansion of Alpine glaciation in the middle Pleistocene (Selli, 1967). More recently, Herman and Hopkins (1980) have suggested that perennial sea-ice cover in the Arctic began around 900,000 years ago. It has also been proposed that the establishment of this Arctic Ocean ice sheet combined with large continental ice sheets is responsible for the observed middle

Pleistocene climatic shift and the intensification of glacial–interglacial cycles (Williams et al., 1981; Fillon and Williams, in press).

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STABLE CARBON ISOTOPES IN QUATERNARY FORAMINIFERA FROM THE GULF OF AQABA (ELAT), RED SEA

B. LUZ and Z. REISS

ABSTRACT

Carbon isotopic composition of perforate-lamellar and porcelaneous smaller benthic foraminifera in Late Quaternary sediments from the Gulf of Aqaba record systematic variations with time. The last glacial is characterized by depletion of ^{13}C in all groups, but with different magnitudes. The largest departure from present-day $\delta^{13}C$ is observed in (the probably epifaunal) *Cibicides*. Smaller departures are recorded by (the probably infaunal) buliminaceans and miliolaceans. The general ^{13}C depletion indicates lowering of oxygen-levels in the deep waters of the glacial Gulf due to higher fertility of the photic zone and larger particulate flux to the bottom. Independent evidence from assemblages of planktic foraminifera, pteropods and coccolithophorids, as well as from oxygen isotopes in planktic and benthic foraminifera, supports this interpretation. Mode of shell formation is suggested as a factor influencing stable isotope fractionation.

INTRODUCTION

Stable isotope composition of skeletal carbonate, especially of foraminifera has become a major tool in the reconstruction of marine paleoenvironments. Oxygen isotope ratios have been widely studied and successfully used for the interpretation of the thermal history of the oceans, of past fluctuations in sea-level and ice volume, evaporation/precipitation rates and density stratification. Carbon isotope ratios in skeletal material, although less well studied, are used in interpreting the organic fraction of the total CO_2 in the ambient water, hence the latter's fertility and, implicitly, dissolved oxygen levels. Difficulties arise in interpretation of both oxygen and carbon isotope ratios especially because of incorporation into the foraminiferal shell of metabolic CO_2 derived from the photosynthetic activity of symbionts hosted by many planktic and benthic species and/or from food. Furthermore, skeletal carbon isotope ratios are influenced by the nature (marine or terrestrial) and diagenetic stage of the organic material (kerogen, methane) oxidized and incorporated through the bicarbonate of the ambient water. Additional problems arise because of changes in oxygen and carbon isotope disequilibrium values in skeletal carbonate due to changes in growth rates and metabolic activity and seasonal environmental changes, during ontogeny, as well as due to specific departures from equilibrium values ("vital effect") explained in part by chemical composition of the skeletal carbonate (e.g. magnesium content), but actually not well understood (for recent reviews of progress and problems in stable isotope research see Berger et al., 1981; Savin and Yeh, 1981; and Vincent and Berger, 1981).

The present contribution summarizes an attempt to use carbon isotopes in smaller benthic foraminifera from deep-sea cores as an aid in interpreting paleoenvironmental changes during the Late Quaternary in the Gulf of Aqaba. The analytical procedure employed is according to Shackleton (1974) and the results are expressed in permil deviations from PDB. In calculating $\delta^{18}O$ and $\delta^{13}C$ of equilibrium calcite, equations (1) and (2), which are based on Craig (1965) and Emrich et al. (1970) respectively, have been derived.

$$\delta^{18}O_{\text{equilibrium calcite}} = \delta^{18}O_{H_2O} + 16.15 - (130.95 + 7.69T)^{\frac{1}{2}} \tag{1}$$

$$\delta^{13}C_{\text{equilibrium calcite}} = \delta^{13}C_{\text{dissolved } HCO_3^-} + 1.15 + 0.035T \tag{2}$$

where T is temperature in °C.

THE GULF OF AQABA'S PRESENT-DAY CONDITIONS

Extremely high evaporation rates ($4 m\ y^{-1}$) in the arid setting determine an inverse estuarine, thermohaline circulation pattern in the 180 km long, 24 km wide and 1,830 m deep Gulf of Aqaba (fig. 1) with rapid and large volume transport over the 252 m deep sill of Tiran. The Gulf is filled with warm, upper Red Sea waters with a residence time of 4–8 months. Evaporation rates and circulation pattern (which includes a vertical vortex in the deep waters) lead to a water column in the Gulf which is highly saline (41‰), warm (min. 21°C) and highly oxygenated to greatest depth throughout the year. The upper waters of the northern Red Sea filling the Gulf are extremely nutrient-poor and since there is no other source (like rivers) for nutrients in the Gulf of Aqaba, the latter is oligotrophic. Strong insolation throughout the year, low biomass and lack of substantial transport of abiogenic material from land lead to considerable light penetration and a photic zone of about 170 m depth (Klinker et al., 1976, 1978; Levanon-Spanier et al., 1979; Reiss et al., 1977). A comparison of the hydrographic characters of the Gulf of Aqaba with those of the northern Red Sea and the Gulf of Aden is summarized in figure 2.

Present-day assemblages (low-diversity ones) of planktic foraminifera (mostly symbiont-bearers) and of pteropods are epi- to shallow mesopelagic, similar to those of oceanic gyre-centers. Deeper water species appear in the Red Sea south of lat. 22°N and become abundant in the southern Red Sea and especially in the Gulf of Aden, where assemblages resemble those of equatorial current systems. The change in assemblages is best explained by the gradients of nutrient content and primary production, from oligotrophic conditions in the strongly illuminated Gulf of Aqaba, coupled with specific

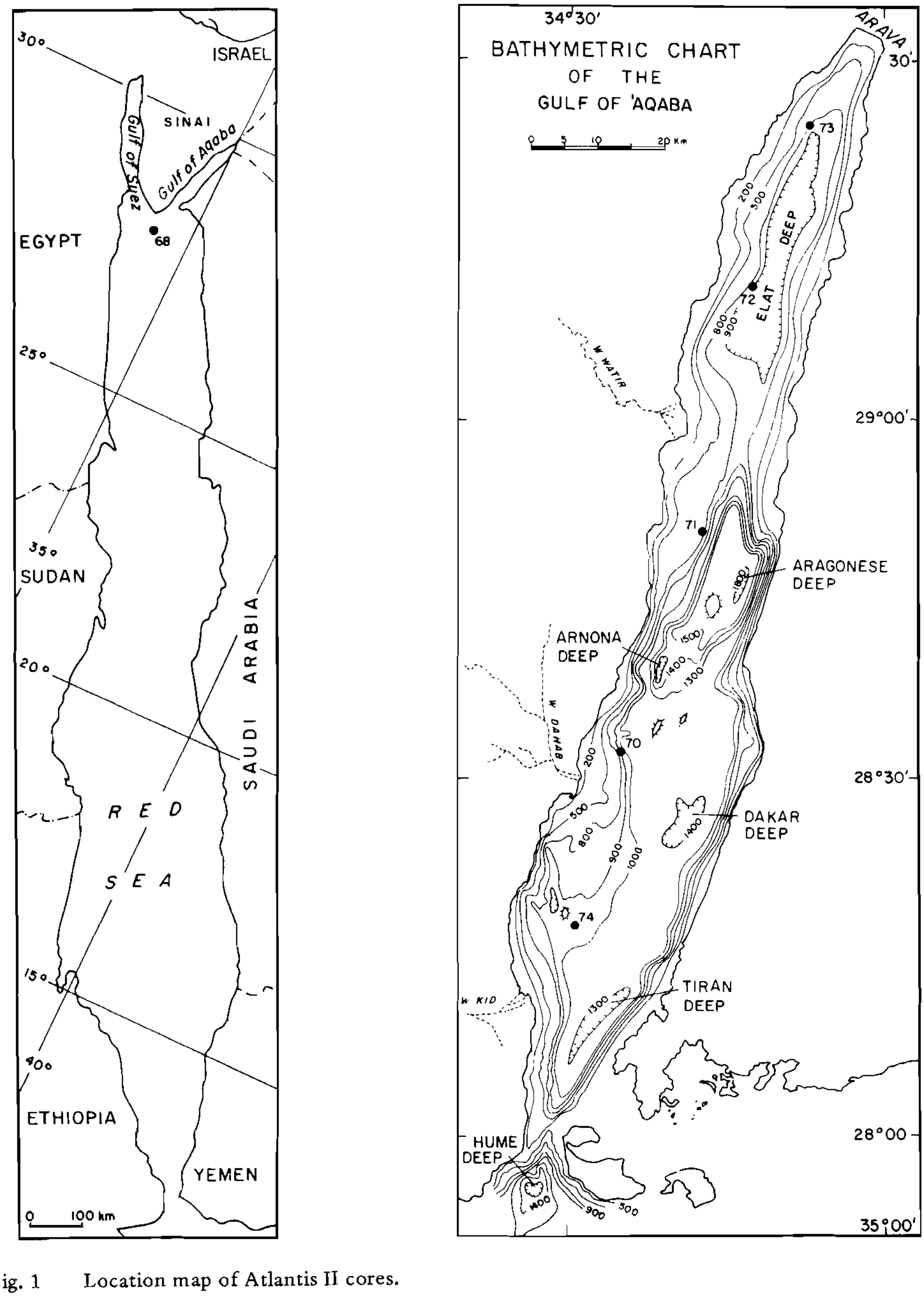

Fig. 1 Location map of Atlantis II cores.

nutritional requirements of various taxa, to increasingly normal, highly productive conditions in the Gulf of Aden. Changes in assemblages of coccolithophorids along the stretch Gulf of Aden-Red Sea-Gulf of Aqaba can also be explained mainly by the associated gradient of nutrient content (Almogi-Labin, 1981, 1982; Halicz and Reiss, 1981; Reiss et al., 1974; Winter et al., 1979; Winter, 1982).

DEEP-SEA CORES: OXYGEN ISOTOPES AND PLANKTIC ASSEMBLAGES

Deep-sea cores from the Gulf of Aqaba and the northernmost Red Sea (fig. 1) have provided information on the paleoceanographic evolution of the Gulf of Aqaba during the last 150,000 years. Rates of sedimentation of about 10 cm per 1,000 years facilitate a high-resolution eco-stratigraphic record based on stable oxygen isotopes and on qualitative and quantitative changes in assemblages of planktic and benthic foraminifera, pteropods and coccolithophorids (Almogi-Labin, 1982; Halicz and Reiss, op. cit.; Reiss et al., 1980; Winter, 1982). A composite, generalized core-record is given in figure 3.

The shape of the oxygen isotope curve from planktic foraminifera (*G. ruber*) and from pteropods in the cores makes it possible to recognize isotope stages 1 to 6 and to date (beyond the radiocarbon range) several points in the sequence. However, the difference in $\delta^{18}O$ between the last glacial maximum, about 18,000 y BP and the present is about 1.5‰ in the open ocean and in excess of 5‰ in the Red Sea and in the Gulf of Aqaba (Deuser et al., 1976; Reiss et al., 1980). This difference expresses the glacial-post glacial change in sea water composition and does not provide a direct clue to changes in temperature and/or salinity. On the other hand, throughout the deep-sea cores studied from the Gulf of Aqaba and northernmost Red Sea, displaced shells of shallow-water, benthic tropical, symbiont-bearing foraminifera occur, among them *Amphisorus*, whose present-day minimum winter isotherms are about 17°C. This indicates that a) throughout glacial times minimum winter temperature of the upper waters in the Gulf were never lower than at most 4°C below that at present, and b) that the $\delta^{18}O$ values reflect a rise in salinity of about 10‰, to more than 50‰ during the glacial maximum. This salinity rise is attributed to lowering of sea level and strait dynamics. The total absence, in strata corresponding to glacial maxima, of planktic foraminifera whose upper salinity tolerance limit is shown by laboratory experiments to be approximately 48‰, supports this interpretation. The abundance of well-preserved aragonitic pteropods in the same strata indicates that no dissolution of calcium carbonate affects the assemblage composition. The domi-

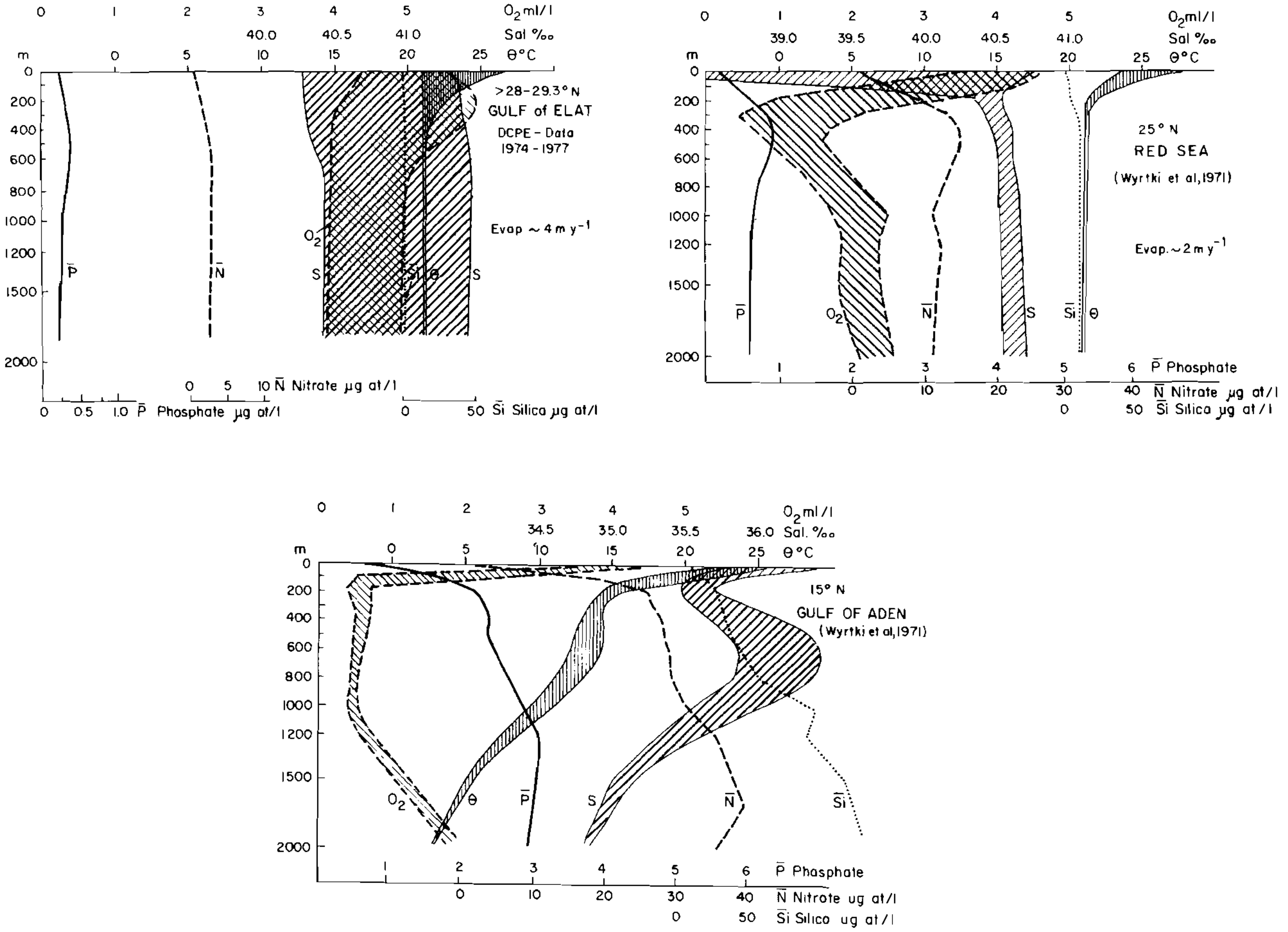

Fig. 2 Comparison of hydrographic characters of the Gulf of Aden, Red Sea proper and Gulf of Aqaba (from Halicz and Reiss, 1981).

nance of *G. ruber* and virtual absence of *G. sacculifer* in glacial intervals is attributed to water temperature at depth of reproduction and not to salinity (*G. sacculifer* dominates over *G. ruber* at present in the hypersaline Gulf of Aqaba).

Peaks of the *G. bulloides-falconensis* group, indicative of highly productive waters, seem to reflect higher fertility of the upper waters in the Gulf during glacial times. This is supported by the dominance of the pteropod *Limacina trochiformis* known to characterize at present high productive regions, over *L. inflata*, abundant mostly in low-productive waters and in interglacial intervals of the Aqaba cores. Abundance of *Creseis acicula* and absence of other pteropods during glacial maxima is attributed to its well-known euryhalinity as well as to its affinity to productive waters. Higher fertility of the upper waters during glacial times is furthermore indicated by dominance of – the more euryhaline in the upper reaches – *Gephyrocapsa oceanica* over *Emiliania huxleyi*, which is more euryhaline at low salinities. Higher fertility during glacial times can be explained by an increase in residence time of the waters and by a change of input/output ratio of nutrients, as well as by the probably higher fertility of the ocean during the glacial. Upwelling during glacial maxima in the northernmost Red Sea, outside the sill of Tiran, is indicated by layers extremely rich in coscinodiscid diatoms occurring in core 68 (fig. 1).

CHANGES IN THE BENTHIC ENVIRONMENT

The ecological changes of the upper waters are reflected in the benthic assemblages, and in isotopic composition of their calcitic shells. The glacial intervals are characterized by strong dominance of buliminaceans over other benthic perforate foraminifera. This seems to indicate reduction of O_2-levels due to greater particulate influx of organic matter, and due to less vigorous vertical mixing of the water column. The strong increase during glacials in abundance of small miliolaceans indicates that they, too, are able to withstand low oxygen conditions and the extreme high salinities of the glacial maxima. Since various buliminaceans and especially the bolivinids are known to be infaunal, the parallel trends of buliminaceans and miliolaceans (especially small ones) may indicate that the latter are also infaunal and thus are able to thrive at minimum oxygen levels. This in contrast to the "rotaliform" epifaunal foraminifera (see caption fig. 3), whose abundance decreases drastically during glacials.

Reduced vertical mixing is indicated by $\delta^{18}O$ of planktic and benthic foraminifera (fig. 4). In the glacial interval there is greater separation in $\delta^{18}O$

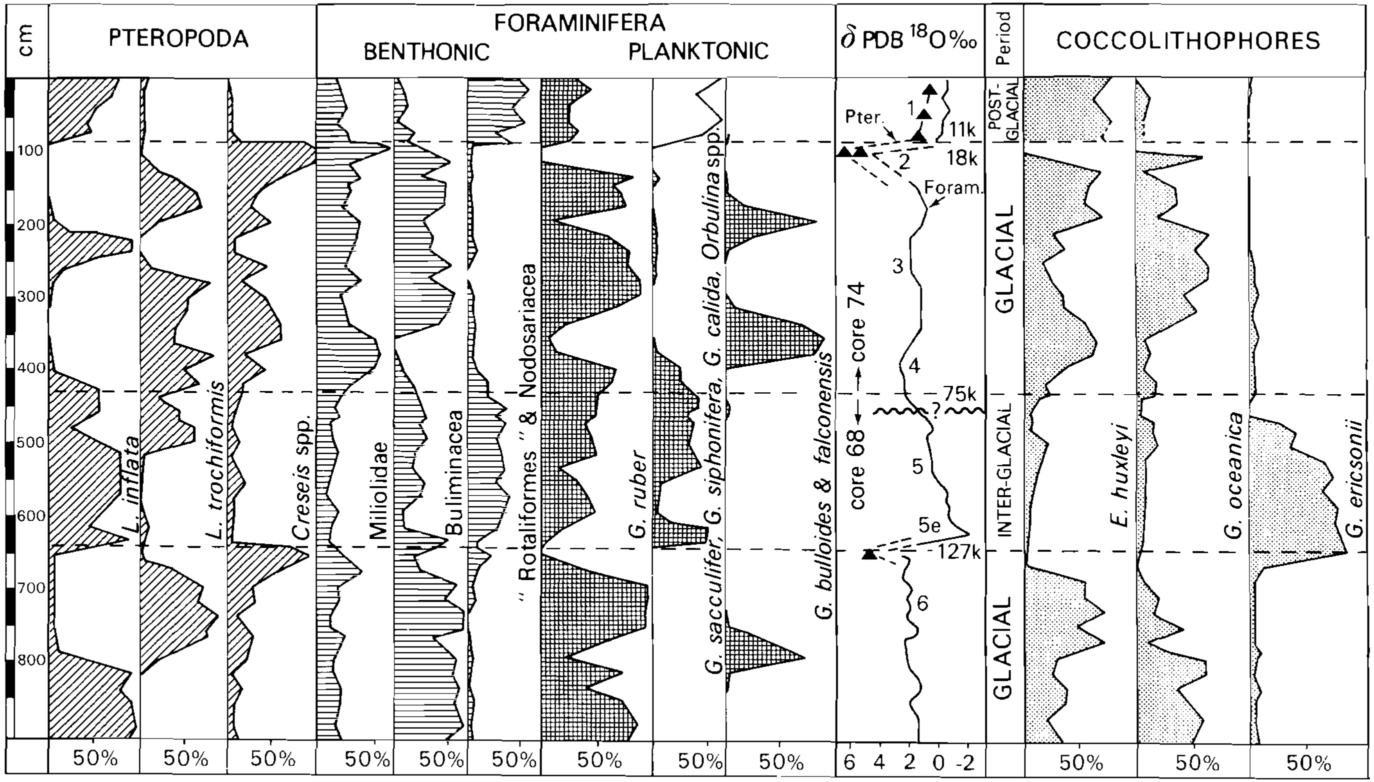

Fig. 3 Generalized composite core record (based on cores 74 and 68; see fig. 1). Stable isotope curve based on *Globigerinoides ruber* ("Foram") and on *Limacina trochiformis* and *Creseis acicula* ("Pter.") (modified from Reiss et al., 1980; Halicz and Reiss, 1981; Almogi-Labin, 1982, and Winter, 1982).

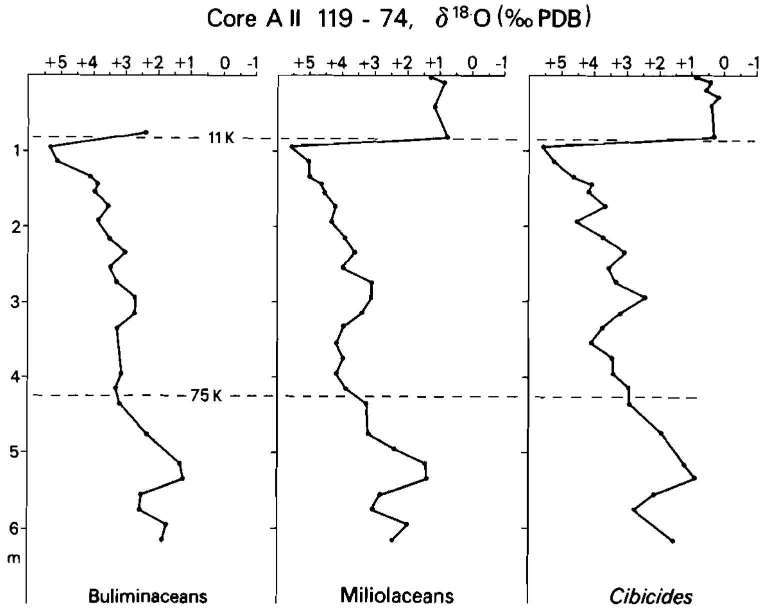

Fig. 4 Oxygen isotope record of benthic foraminifera, core AII 119–74 (see fig. 1).

of the two groups. Thus, there was either a larger temperature or a larger salinity difference between surface and deep waters. Parametrization of sea-straits (Anati, 1980) for lower sea level (during glacials) supports the second possibility, because it suggests stronger salinity stratification due to restricted water exchange through the straits.

It is interesting to note that the absolute $\delta^{18}O$ values of the three foraminiferal groups differ considerably (fig. 4), and only the miliolids seem to be close to isotopic equilibrium (based on the post-glacial data). Nevertheless, all the groups show very similar trends. Thus, regardless of the biological effect causing disequilibrium, the fluctuating isotopic ratios can be interpreted in terms of past environmental conditions. The possibility is not excluded that the *fundamentally different mode of shell-formation* in perforate-lamellar and porcelaneous foraminifera (Berthold, 1976; Berthold and Spindler, 1979), influences oxygen isotopic fractionation.

CARBON ISOTOPES

The carbon isotopic ratios of benthic foraminifera in core 74 (fig. 5) show systematic fluctuations in all the groups, which correspond to the major environmental changes discussed above. On the other hand, the planktic

$\delta^{13}C$ record shows small, seemingly random deviations (± $0.4^0/_{00}$) from an average of $1.3^0/_{00}$. This rules out the possibility that the $\delta^{13}C$-changes were an ocean-wide phenomenon which affected the entire water column and influenced the Red Sea and the Gulf of Aqaba by exchange of upper waters across sea straits. Clearly the changes had to result from a mechanism that operated in the basin itself.

The samples examined are multispecific ones comprising in the Miliolidae several species of *Quinqueloculina*, *Triloculina* and *Spiroloculina*; in the Buliminacea mainly Bolivinidae with varying proportions of *Brizalina* cf. *B. subargentea* Uchio, *Brizalina amygdalaeformis* (Brady), *Bolivina hebes hebes* Macfadyen and *B. hebes suezensis* Said, and small numbers of *Bulimina marginata* d'Orbigny; and in the Cibicididae mainly *Cibicides mabahethi* Said and small numbers of *C. tabaensis* Peralis & Reiss.

The Holocene specimens are all in disequilibrium if compared to present-day conditions in the deep water of the Gulf of Aqaba (table 1).

Departures from carbon-isotopic equilibrium are common in perforate foraminifera (Berger et al., 1981) and might be related to internal cycling of organic carbon within the living foraminifera. However, many porcelaneous species are known to be at or close to isotopic equilibrium (Berger et

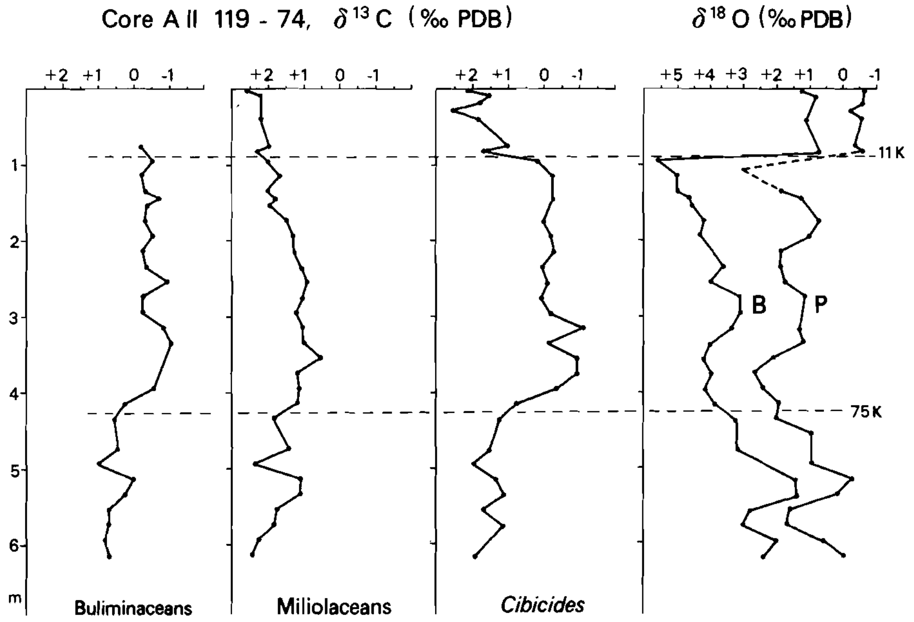

Fig. 5 Carbon isotope record of benthic foraminifera, core AII 119–74, compared with oxygen isotope record of planktic (P) and benthic (B) foraminifera.

	Present (and Post-Glacial)	Glacial (75,000–11,000 year BP)
O_2 (mmole/l)	0.2[1]	0.03[4]
ΣCO_2 (mmole/l)	2.1[2]	2.27[4]
$\delta^{13}C$ of ΣCO_2 ($^{0}/_{00}$ PDB)	1.5[2]	−0.3
$\delta^{13}C$ of equilibrium calcite ($^{0}/_{00}$ PDB)	3.4[3]	1.6

Table 1 Measured deep-water parameters and inferred ones for the glacial interval
1. after Klinker et al. (1976).
2. after Shemesh (1981).
3. calculated according to Emrich et al. (1970) (eq. 2) for 20°C.
4. calculated with eq. 3 assuming $\delta^{13}C_{org.} = -23^{0}/_{00}$.

al., op. cit.; Luz, Reiss and Zohary-Segev, this volume). Like in the case of oxygen isotopes (see above) mode of shell formation may equally influence carbon-isotope fractionation.

The apparent deviation from equilibrium (by $1.4^{0}/_{00}$) with the deep water of the miliolids may thus indicate their infaunal habitat. If this is true then they live in a micro-niche whose $\delta^{13}C$ of the total dissolved CO_2 (ΣCO_2) is $1.5-1.4 = 0.1^{0}/_{00}$ (table 1). Assuming that $-23^{0}/_{00}$ organic carbon ($\delta^{13}C_{org}$) is oxidized in the sediment, then the resulting changes in both O_2 and CO_2 with respect to the deep water can be calculated from simple material balance considerations. Let D be the increase in ΣCO_2 or decrease of O_2 in mmole/l in the sediment and Δ the difference between $\delta^{13}C$ of the miliolid calcitic shell and the calculated $\delta^{13}C$ of deep-water equilibrium-calcite ($-1.4^{0}/_{00}$). At present, $\delta^{13}C$ in the CO_2 of the deep water is $1.5^{0}/_{00}$ and ΣCO_2 is 2.1 mmole/liter (table 1).

$$\Delta + (\delta^{13}C_{CO_2})_{present} = \frac{D \times \delta^{13}C_{org} + (\delta^{13}C_{\Sigma CO_2} \times \Sigma CO_2)_{present}}{D + (\Sigma CO_2)_{present}} \qquad (3)$$

By solving for D, a value of D = 0.13 mmole/l is obtained, indicating that the O_2 concentration in the miliolid micro-niche is at present 0.07 mmole/l or 1.6 ml/l. This estimate is not very sensitive to small changes in $\delta^{13}C_{org}$. For example for $\delta^{13}C_{org} = -26^{0}/_{00}$, D is calculated as 0.11 mmole/l, corresponding to 2.0 ml O_2/l in the miliolid micro-niche.

	Interglacial	Glacial	$\Delta_{G\text{-}IG}$
Cibicididae	1.66	–0.15	–1.81
Buliminaceans	0.52	–0.49	–1.01
Miliolaceans	2.00	1.34	–0.66

Table 2 Average $\delta^{13}C$ ($^0/_{00}$ PDB) of benthic foraminifera in glacial and interglacial intervals and the difference between these periods ($\Delta_{G\text{-}IG}$) in core AII 119–74.

Averaging the $\delta^{13}C$ values for glacial and interglacial intervals and comparing the glacial-interglacial changes in each group (table 2) it is of interest to note that the change in both miliolaceans and buliminaceans (despite the difference in absolute values) is the same ($-1^0/_{00}$), while the strongest change occurs in the (largely monospecific) *Cibicides* assemblage ($-1.8^0/_{00}$). This may support the suggestion that both miliolaceans and buliminaceans share an infaunal habitat, while epifaunal *Cibicides* is affected by considerable changes in the deep water. It follows that equilibrium calcite with the glacial deep-water had a $\delta^{13}C$ of $1.6^0/_{00}$ ($3.4^0/_{00}$ present + $\Delta_{G\text{-}IG}$). Because temperature fractionation of carbon isotopes is relatively small, the same change ($\Delta_{G\text{-}IG}$) can be assigned to $\delta^{13}C$ of ΣCO_2 of glacial and interglacial times (table 1). One can now use equation 3 for calculating ΣCO_2 and O_2 concentration of the glacial deep waters in the Gulf of Aqaba. Let D be the change in O_2 or CO_2 between the glacial and the present and substitute $\Delta_{G\text{-}IG}$ for Δ. Solving for D we obtain D = 0.17 mmole/l or 3.8 ml O_2/l. Thus, the glacial deep water in the Gulf of Aqaba had very low O_2 levels, viz. about 0.7 ml/l.

Recalling that this estimate depends on the $\delta^{13}C$ of the oxidized organic carbon ($\delta^{13}C_{org}$) it is possible that at least part of the glacial-interglacial change results from a difference in $\delta^{13}C_{org}$. However, it is unlikely that this would greatly affect the estimated O_2 reduction. Calculation with equation 3 demonstrates that in order to decrease the change in O_2 level by one-half, $\delta^{13}C_{org}$ has to be about $-45^0/_{00}$. In the same way the differences among the cibicidids, miliolaceans and buliminaceans in the cange between glacial and interglacial $\delta^{13}C$ (table 2) may be related to changes in food sources with the latter's own (considerable) difference in $\delta^{13}C$.

It is not known whether this consideration is realistic, and whether the spectrum of $\delta^{13}C$ of the available food sources for benthic foraminifera is large enough. The fact that the lowering of $\delta^{13}C$ in the benthic foraminifera corresponds to increase in fertility of the upper waters, points to increased particulate flux to the deep water as the most probable mechanism.

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RECENT ADVANCES IN RESEARCH ON LIVING PLANKTONIC FORAMINIFERA

CHRISTOPH HEMLEBEN and MICHAEL SPINDLER

ABSTRACT

Biological studies of planktonic foraminifera are necessary for any reliable interpretation of their oceanic paleoenvironments. These studies include both field and vital observations to explain vertical and horizontal distributions and to evaluate the role of symbionts, commensals and parasites in determining life habitat and in influencing the calcification process. Food source is apparently most important for explaining the distribution of planktonic foraminifera. Their growth (both calcification and resorption) is strongly influenced by their general life habitat. Reproduction may be linked to the lunar cycle and in some cases influences their distribution or causes additional calcification. The depth habitat of planktonic foraminifera is determined by, and thus can be used to decipher, measurable environmental factors.

INTRODUCTION

Very little is known about the biology of the planktonic protozoans, such as radiolarians and planktonic foraminifers, even though they are abundant throughout the world's oceans. Planktonic foraminifers have been known ever since they were described by d'Orbigny (1826), although he believed that he was dealing with benthic organisms. It took another sixty years before Brady (1884) established their planktonic mode of life from material collected during the "Challenger" Expedition (1872–1876). Tremendous knowledge has been gained since then, mainly of their distribution in the water column and on the sea floor in recent and in fossil sediments.

Planktonic foraminifers are now widely used to decipher the ocean's ecosystem in the past and, thereby, to help reconstruct global events in paleoclimatology and plate tectonics. However, our knowledge of the physiology and life cycle of the approximately 40 living species (or subspecies) has increased only very little since the time of the "Challenger".

Most data have been obtained from specimens collected with plankton nets that destroy the natural microenvironment of the animal. However, Murray (1897) and Rhumbler (1911) did describe the gross morphology of living specimens from both plankton hauls and dipping jars. Rhumbler (1911) was the first to publish results of a cytological light microscopical study showing ingested muscle fibers and incorporated zooxanthellae (symbionts). More recently, Fèbvre-Chevalier (1971), Zucker (1973), Leutenegger (1977), Anderson and Bé (1976) and our group (see references) have reported cytological aspects of the feeding process, symbionts, pore structure, chamber formation and reproduction. Attempts to culture and maintain planktonic foraminifers in the laboratory were first made by Adshead (1967). A new collecting method, the collection of planktonic organisms by hand during scuba diving, was introduced by Alldredge and Jones (1973) and by Bé et al. (1977).

Since 1975, we have tried to combine field observations, laboratory experiments and subsequent scanning and transmission electron-microscopic and mass spectrometric studies for a better understanding of the physiology, nutrition, shell growth, reproduction and ecological adaptation of planktonic foraminifers. In this paper we shall try to summarize the "present state of the art".

MATERIAL AND METHODS

Our present knowledge is based on only 16 of the living species of planktonic foraminifers from the Atlantic Ocean. Field observations and laboratory experiments with living planktonic foraminifers were performed mostly at the Biological Station of Bermuda (BBS) and at Bellairs Research Institute, Barbados (BRI). To a lesser extent we did comparative research at the Heinz Steinitz Marine Biological Laboratory (HSMBL) in Elat, Israel. Following Bé's classification (1977) with minor modifications, we subdivide the recent planktonic foraminifers into three groups emphasizing the terms spinose and non-spinose.

A. The *spinose* family Hastigerinidae
B. The *spinose* family Globigerinidae s.l.
C. The *non-spinose* family Globorotaliidae s.l.

Figure 1 lists all species we have worked with; species about which little is known are indicated by an asterisk. Seasonal occurrence and laboratory are also listed.

For the collecting methods and maintaining procedures see Bé et al. (1977). In culture experiments, performed at BBS during the years 1975–1983, we used open ocean seawater of 36‰ (± 0.5‰) salinity. The temperature of the culture room was continuously adjusted to that of the open ocean (3–5 miles offshore Bermuda) during the course of the year. From the fall of 1979 we used accurately adjustable (± 0.5°C) culture containers and open ocean seawater of different salinities (Hemleben, 1982). Laboratory light conditions were adjusted to those at approximately 25 m water depth in the blue open ocean. The following observations, data and conclusions are based on 15,000 individuals collected while scuba diving or derived from plankton tows. All specimens were kept and monitored individually. The SEM and TEM work was done in Tübingen; micrographs were taken either with a Stereoscan Mark II and 250 S operated at various KV or with an EM 9 operated at 60 KV.

Spinose species

	Occurrence	Frequency	Laboratory
Hastigerina pelagica (d'Orbigny)	summer (winter)	f (r)	BBS
	winter	r	BRI
Globigerinalla aequilateralis (Brady)	summer (Apr-Nov)	c-r	BBS
	year-round	r	BRI
Orbulina universa (d'Orbigny)	year-round	f	BBS, BRI
Globigerinoides conglobatus (Brady)	summer (Apr-Nov)	c	BBS
	winter	r	BRI
G. *ruber* (d'Orbigny)	year-round	f	BBS, BRI
G. *sacculifer* (Brady)	year-round	f-r	BRI
*Globigerina cristata** (Heron-Allen and Earland)		traces	BBS
G. *falconensis** Blow	summer	r	BBS, BRI

Non-spinose species

	Occurrence	Frequency	Laboratory
Globorotalia hirsuta (d'Orbigny)	winter (Feb-Mar)	f	BBS
G. *inflata* (d'Orbigny)	spring (Mar-Apr)	f	BBS
G. *menardii** (d'Orbigny)	summer	r	BRI
G. *truncatulinoides* (d'Orbigny)	winter (Dec-Feb)	f	BBS
Neogloboquadrina dutertrei (d'Orbigny)	year-round	c-r	BBS
	winter	r	BRI
Globigerinita glutinata (Egger)	year-round	r	BBS, BRI
Pulleniatina obliquiloculata (Parker and Jones)	summer	c	BBS
*Candeina nitida** d'Orbigny	summer	c	BRI

Fig. 1 Occurrence and frequency of spinose and non-spinose species off Bermuda (BBS) and Barbados (BRI). f = frequent, c = common, r = rare; *: species where only few observations are available.

FIELD AND VITAL OBSERVATIONS

Both Bermuda and Barbados are oceanic islands. There is no or only very little terrigenous influx from the land to the surrounding water mass. Only during very high energy situations, such as during storms or hurricanes, is there any effect on the water masses from which we collected our specimens. Under normal conditions, the abundances of specimens would be expected to be rather constant. To the contrary, we observed a distinct patchiness in the occurrences of planktonic foraminifers as well as radiolarians. This is demonstrated by plankton samples taken regularly at the same location by the same diver (fig. 2). Although the diver's results are semiquantitative, they show daily (and weekly) changing abundance patterns. Similar observations have been made by Boltovskoy (1971, 1973).

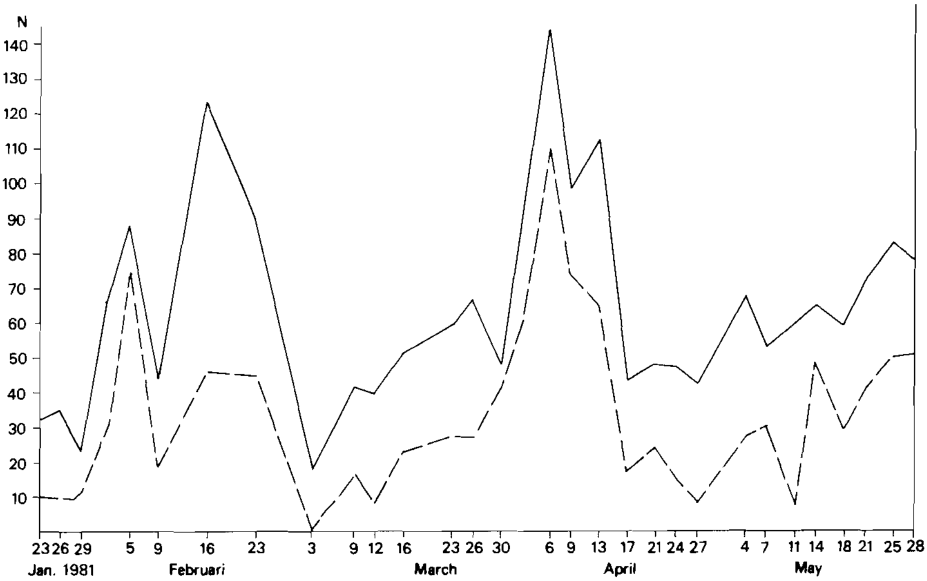


Fig. 2 The patchy occurrence of spinose planktonic foraminifers two miles off Barbados, demonstrated by regular sampling by the same scuba diver. Solid line: all specimens; dashed line: *G. sacculifer.*

The causes of this patchiness are quite variable and the extent of their influence is of different magnitude.

1. Current systems changing on a small scale can split off watermass bodies, such as eddies.

2. Watermass conditions around Barbados are strongly affected by Amazon River discharge (Steven and Brooks, 1972; Kidd and Sander, 1979), at times forming "freshwater" lenses of low salinity (< 32‰) that force a change in the foraminiferal assemblages. Normally *G. sacculifer* is dominant in high salinity surface water. But during low salinity periods, *G. ruber* dominates at the surface, while *G. sacculifer* lives mostly below the 50 m to 80 m thick "freshwater" lenses.

3. Spine shedding and gerontic calcification during reproduction cause

sinking, resulting in a change of the depth habitat. Absence or presence in surface waters depends highly on the moon cycle (lunar periodicity) which triggers the reproductive cycle of possibly most symbiont-bearing spinose planktonic foraminifers. This is true for *H. pelagica* (figs. 3, 4) (Spindler et al., 1979) and may be possible for *G. sacculifer* and *O. universa* (Hemleben et al., unpubl. data).

4. Changes in the food chain affect the numbers of planktonic foraminifers. Changing amounts of nitrates and phosphates influence the growth of phytoplankton, which is the main food source for the non-spinose species, and the copepods. The latter are the main food source of the spinose species.

5. Migration of the foraminifers in pursuit of their food source may play another important role.

In summary, the actual condition of the water mass in space and time plays a most important role for any field observation and during experi-

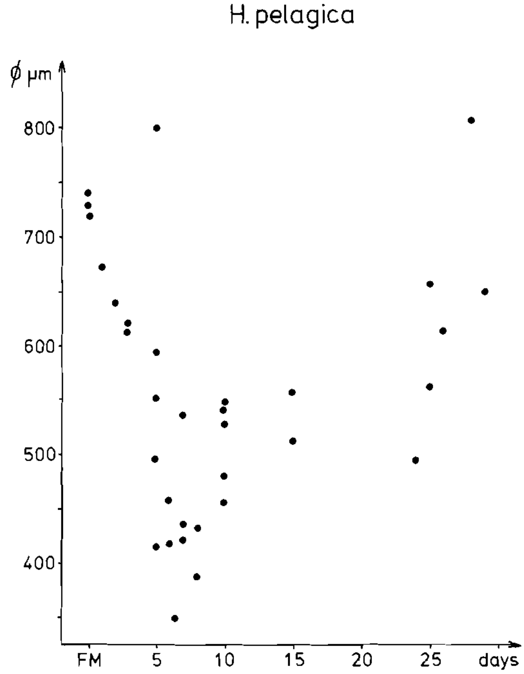


Fig. 3 Size variation of *H. pelagica* samples during the lunar month. Data summarized from various collections in surface water (0–20 m) off Bermuda in 1977 and 1978. Prior to reproduction which occurs about 3–6 days after full moon the mean size of the *H. pelagica* population is relatively large. After reproduction the population consists of more or less juveniles and the mean size has dropped considerably. Prior to the next reproductive phase the mean size of the population has increased to the normal adult size. FM = day of the full moon.

mental work. This includes post-experimental measurements of the isotopic composition.

By definition, planktonic foraminifers must float in the water column. However, in the laboratory the non-spinose species behave like benthic foraminifers, crawling on the bottom of the culture vessel. Only at very few occasions non-spinose species, e.g. *G. inflata* or *N. dutertrei*, have been seen floating in the culture dish. In contrast, the spinose species always float under normal conditions in our cultures. Macroscopically most spinose species exhibit a typical appearance which is characterized by the shape of the test including length and density of spines, the extension of the rhizopodial network and the distribution of the symbionts (pl. 1, figs. 1, 3, 4). In laboratory experiments most species we have worked with exhibited a species-specific behavior with respect to different environmental parameters.

Spinose specimens caught with a plankton net normally shed their spines during collecting. After cleaning and transferring them into water from the collecting site they regenerate their spines. However, they are differently sensible to disturbances; e.g. *G. ruber* sheds the spines very quickly after being disturbed with a pipette, whereas *G. sacculifer* shows no reaction at all. *G. ruber* can survive several weeks (more than 60 days) under "unhealthy" conditions without any spines, as has been nicely demonstrated by Adshead (1980). Non-spinose species are much more robust. They retract the rhizopods when disturbed, but after less than a minute their former state is restored (pl. 1, fig. 2).

Up to 50% of newly caught specimens carry food organisms in various stages of digestion in between their spines. According to the kind of food, the cytoplasm exhibits different colors. A greenish color is caused by feeding on green algae, a reddish orange is caused by diatoms and a red color by fat of copepods or amphipods (see food chapter below).

SYMBIONTS, COMMENSALS AND PARASITES

Since Murray (1897) and Rhumbler (1911) and more recently by the papers of Lee et al. (1965), Zucker (1973), Anderson and Bé (1976), Bé et al. (1977) and Spindler and Hemleben (1980), photosynthetic symbionts are known to occur in planktonic foraminifers. The fact that planktonic species bear photosynthetic symbionts implies that they must, at least for a certain time, live within the photic zone. Bé et al. (1983) published some preliminary results indicating that the symbionts are somehow involved in the calcification process during chamber growth. Further work on this topic is in progress by H. J. Spero (University of California, Santa Barbara).

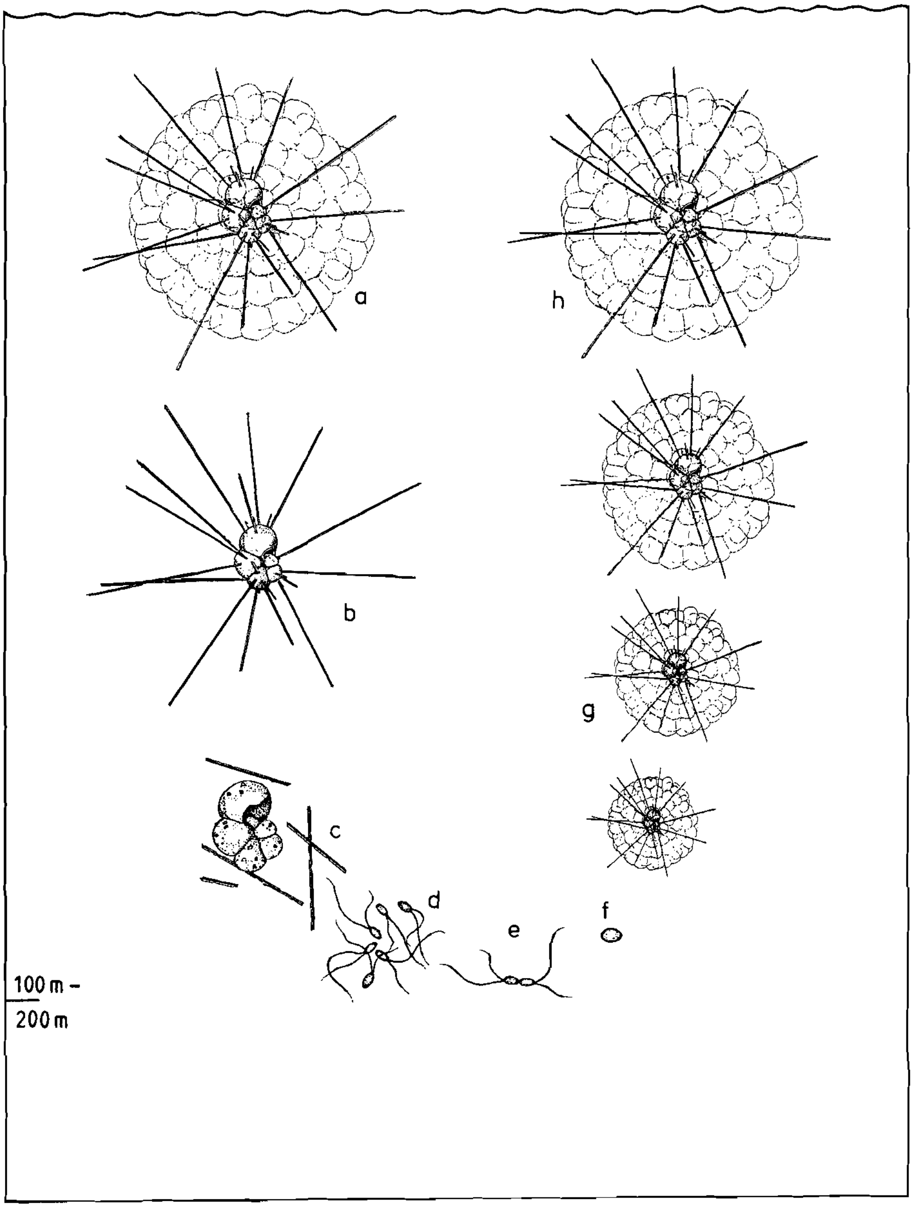


Fig. 4 Reproductive cycle of *H. pelagica*. Gametogenesis is linked to the lunar cycle, the gametes are released 3–5 days after full moon.

a) Specimen prior to gametogenesis with long spines and bubble capsule.

b) About 12 hours before gamete release the bubble capsule gets resorbed and the animals sink to deeper water.

c) Shortly afterwards the spines and the septal walls get resorbed.

d) 300,000–400,000 biflagellated gametes are released.

e) Fusion of gametes.

f) Zygote

g) Growing juveniles ascending to surface waters.

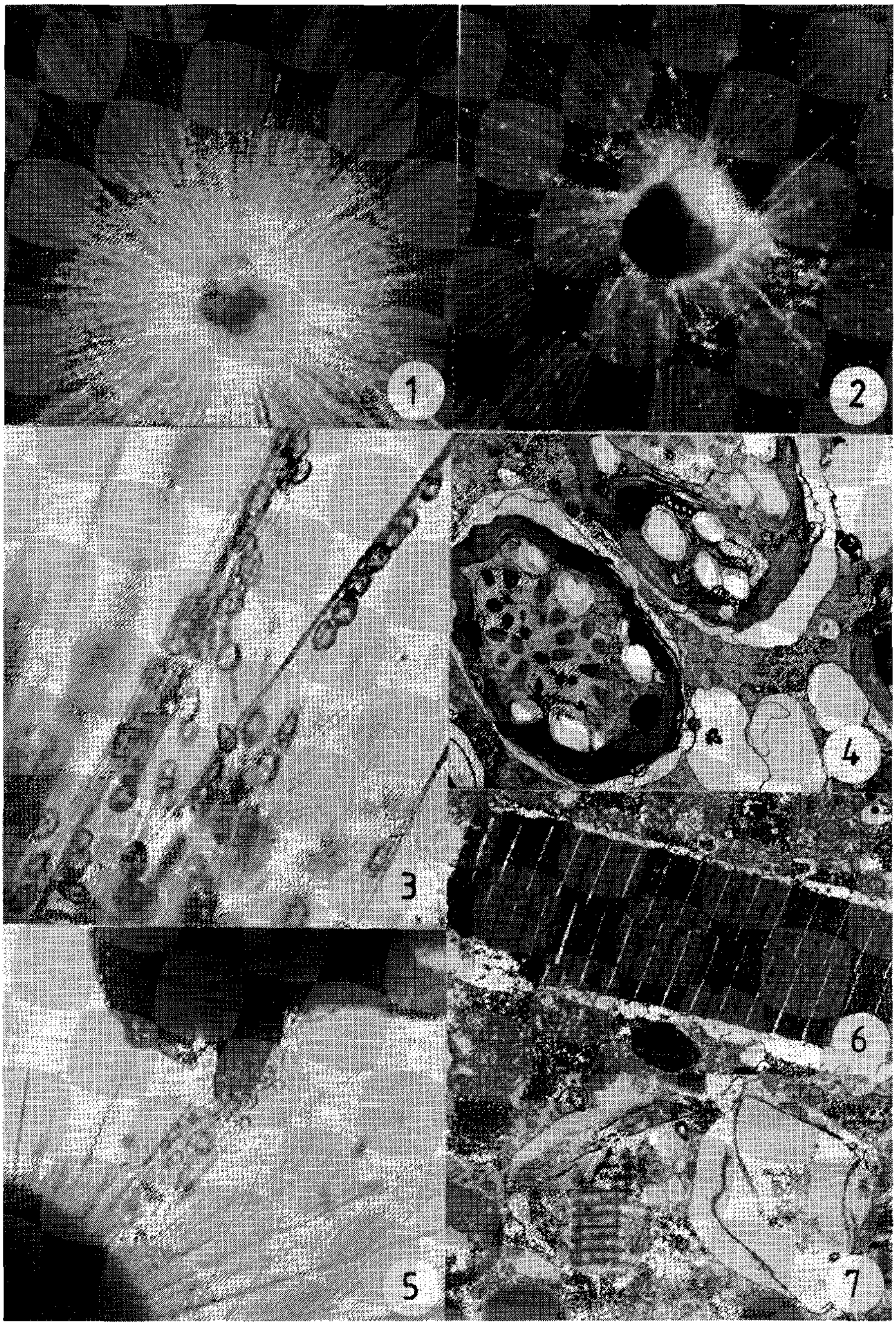
h) Adult specimen.

Stages e) and f) are hypothetical, not yet observed.

Plate 1

Fig. 1	Spiral O. *universa* (spinose) exhibiting the dinoflagellate symbionts surrounding the test halo-like (X 25).
Fig. 2	The non-spinose G. *inflata* exhibiting long stiff rhizopods internally being reinforced by microtubuli (X 45).
Fig. 3	Dinoflagellate symbionts living in vacuoles and moving along the spines of O. *universa* (X 320).
Fig. 4	TEM micrograph of dinoflagellate symbionts enclosed in cytoplasmic vacuoles (X 4700).
Fig. 5	*G. sacculifer* feeding on *Artemia salina*; rhizopods transporting prey tissue towards the test (X 200).
Fig. 6	TEM micrograph of a muscle being partially digested by *H. pelagica* (X 4700).
Fig. 7	TEM micrograph of digested diatom frustule incorporated within the cytoplasm of *G. truncatulinoides* (X 3750).

Plate 1



To date we know at least 6 spinose species of planktonic foraminifers that incorporate symbionts in their cytoplasm (fig. 5) (*G. bulloides* has been erroneously quoted in Spindler and Hemleben, 1980). They live within vacuoles surrounded by the host's cell membrane (pl. 1, fig. 4) and move in and out of the shell according to the day/night cycle. The symbionts occurring in *G. ruber*, *G. sacculifer*, *G. conglobatus* and *O. universa* are dinoflagellates with the typical dinokaryon showing the chromosomes. The symbionts of *G. aequilateralis* and *G. cristata* are different, probably belonging to the Haptophycea (see also fig. 5). It remains still an open question whether or not these dinoflagellates are different species. Morphological differences are difficult to detect, but the light absorption by the symbionts in *G. ruber* is characteristically different from that by the symbionts in *G. sacculifer*.

Quite recently Bé et al. (1983) published the results of some experiments carried out on the shell growth, longevity and reproductive potential of *G. sacculifer*. Elimination of symbionts by a photosynthetic inhibitor (DCMU) and reinfection indicated that the symbionts are somehow involved in the calcification process. In contrast, Erez (1983) stated that "calcification in these organisms is enhanced by light, and probably not by photosynthesis of their symbiontic algae". Elimination of symbionts had the same effect as total darkness: a shortening of life span (early gametogenesis) and a smaller shell size than under normal conditions.

Algae associated with the bubble capsule of *H. pelagica* or the rhizopodial network of *G. sacculifer* and *G. ruber* without producing any obvious advantage or disadvantage to the host have been called commensals. They occur together with all the forementioned spinose species and belong to the cocale dinophytes *Pyrocystis noctiluca* and *P. robusta*. They are autotrophic dinophytes which may have been "caught" by chance. This explains why more than 80% of the planktonic foraminifers are associated with no less than 2 individuals. Additional species mentioned by Bé et al. (1977), living within the bubble capsule of *H. pelagica* include *P. fusiformis*, *Dissodinium lunula* and *D. elegans*. Clone cultures of isolated commensals taken from *G. sacculifer* revealed that *D. elegans* and *D. lunula* are probably variants of *P. robusta* (Elbrächter et al., in press).

Smaller free-swimming dinoflagellates occur together with *G. aequilateralis*, *G. ruber*, *G. sacculifer*, *H. pelagica* and *O. universa*. They belong to different genera of the gymnodiniales and peridiniales (dinoflagellates). Light microscopic studies revealed their parasitic nature feeding on the foraminiferal cytoplasm.

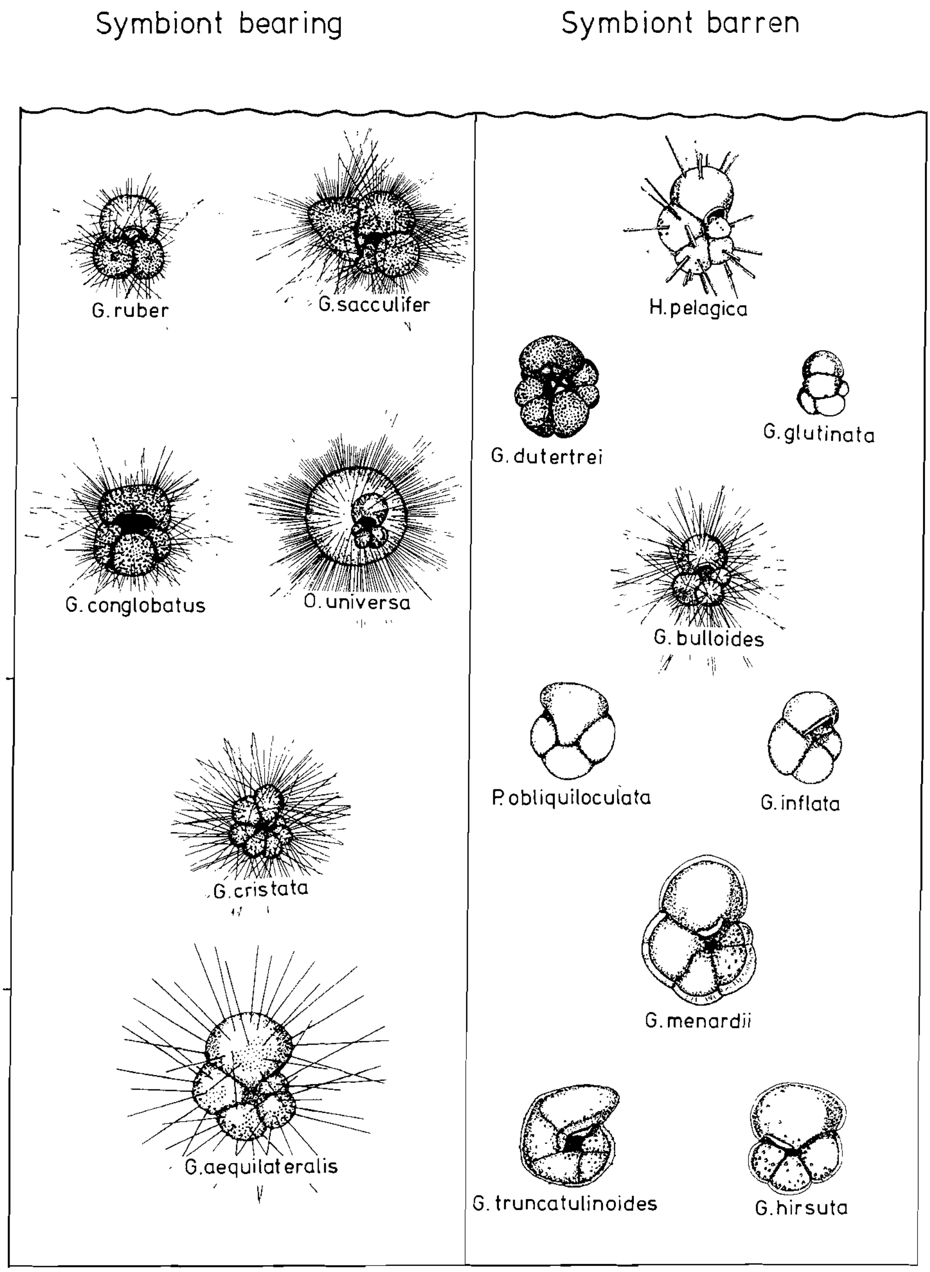


Fig. 5 Relationship between planktonic foraminifers and symbiontic algae. So far 15 species of planktonic foraminifers were checked by transmission electron microscopy for symbiontic algae. Most spinose species are associated with symbionts, all non-spinose species checked so far are symbiont barren. Species preferring different depth habitats live in symbiosis with different types of algae. The symbionts of *G. ruber*, *G. sacculifer*, *G. conglobatus* and *O. universa* are dinoflagellates, while those of *G. cristata* and *G. aequilateralis* probably belong to the haptophyceans.

As published earlier (Bé et al., 1977; Hemleben and Spindler, 1978; Anderson et al., 1979; Hemleben, 1982), planktonic foraminifers are basically omnivorous, but the non-spinose species prefer herbivorous food, whereas the spinose species prefer a more carnivorous diet. Feeding experiments (Anderson et al., 1979; Bé et al., 1981) seem to demonstrate that the feeding frequency highly influences the life span and the final shell size. Thus, the availability of food in the natural environment seems to influence the life span and the final shell size.

Additional experiments showed a more complex relation between predator and prey. Observations on freshly scuba-collected spinose species revealed that calanoid copepods are the main constituent of their diet. Cyclopoid copepods were less preyed on and harpacticoid copepods only sporadically. Feeding experiments (Spindler et al., in prep.) demonstrated that calanoid copepods were digested in 7–9 hours, whereas the digestion of cyclopoid copepods took 9.5–26 hours (fig. 6). In addition, most spinose species digested other organisms, including polychaete larvae, pteropods and heteropods, tunicates and chaetognathes, as well as diatoms and radiolarians,

Foraminiferal species	Food remains %	Food organisms			
		A. salina Nauplius	Calanoid Copepod	Cyclopoid Copepod	Harpacticoid Copepod
O. universa	36	2:26	7:07	16:32	11:05
G. sacculifer	30	3:34	7:10	9:39	(+)
G. ruber	25	3:55	7:45	–	–
G. aequilateralis	27	3:47	7:57	9:27	–
H. pelagica	53	3:34	8:54	25:49	–

Fig. 6 Digestion times (hours) of different food organisms by planktonic foraminifers and percentages of freshly collected foraminifers with prey in between their spines. Digestion times for *A. salina* nauplii (without a chitinous carapace) account for the time from catching the food to total digestion. Digestion times for the other copepods include the ejection time of the empty carapace.

— = never accepted; (+) = digestion once observed but without exact time duration.

flagellates and ciliates. From these observations it is concluded that spinose planktonic foraminifers catch and digest a prey once every 24 hours (Spindler et al., in prep.).

The non-spinose species obviously prey on diatoms and dinoflagellates. Transmission electron microscopic observations of freshly collected specimens revealed that species like *Globigerinita glutinata* or the globorotaliids (e.g. *G. hirsuta, G. inflata* or *G. truncatulinoides*) contain several tens or hundreds of diatom frustules in their cytoplasm (pl. 1, fig. 7). However, some muscle tissues were observed as well. In laboratory culture both groups were fed with *Artemia salina* nauplii, a food organism which is very easily digested (fig. 6) because it lacks a chitinous carapace (pl. 1, figs. 5, 6).

In summary, we conclude that in general non-spinose species are herbivorous and spinose species prey on zooplankton. This implies that, for any synecological approach in foraminiferal research, absolute abundance and the distributional pattern depend highly on the occurrence of zoo- and phytoplankton. This can be substantiated by for instance the distribution pattern in the Red Sea. Plankton tows and Pleistocene to Holocene cores show a distinct boundary near the latitude 20° North. Moreover, the boundary is associated with a distinct abundance break (spring) of phytoplankton (Tardent, 1979). Southward the planktonic foraminiferal assemblage is similar to that of the adjacent Indian Ocean (Zobel, 1973) including spinose and non-spinose species. In contrast, northward, only spinose species occur, with one exception: *Neogloboquadrina pachyderma,* for which species we do not yet know the food requirements.

Similar observations have been made concerning the vertical distribution of the non-spinose species *G. hirsuta, G. inflata* and *G. truncatulinoides* in the western Atlantic off Bermuda. Fairbanks and Wiebe (1980) related the deep chlorophyll maximum (DCM) to the pycnocline where they found it associated with a maximum abundance of planktonic foraminiferal species. However, the DCM moves up and down (in the Sargasso Sea between 0 m and 95 m) depending on the seasons; therefore the non-spinose foraminifers have to follow their food source. This is what we find during the different seasons in plankton tows. Unfortunately, the forementioned authors do not differentiate between non-spinose and spinose forms concerning the food requirements; thus no depth differentiation could be noticed within the euphotic zone.

Chamber formation; primary wall formation

Polythalamous calcareous foraminifers grow by adding chambers. Most of them secrete an organic precursor of the chamber prior to calcification of a primary wall. In the case of planktonic foraminifers (Bé et al., 1979), the development of a so-called "anlage" (Angell, 1967), which consists of the primary organic membrane (POM) and an outer organic protective envelope, precedes calcification. Visible calcification starts with calcite plaques on either side of the POM. As the plaques increase in size they finally coalesce to form the bilamellar wall (Reiss, 1957). Each chamber formation takes some 4–8 hours. When the calcification process is nearly finished the whole test becomes covered with a new calcite layer, which mostly is rather incomplete (Hemleben, 1969). This general type of calcification takes place in all observed species, except in *H. pelagica.* This species seems to secrete an "anlage" where calcification occurs only on the outside of the primary organic membrane.

Newly built chambers or chambers of the early juvenile stage of *G. ruber* often show incompletely calcified walls (Towe, 1971) and contain a certain amount of organic material. The same is true for the spiral (juvenile) form of *O. universa,* since most freshly collected specimens collapse when dried for SEM preparation (pl. 2, fig. 4). Spherical chambers of the adult form are completely calcified and contain relatively small amounts of organic material.

Pores

Simultaneously with wall calcification, pore formation procedes. Areas where, in a later stage, normal pores will occur are marked by micropores, which are formed by wall protruding rhizopods (Hemleben et al., 1977). Hence, the incipient wall is non-porous in the normal restricted sense and the later pore area is slightly calcified. Subsequently, partial resorption seems to form the pores, which are still irregular after chamber formation has been finished. This mode of pore formation has so far been observed in *H. pelagica, G. ruber* and *G. menardii* only, which may be due to the very short period available for observation. Therefore it is not known whether this is a general phenomenon valid for all planktonic foraminifers. In the final stage the pores are tubular or funnel-shaped wall perforations closed by an organic pore plate (pl. 2, fig. 1). The pore walls are lined with an organic sheet (pl. 2, fig. 2).

In general, the pores in planktonic foraminifers (except in *H. pelagica*) show two distinct patterns. The spinose species exhibit a pore plate formed by the POM and the IOL with micropores of less than 0.1 μm (Towe, 1971; Bé et al., 1980) (pl. 2, fig. 3). In the non-spinose species the IOL is clearly separated from the pore plate and is rather thick without any obvious connection with the outer cytoplasm (pl. 2, fig. 2).

Spines, pustules

After the primary wall has been completed, spine formation in the spinose species starts on the newly formed chamber. The spines are planted into the wall like telephone poles into the earth, fixed by surrounding plate-like crystals (Hemleben, 1969). Thus, they can easily be pulled out. They grow rather fast up to a length of 2 cm enabling the animal to catch food with a "spine surface area" of 50 cm^2 (Spindler et al., in prep.).

The pustules (pseudospines, rugosities, etc.) in the non-spinose species become visible independently of the chamber formation, mostly on previously formed chambers. They are part of the wall showing the same lamellar wall construction as the primary wall (Hemleben, 1975; Benjamini and Reiss, 1979).

Secondary wall formation

The primary wall originates from regularly repeated chamber formation forming multilayered walls. The secondary wall is due to a drastic environmental change. In general, all observed species live, or at least reproduce, in the upper few tens of metres of the water column. However, species migrating to deeper and thus colder water during their life, secrete a different wall type: a so-called calcite crust (Bé and Ericson, 1963; Bé and Hemleben, 1970). This crust shows a typically euhedral crystalline surface texture and, in cross section, elongated prisms perpendicular to the surface. Experiments (unpublished data) undertaken with the species *G. hirsuta*, *G. truncatulinoides* and *N. dutertrei* demonstrate a growing calcite crust under controlled conditions at temperatures below 10°C for both globorotaliids and below 15°C for *N. dutertrei.* In general, the formation of a calcite crust indicates a colder environment compared to that where the animal had spent the first part of its ontogeny (pl. 2, fig. 5).

Resorption and regeneration

Resorption of calcitic material seems to be an integrated capability, as calcification and resorption can occur in one specimen at the same time.

Plate 2

Fig. 1 Wall cross section of G. *menardii* showing the calcite crust (CC) added to the normal wall (× 1050).

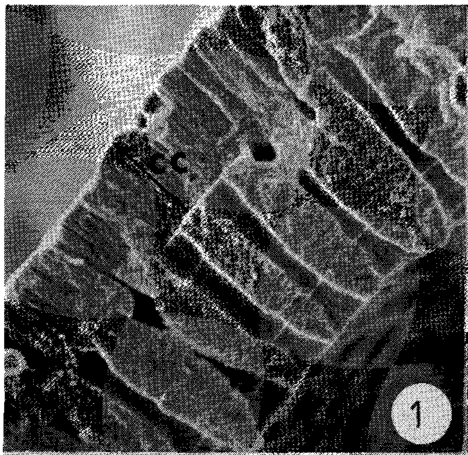
Fig. 2 TEM micrograph of a cross section of N. *dutertrei* (non-spinose); note that the inner organic layer (IOL) is not in contact with the pore plate (pp); there is an open space between IOL and pore plate (× 4700).

Fig. 3 TEM micrograph of G. *ruber* (spinose); note that the IOL fuses with the pore plate (× 9500).

Fig. 4 TEM micrograph of a spiral O. *universa.* A high amount of organic material in the wall indicates an incomplete wall calcification (× 19000).

Fig. 5 G. *truncatulinoides* showing an intermediate stage of a growing calcite crust of a specimen kept under controlled laboratory conditions below 10°C (× 700/× 2200).

Plate 2



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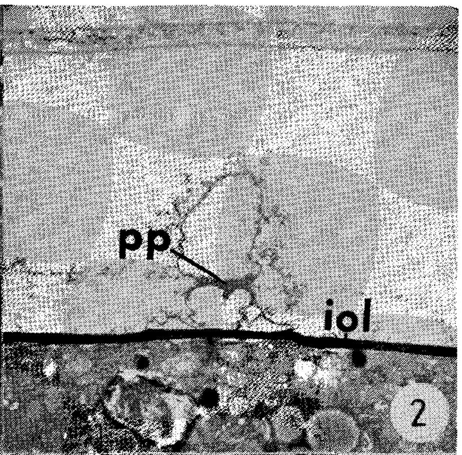

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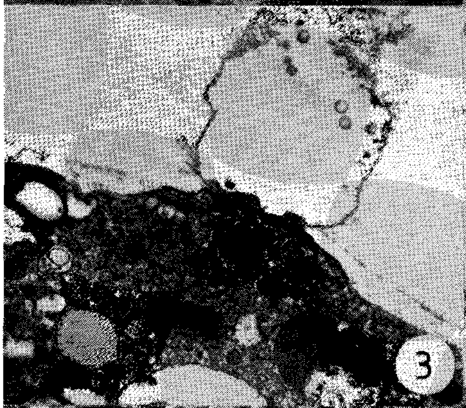

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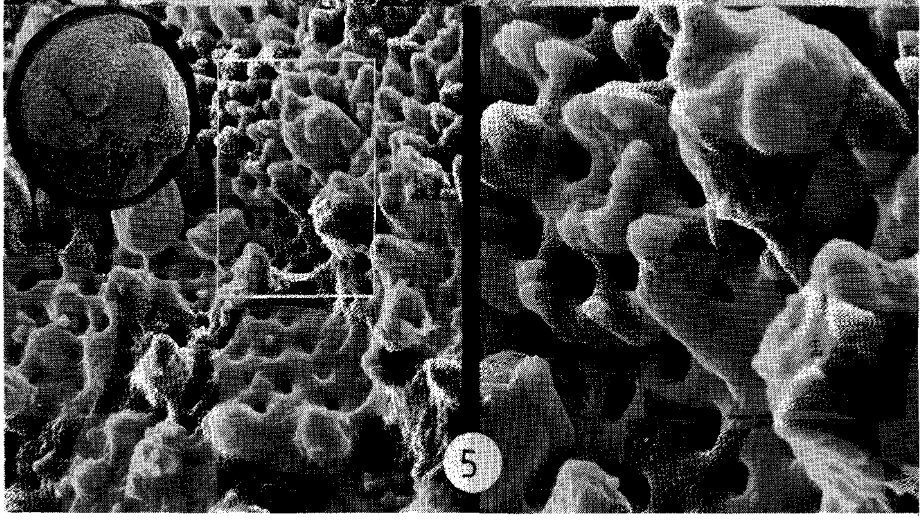

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Disturbances during chamber formation may lead to resorption, as do, for instance, drastic salinity changes. The most common resorption occurs among the spinose species when they shed their spines during collection with a plankton net, or prior to gametogenesis. The same will happen in laboratory cultures under unfavorable conditions. Even chambers become fragmentized or shed as whole chambers. Physical injury in nature by large copepods or by damage in laboratory cultures leads primarily to short resorptional processes "in order" to smoothen the edges and then to regrowth (Bé and Spero, 1981).

Everything resorbed can be recalcified: broken spines, shed spines, broken chambers or even totally resorbed spheres of *O. universa*. In our laboratory experiments a specimen of *O. universa* has been observed which calcified 4 times and resorbed 3 times the spherical, last chamber. This shows that calcification and resorption are reversible processes and are controlled and monitored by the cell. Furthermore, resorption and calcification are integrated processes during gametogenesis: all spinose species shed their spines through resorption; some species even resorb septa (e.g. *H. pelagica*) or parts of them (e.g. *G. aequilateralis*). Other species (e.g. *G. sacculifer*) seem to cover the whole test with a new calcite layer after spine shedding (Bé, 1980).

REPRODUCTION

The complete life cycle of planktonic foraminifers is still unknown. Nevertheless, tracing early juvenile stages to the adult and gerontic stages, and studies on the formation and release of gametes help to understand the biology of these creatures. Gametogenesis was described by Rhumbler (1911) and by Le Calvez (1935) and more recently by Bé and Anderson (1976). So far reproduction is best documented for *H. pelagica*, partially because of their high abundance off Bermuda. On the other hand, reproduction is linked to the synodic lunar cycle and therefore most steps during the reproductive differentiation of the cytoplasm are precisely timed (Spindler et al., 1978; Spindler et al., 1979; Hemleben et al., 1979; Spindler and Hemleben, 1982).

A first indication of the impending gametogenesis in *H. pelagica* (about 30–24 hours before gamete release) is a drastic color change from indifferent orange and brownish colors to a bright red, which is due to more dispersed lipids. About 20–15 hours before gamete release (GR) cytological changes occur (Spindler and Hemleben, 1982). Simultaneously the animal sheds the spines and resorbs the septa. This causes sinking from shallow to deeper water. Between 12–10 hours before GR the nucleus divides into 300,000 to 400,000 gamete nuclei. During the last stage, approximately 10–2 hours before GR, the nuclei are surrounded by small portions of cytoplasm, two flagella develop, and the newly formed gametes become separated from each other (Spindler et al., 1978). The gamete release itself occurs rather explosively, very often destroying what is left of the original test. This partially explains why *H. pelagica* has a very low fossilization potential and ranks highest in the dissolution susceptibility among the planktonic foraminifers (Hemleben et al., 1979). Together with the gametes, the so-called spherical bodies are released. These spherical bodies are believed to be receptacles of waste material (Spindler et al., 1979).

Between gamete release and the occurrence of the first small juveniles in plankton tows there is a gap of some 5 days (see figs. 3, 4) during which no *H. pelagica* are found in the water column. The occurrence of high numbers prior to gametogenesis and the absence after reproduction should be taken into account in interpreting patchiness of planktonic foraminifers.

In general, the reproductive sequence of *H. pelagica* is representative for all spinose species we observed. However, several differences are to be noted. Instead of resorbing parts of the test, calcification may occur 48–12 hours prior to gametogenesis. The following gerontic "calcite deposits" have been observed:

1. One normal last chamber larger than the previous one.
2. One normal last chamber equal in size with the previous one.
3. In the case of *G. sacculifer* one polymorphous sac-like chamber, including the fistulose type.
4. One or more (up to 4) chambers smaller than the previous chamber (kummerform). The kummerform very often lacks spines and sometimes it is either incompletely calcified or it is rather thick-walled with scarce and scattered pores, but still it possesses spines.
5. An additional patchy calcite layer covering the whole test after shedding of the spines may be formed 16 hours before GR (e.g. Bé, 1980).

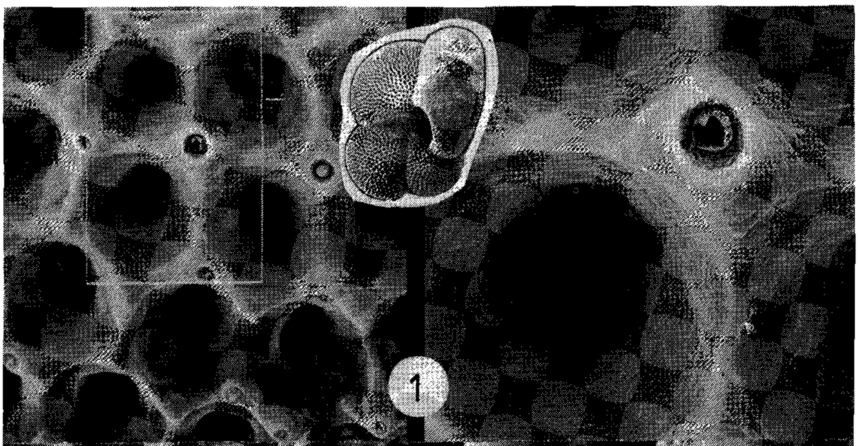
In addition, spherical bodies, released together with the gametes contain calcium.

The amount of $CaCO_3$ deposited prior to gametogenesis seems to vary widely; especially the amount of gametogenic calcification described by Bé (1980) is rather variable. Spine holes may or may not be closed by additional calcification as demonstrated by specimens in laboratory cultures and from the sea floor (pl. 3, 4). SEM studies of all forementioned spinose species revealed a very variable gametogenic calcification. The enormous variation in the amount of gerontic calcite deposits requires a general process prior to gametogenesis; this needs further investigation.

Plate 3

Figs. 1 and 2	G. *sacculifer*, specimens which underwent gametogenesis in laboratory culture.
Fig. 1	Resorbed spine holes are visible on all chambers (X 1000/X 3000).
Fig. 2	During proceeding gametogenesis and after spine resorption the spine holes were covered by calcite secretions. This gametogenic calcification takes place while the test sinks to deeper water (X 900/X 1800).
Fig. 3	G. *sacculifer* from sediment trap off Barbados, water depth 3200 m. The spine holes are visible, last chamber rather thin (X 600/X 1500).

Plate 3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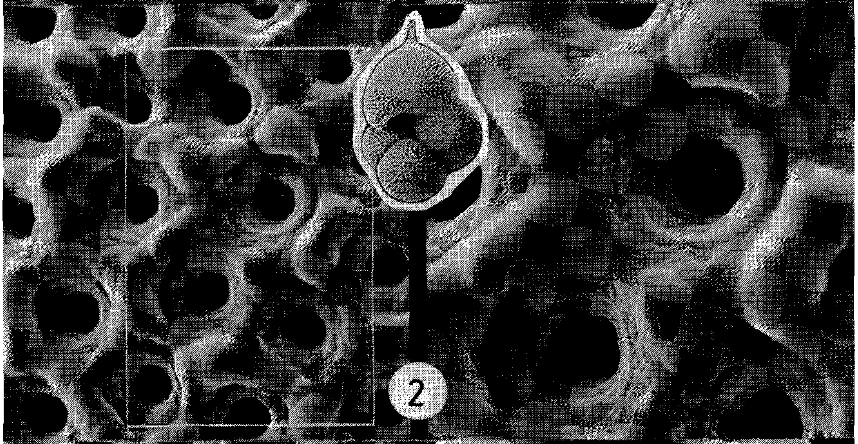
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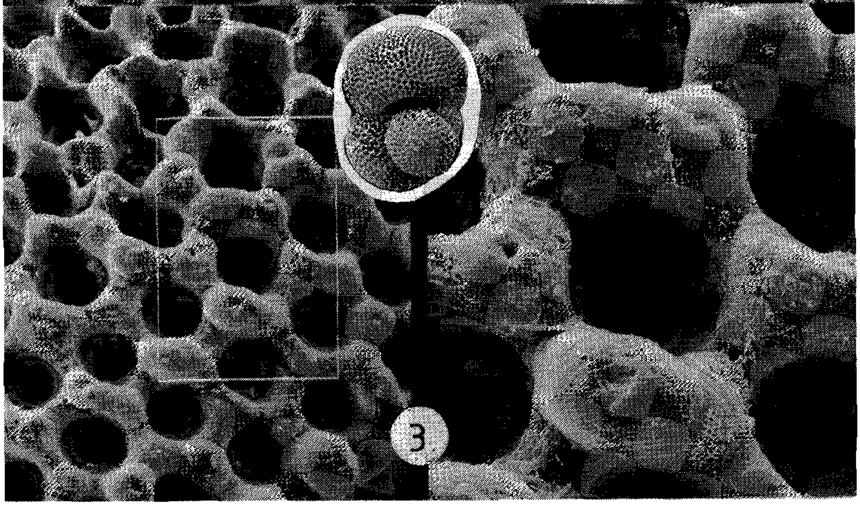
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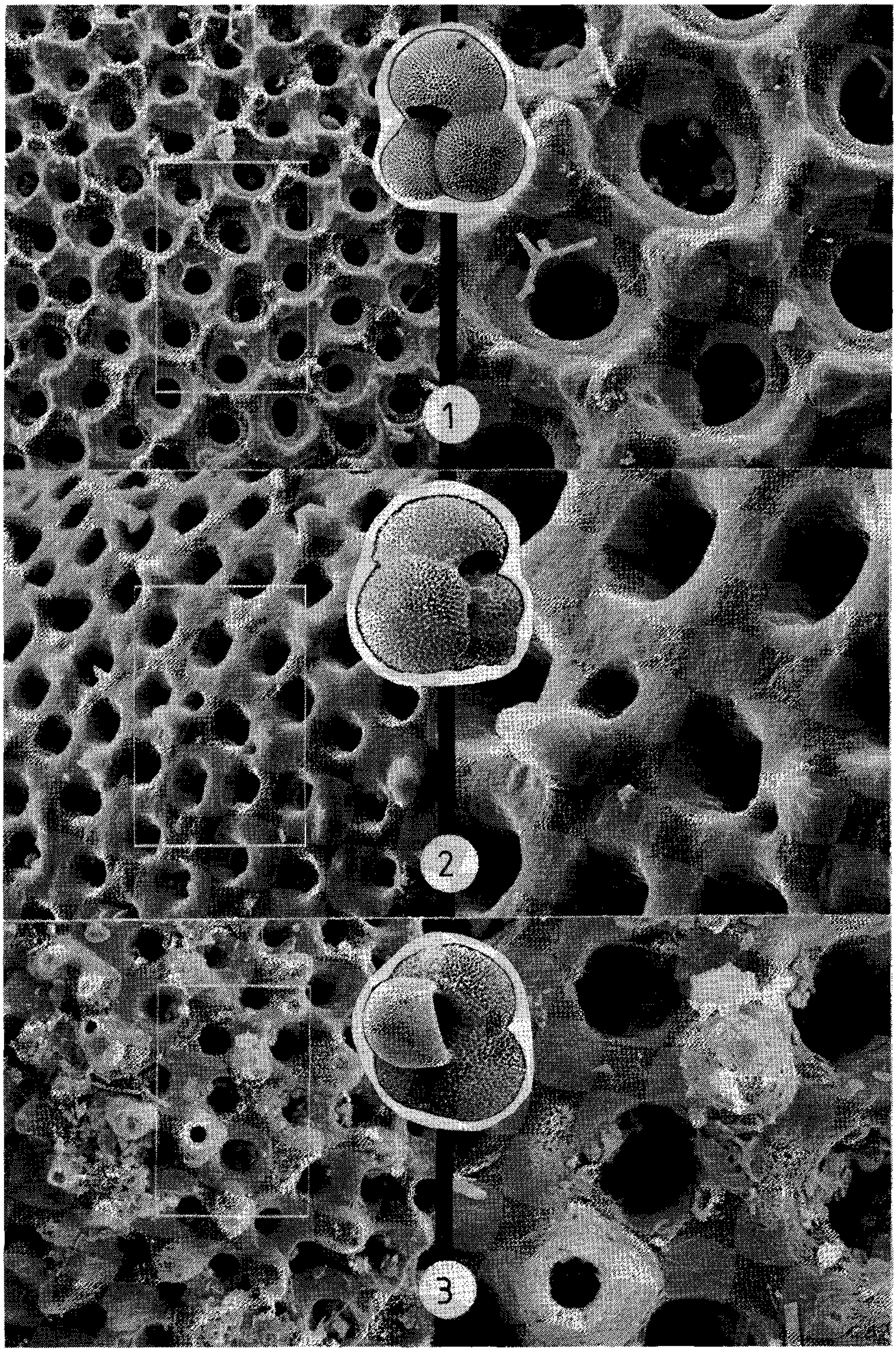
Plate 4

Fig. 1	G. *sacculifer* from sediment trap off Barbados showing spine holes covered by calcite layers; compare pl. 3, figs. 1–3 (X 300/X 1325).
Figs. 2 and 3	G. *ruber* from laboratory culture (fig. 2) and from sediment trap (fig. 3) showing no gametogenic calcification; either spine remnants (fig. 2) or spine holes (fig. 3) are visible (X 900/X 2600).

Plate 4



In summary, spine shedding and gerontic calcification change the morphology rather distinctly and may cause sinking to deeper water. The actual depth is not really known, but it seems likely that somehow the thermocline is involved; a rather small zone of the same density (pycnocline) may facilitate the fusion of the widely dispersed gametes for the initiation of the new generation.

In laboratory cultures we have not yet succeeded in obtaining the next generation despite a variety of changing culture conditions. In the natural environment we tried to follow changes in mean test size by sampling in short intervals at various depths. This revealed a growing population of, e.g., *H. pelagica* (fig. 3) or *G. sacculifer.* Furthermore, this method enabled us to trace the determinable adult specimens back to their juvenile stage smaller than 75 μm. Such non-diagnostic juveniles exhibit a typical allometric coiling of a logarithmic spiral. Protoconch measurements of each species show characteristic size ranges, although no indication for the occurrence of micro- and megalospheric generations could be detected. This supports our observation that planktonic foraminifers reproduce by forming gametes only (Brummer et al., 1983).

DEPTH DISTRIBUTION

The general depth habitat of planktonic foraminifers has been of interest since Rhümbler (1911) published the co-occurrence of zooxanthellae (symbionts) and planktonic foraminifers. More recently Berger (1969) and Bé (1977) compiled the available data based on plankton tows and the oxygen isotope composition of the tests; they separated the "shallow water" species which live in the upper euphotic zone (< 50 m) from the "intermediate water" species living predominantly in the lower euphotic zone (50–100 m). The "deep-water" species "living in the upper few hundred meters and whose adult stages occur predominantly below 100 m" (Bé, 1977) represent the third group. However, a depth distribution obtained by these methods indicates the average habitat only, since all species under observation with the exception of *G. ruber* change their depth habitat during ontogeny.

G. ruber seems to live in the uppermost layer of the water column during its total life span. Unpublished data from offshore Barbados reveal no shifts in the size for the *G. ruber* population over a period of several months, whereas *G. sacculifer* shows a distinct size change during the course of a month. This can be interpreted as a continuously occurring reproductive cycle in the case of *G. ruber*, and as a monthly reproduction in *G. sacculifer*, possibly triggered by the lunar cycle. For *H. pelagica* we could definitely demonstrate the lunar periodicity of the reproductive cycle (Spindler et al., 1979). During their reproduction, *G. sacculifer* and *H. pelagica* vanish from surface waters by sinking into deeper water. This may be caused by spine shedding, and/or break-down of the cytoplasm, but mostly by gametogenic calcification. *G. ruber* shows only very little gametogenic calcification or none at all which may account for their not sinking into deeper water.

Some conclusions may be drawn from isotopic data. Most living spinose species from plankton tows show higher values than those having passed gametogenesis (Duplessy et al., 1981), indicating different depth habitats during ontogeny (Emiliani, 1971). In addition, Fairbanks and Wiebe (1980), and Bé et al. (1980) demonstrated the association of peak relative abundances of planktonic foraminifers with the pycnocline and the deep chlorophyll maximum governed by the seasons. However, this can be true for the non-spinose species only during reproduction as most spinose species, e.g. *G. sacculifer* and *G. ruber*, "could preferentially develop in the upper part of the chlorophyll maximum" (Duplessy et al., 1981), that means above the maximum. The uppermost living species seems to be *G. ruber*, as this species reflects very well the changing temperatures of the environments (Deuser et al., 1981). *O. universa* exhibits, by wall thickening, additional calcification after building the last spherical chamber. The $\delta^{18}O$ values indicate increasing wall thickness during migration to deeper water. *G. aequilateralis* builds 1–3 more chambers while migrating downwards (Deuser et al., 1981).

The non-spinose species, e.g. the globorotaliids *G. truncatulinoides*, *G. hirsuta* and *G. inflata*, appear in surface waters near Bermuda during December through April for reproduction. After that, they sink into deeper water while still calcifying. How deep seems to be species specific. Our experimental experience with these species seems to indicate that, e.g., *G. truncatulinoides* (Deuser et al., 1981) adds chambers while sinking to more than 800 m; and coming into watermasses of less than 10°C, they may add the calcite crust. In contrast, *N. dutertrei* starts adding the calcite crust already at water temperatures below 15°C. This again demonstrates the stratification or migration during ontogeny.

From these briefly summarized data and observations, we must conclude that only very little knowledge is available on the ontogeny of planktonic foraminifers in respect to their actual life habitat; most data are derived from a few points in the North Atlantic and we do not know anything about their behavior in, e.g., the Red Sea or off West Africa.

Figure 7 summarizes our present knowledge of life habitat taking into consideration the following influencing parameters:

species	main habitat	reproduction habitat	juvenile habitat	seasonal reaction
H. pelagica	0–50 m	deeper than 100 m	above 100 m	no
G. ruber	0–30 m	0–30 m	0–30 m	no
G. sacculifer	0–80 m	100 m or deeper	above 100 m	no
G. conglobatus	0–?50 m	?100 m and deeper	100 m	yes
O. universa	0–150 m	100–200 m	100 m	yes
G. aequilateralis	0–400 m	0–100 m	100 m	yes
N. dutertrei	?50–100 m	100 m	?	?
G. glutinata	0–?30 m	?	?	?
G. bulloides	50–200 m	?	?	?
G. obliquiloculata	0–100 m	?	?	?
G. inflata	0–?800 m	0–50 m	0–50 m	yes
G. menardii	appr. 200 m	?	?	?
G. truncatulinoides	0–1000 m and deeper	0–150 m	0–150 m	yes
G. hirsuta	0–1000 m and deeper	0–150 m	0–150 m	yes

Fig. 7 Habitats of different planktonic foraminifers compiled from our observations at Bermuda and Barbados.

1. Symbiosis with photosynthetic algae determines a habitat within the photic zone (Bé et al., 1977).
2. Lunar cycle causes time predictable size shifts; ontogenetic migration (Spindler et al., 1979).
3. Changing morphology, e.g. calcite crust induced by low temperature (Bé and Ericson, 1963; this paper).
4. Gametogenic calcification may cause sinking (Bé, 1980; this paper).
5. Shift of food sources causes migration (horizontal and vertical); chlorophyll maximum shift (Fairbanks and Wiebe, 1980).
6. Seasonal temperature changes; species following the optimum temperature (Deuser et al., 1981).
7. Salinity changes; "freshwater" lenses of low salinity cause a habitat shift to deeper water (this paper).

The data in fig. 7 are mostly derived from our work at the Bermuda and Barbados Biological Stations. Incorporated are data not yet published or being in press. However, in general the data are well comparable with those previously published (Berger, 1969; Bé, 1977). In addition, we would like to emphasize the changing life habitat during ontogeny, which increases the difficulties in interpreting the isotopic data. A lot of question marks should stimulate progress in filling up the table and encourage comparison of the data with results from other areas of the world's oceans.

ACKNOWLEDGEMENTS

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MODERN NANNOFOSSIL ASSEMBLAGES IN SEDIMENTS OF COASTAL AND MARGINAL SEAS ALONG THE WESTERN PACIFIC OCEAN

HISATAKE OKADA

ABSTRACT

The ecology and biogeography of Recent calcareous nannoplankton are briefly reviewed, and the results are presented of a study of the composition of nannofossil associations collected in various environments ranging from marginal to open seas along the western Pacific Ocean.

Florisphaera profunda has become a major component of the flora since the Late Miocene. Its abundance shows a positive correlation with depth; the species is absent in shallow water, whereas it constitutes more than half of the total associations recovered from deep, pelagic sediments. *Gephyrocapsa oceanica*, on the other hand, dominates the flora in shallow, marginal seas and in inland seas.

A triangular coordinate diagram is constructed by using *F. profunda* and *G. oceanica* as environmental markers, while a third category represents all other species. The diagram clearly illustrates provincialism in the composition of the nannoflora associations; a discussion is given on the applicability of this analytical method.

INTRODUCTION

The ecology and distribution patterns of living calcareous nannoplankton have been studied in various marine environments. Their ocean-wide distribution is controlled by the geography of water masses (McIntyre and Bé, 1967; Okada and Honjo, 1973; Honjo and Okada, 1974); seasonal fluctuations in the composition of nannoplankton communities were documented by Okada and McIntyre (1979) for the northern Atlantic. Okada and Honjo (1975) reported conspicuous differences in the community structure between marginal seas and their pelagic counterparts along the western Pacific.

The ocean-wide distribution of calcareous nannofossils in surface sediments of the Atlantic was studied by McIntyre (1967) and McIntyre and Bé (1967); similar studies were performed for the Pacific by Geitzenauer et al. (1976), McIntyre et al. (1970), Roth and Berger (1975), Roth and Coulbourn (1982) and Ushakova (1970), while Geitzenauer et al. (1977) reported on both the Atlantic and Pacific Oceans. The results of these studies clearly demonstrate a good correspondance between the species distribution patterns in sediments and the nannoplankton in the water column. The cause of such a good correspondance has to be looked for in the rapid transfer of coccoliths through the water column by faecal pellets. This mode of transport is now a well-known fact (Roth et al., 1975; Honjo, 1976) and quantitatively the most important mechanism of coccolith deposition (Honjo and Roman, 1978). Selective dissolution of coccoliths in the deep sea water column and in deep sea sediments was subject to studies by Honjo (1975), and by McIntyre and McIntyre (1971), Roth and Berger (1975), and Schneidermann (1973), respectively.

Until now there have been only a few studies dealing with nannofossils recovered from surface sediments of neritic and marginal seas. Scholle and Kling (1972) investigated the flora from lagoonal sediments in British Honduras; Bukry (1974) reported the predominance of *Emiliania huxleyi* in the flora from the top layer of the Black Sea floor. There are several reports on nannofossils from various parts of the coastal floor of the Indian Ocean, but these reports lack a quantitative analysis of data (Guptha, 1976, 1979, 1981; Shafik, 1978). Such quantitative studies have been made for sediments in marginal seas along the western Pacific, e.g., for the Sendai Bay (Takayama, 1972), the Okinawa Trough (Chen, 1979), and the South China Sea (Chen and Shieh, 1982). The fossil association from the continental shelf of the South China Sea is dominated by *Gephyrocapsa oceanica*; the same applies to the living communities, studied by Okada and Honjo (1975).

Okada and Honjo (1973) first described *Florisphaera profunda* from the Pacific Ocean and observed its depth-sensitiveness. The species was only found in the lower part of the euphotic layer, usually below 100 m, of the Equatorial to Transitional zones. A large form of the species was described by Okada and McIntyre (1977, 1980) as *F. profunda* var. *elongata.* Since coccoliths of *F. profunda* are abundant in deeper waters of the Pacific Ocean (Honjo, 1975) they may be expected to be a good depth indicator in basin analysis. Because of the unique (perhaps too simple) shapes of these coccoliths, however, not many paleontologists recognized them as such, and in none of the papers listed above has *F. profunda* been counted as a member of the nannoplankton community. The coccoliths of another "deep layer species", *Thorosphaera flabellata,* are less frequent in the aphothic water column than those of *F. profunda* (Honjo, 1975), and they can hardly be recognized under a normal light microscope.

This paper mainly deals with the frequency distribution and ecological interpretation of *Florisphaera profunda* in sediments, and with general environmental aspects of nannoflora associations, in particular from neritic and marginal seas. Coccospheres and nannofossils of *F. profunda* from various localities are illustrated on Plate 1.

SAMPLES AND TECHNIQUES

Twenty-seven core samples which cover the Upper Miocene to Holocene sequences of DSDP sites 289 and 445, and 97 surface sediment samples recovered from the Sea of Kumano were studied for the analysis of the frequency distribution patterns of *Florisphaera profunda* (figs. 1, 3, 4). Ten surface samples were obtained from the Tokyo Bay, the Inland Sea of Seto, the Ohmura Bay and some nearshore and further offshore localities of Japan for the study of nannofloras in the Transitional zone (fig. 5). Surface sediment samples were also collected from the Taiwan Strait and from a locality of bathyal depth at the same latitude (fig. 2). Surface sediments from 18 stations in the Gulf of Thailand (fig. 6) and from 23 stations in the Arafura Sea and in the Gulf of Carpentaria (fig. 7) were sampled for the investigation of associations in tropical, marginal seas.

All determinations and countings were performed with a light microscope; supplementary SEM observations were made for some selected samples. The diversities of the communities are expressed by the Yule Simpson Index (D_p) and by the Shannon-Weaver Function (D_H), which were calculated following the method reported by Berger and Parker (1970).

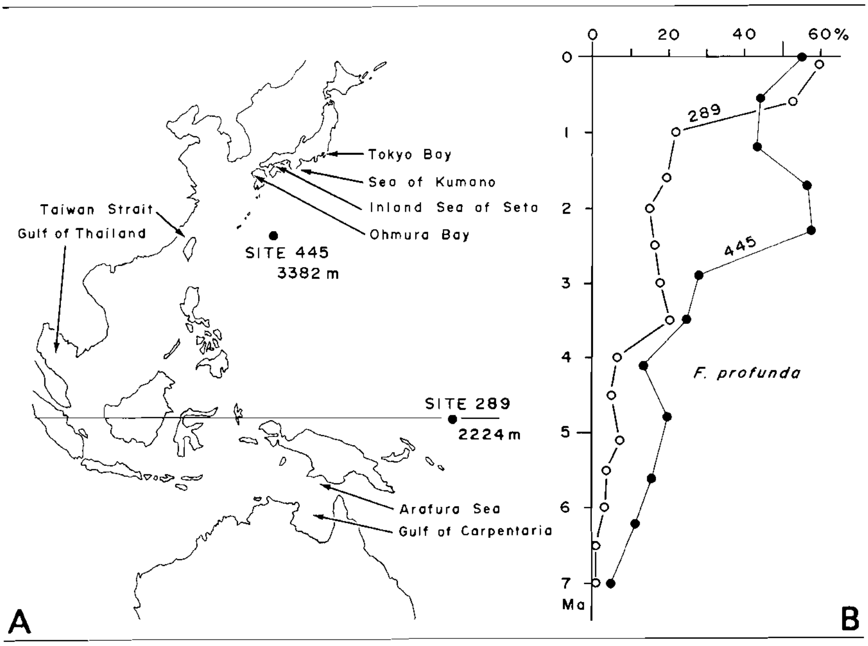


Fig. 1 A) Position of coastal and marginal seas and of DSDP sites 445 and 289; B) Relation between relative frequency of *Florisphaera profunda* and time for Late Miocene to Holocene sediments of DSDP sites 445 and 289. The frequency of *F. profunda* is expressed by percentage values of the total associations.

RESULTS

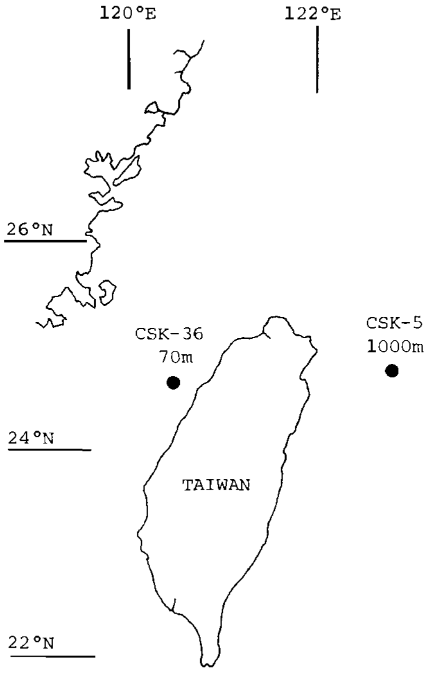
Geological record of Florisphaera profunda in deep sea cores

The lowest occurrence of *F. profunda* in both DSDP sites 289 and 445 (fig. 1) is in the Upper Miocene. Its presence in sediments older than 7 m.y. is uncertain, due to the rather poor state of preservation. In both DSDP profiles a time-transgressive change in frequency of coccoliths of *F. profunda* can be observed. In site 445 they become abundant from the Upper Miocene upward (more than 10% of the association) and they constitute more than 40%, i.e., they become predominant, in the Upper Pliocene and Quaternary. In the equatorial site 289, however, coccoliths of *F. profunda* are not common until the Lower Pliocene, while they become abundant in the Upper Pleistocene (fig. 1).

Abundance of Florisphaera profunda in relation to depth

In order to investigate the use of relative numbers of *F. profunda* as a depth indication in basin analysis, counts were performed on associations recovered from sediments in the vicinity of Taiwan and in the Sea of Kumano. The two samples from the Taiwan area (fig. 2) come from the continental shelf below the Taiwan Strait (water depth 70 m) and from the continental slope off the east coast of Taiwan (approximate water depth 1,000 m). The individual counts for 300 specimens excluding *F. profunda* are fairly similar in the two samples, except for slightly higher relative numbers of *Gephyrocapsa oceanica* and lower relative numbers of *Emiliania huxleyi* in the sample from the shelf (CSK-36). Similar results were obtained by Chen and Shieh (1982) from the South China Sea. If coccoliths of *F. profunda* are counted, the diversity indices are still almost identical in the two samples, but conspicuous differences can be observed in the percentage values of the species between the two samples: almost 70% in the deep sample, less than 3% in the shallow sample.

More data could be obtained from surface sediments in the Sea of Kumano, Japan (figs. 3 and 4). The relative numbers of *F. profunda* show an obvious correlation with depth and with distance from the shore. The percentage values display a strong increase from the sublittoral to the upper bathyal zones (from 60 to 300 m), which is followed by a less strong increase from lower bathyal to abyssal depths (fig. 4A). A comparable trend of increasing percentage values was found concerning the distance from the shore (fig. 4B), but the data display a more scattered picture. Data from deeper and more pelagic sediments in other areas (figs. 1, 2, 5) suggest that the high



Species Name	INDIVIDUAL COUNT		RELATIVE ABUNDANCE	
	CSK-36	CSK-5	CSK-36	CSK-5
Calcidiscus leptoporus	-	1	-	0.1
Emiliania huxleyi	117	142	38.0	14.3
Gephyrocapsa ericsonii	2	7	0.7	0.7
Gephyrocapsa oceanica	171	136	55.5	13.7
Helicosphaera carteri	2	2	0.7	0.2
Umbilicosphaera sibogae	2	4	0.7	0.4
Coronosphaera mediterranea	1	1	0.3	0.1
Syracosphaera pulchra	1	1	0.3	0.1
Umbellosphaera tenuis	-	2	-	0.2
Miscellaneous	4	4	1.3	0.4
Florisphaera profunda var. *elongata*	2	25	0.7	2.5
Florisphaera profunda var. *profunda*	6	668	1.9	67.3
Total	308	993	100.1%	100.0%
Simpson's Index (D_p)			0.53	0.50
Shannon-Wiener Function (D_H)			1.00	1.03

Fig. 2 Location, water depth, and species composition of nannofossil associations for two samples recovered from stations off Taiwan.

percentage values observed in the Kumano set of samples may be rather close to the "maximum" values that can be reached.

Separate counts of *Florisphaera profunda* var. *elongata* do not show any clear correlation between relative numbers and either depth or distance from the shore in the Kumano samples (figs. 4A and B). This may indicate that the variety *elongata* is less sensitive to water depth than the nominate type of *F. profunda.*

Samples from four western stations (figs. 3A and 4A, open circles) display abnormally low percentage values in the depth – frequency diagram, whereas the percentage values fall within the cluster in the frequency - distance from shore diagram. The latter four samples were collected in an area where sedimentation is disturbed by a prevailing bottom current. Due to the exposure of consolidated rocks, attempts to obtain sediment samples failed at several points in this area. The explanation of the aberrant values needs further investigation; a complete analysis of the floral composition of these samples will be published separately.

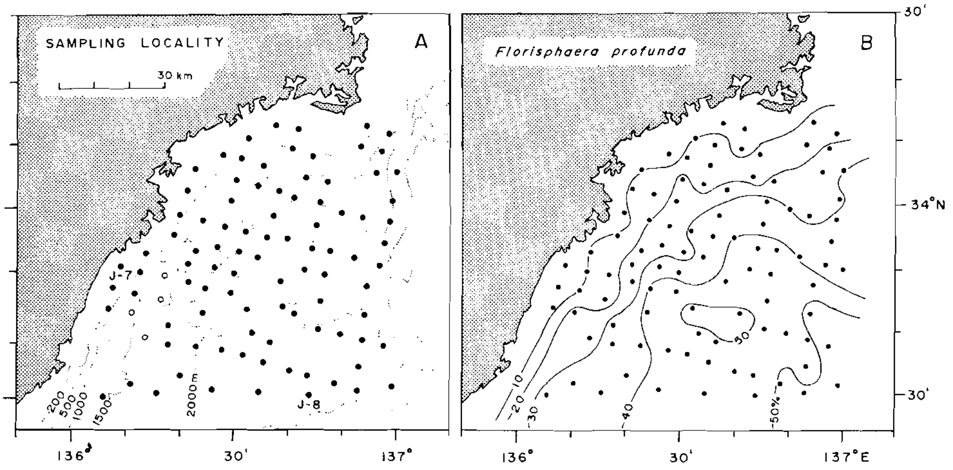


Fig. 3 Sampling localities and water depth (A), and frequency pattern of *Florisphaera profunda* (B) in the Sea of Kumano. The frequencies are expressed by percentage values of the total associations.

Species composition in surface sediments of semi-confined and open sea environments around Japan.

A set of ten surface sediment samples was collected from nearshore and further offshore localities around Japan in order to investigate the compo-

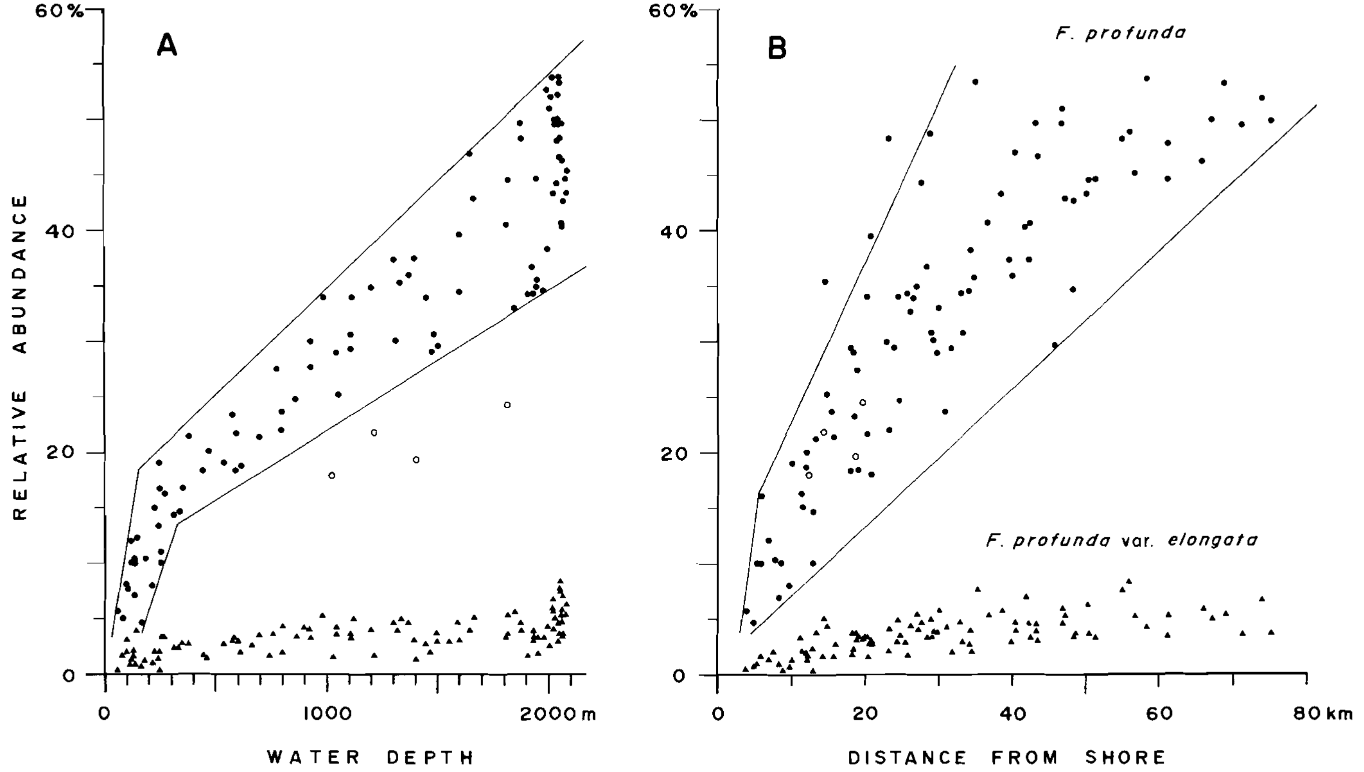
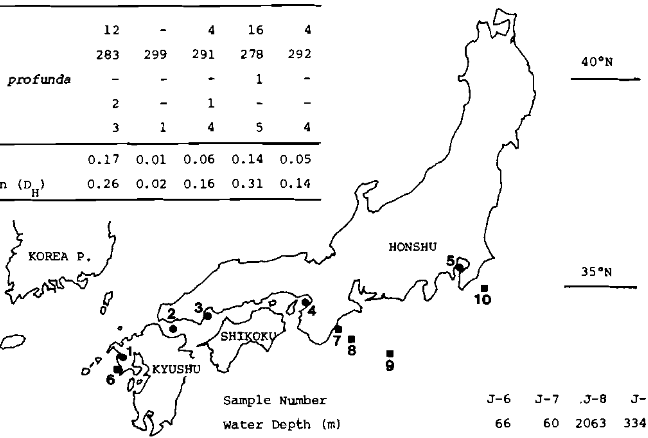


Fig. 4 Relations between relative frequency of *Florisphaera profunda* and water depth (A), and between relative frequency and distance from shore (B) in the Sea of Kumano. The frequencies are expressed by percentage values of the total associations. Closed circles indicate the combined percentage values of the nominate type of *F. profunda* and of *F. profunda elongata*; triangles represent values for *F. profunda elongata* alone; open circles: see text.

sition of the nannofossil association (fig. 5). The collection is meant to represent two different geographical settings. The first group of samples (J1–5) was recovered from semi-confined shallow bay and inland sea environments, whereas the second group (J6–10) was taken in marine open sea, neritic and pelagic environments.

Sample Number	J-1	J-2	J-3	J-4	J-5
Water Depth (m)	16	30	20	18	29
Emiliania huxleyi	12	-	4	16	4
Gephyrocapsa oceanica	283	299	291	278	292
Florisphaera profunda var. *profunda*	-	-	-	1	-
Syracosphaera spp.	2	-	1	-	-
Miscellaneous	3	1	4	5	4
Simpson's Index (D_P)	0.17	0.01	0.06	0.14	0.05
Shannon-Wiener Function (D_H)	0.26	0.02	0.16	0.31	0.14



Sample Number	J-6	J-7	J-8	J-9	J-10
Water Depth (m)	66	60	2063	3345	2020
Calcidiscus leptoporus	-	1	5	5	5
Emiliania huxleyi	95	139	79	56	62
Gephyrocpasa ericsonii	3	-	1	1	-
Gephyrocapsa oceanica	180	116	69	96	87
Helicosphaera carteri	1	7	1	1	2
Helicosphaera hyalina	-	3	1	-	-
Helicosphaera wallichii	3	1	-	-	-
Umbilicosphaera sibogae	3	4	4	1	1
Florisphaera profunda var. *elongata*	3	1	18	13	11
Florisphaera profunda var. *profunda*	9	16	121	122	126
Rhabdosphaera clavigera	-	1	-	-	-
Syracosphaera spp.	-	4	-	-	-
Miscellaneous	3	7	1	5	6
Simpson's Index (D_P)	0.54	0.63	0.71	0.69	0.69
Shannon-Wiener Function (D_H)	1.03	1.29	1.43	1.37	1.37

Fig. 5 Location, water depth and species composition of nannofossil associations for ten samples collected nearshore and further offshore Japan.

The nannoflora associations from the Ohmura Bay (J1), from the inland Sea of Seto (J2–4) and from the Tokyo Bay (J5) all display extremely low diversities; in all samples *Gephyrocapsa oceanica* is predominant. The values of the diversity indices calculated for the five samples from the shallow bay and inland sea environments are always less than one third of the values obtained for the samples of the open marine environments (fig. 5). *Flori-*

sphaera profunda is absent or extremely rare in the first group of samples (J1–5), whereas it is common in the open marine, neritic samples J6 and J7, and predominant in the associations from samples J8–J10, derived from pelagic environments. The rare occurrence of *F. profunda* in sample J4 may be explained in terms of transport from the open sea by strong tidal currents through the Naruto Channel.

Okada and Honjo (1975) investigated living nannoplankton from surface waters in the inland Sea of Seto and from the pelagic, warm Kuroshio current. The authors found an almost monospecific community of *Gephyrocapsa oceanica* in the inland Sea of Seto, which result closely resembles that obtained from surface sediment samples (J2–4).

Species composition in surface sediments of the Gulf of Thailand

Altogether 17 species were identified in the 18 samples studied. The distribution patterns of the three most important species, *Emiliania huxleyi, Gephyrocapsa oceanica* and *Florisphaera profunda* are illustrated in figure 6, along with the diversity indices values. Numerically less important species, not shown in figure 6 are *Acanthoica* sp., *Calcidiscus leptoporus, Calciosolenia murrayi, Discosphaera tubifera, Gephyrocapsa ericsonii, Helicosphaera carteri, H. hyalina, H. wallichii, Neosphaera coccolithomorpha, Syracosphaera pulchra, S.* sp., *Umbellosphaera irregularis, U. tenuis* and *Umbilicosphaera sibogae.*

Figure 6A shows that *Emiliania huxleyi* has its lowest relative frequencies in samples from stations located close to the coast of the Gulf. *Florisphaera profunda* (fig. 6C) is rare in the coastal stations as well, whereas *Gephyrocapsa oceanica* is abundant (fig. 6B). *F. profunda* reaches its highest percentage values in the central part of the Gulf, where *G. oceanica* is less frequent. These data imply opposite distribution patterns for *G. oceanica* and *F. profunda.*

In an earlier study Okada and Honjo (1975) observed coccolithophores with malformed coccoliths to be abundant in the Gulf of Thailand. Unusually low rates of malformed cells, however, appeared to exist in the surface waters of the central part of the Gulf, which area corresponds to that displaying high relative numbers of *Florisphaera profunda* in the sediments. In contrast to what might be expected, *F. profunda* does not have its highest percentage values in the deepest, southern part of the Gulf (approximately 8°N–102°E, see fig. 6C). This may be due to the effects of local geographical conditions, as appeared to be the case in the living communities, but the exact nature of such local conditions is not yet understood.

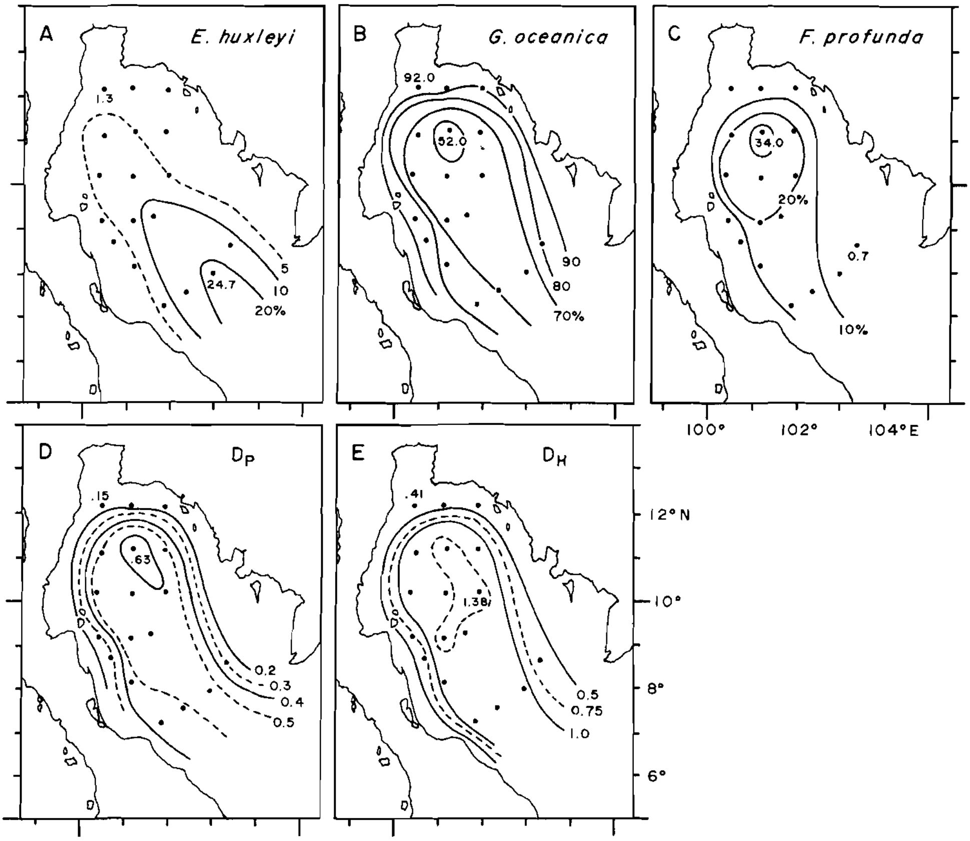


Fig. 6 Distribution patterns of the percentage values of three major species (*Emiliania huxleyi, Gephyrocapsa oceanica, Florisphaera profunda*) and of the values of the two diversity indices in surface sediment samples from the Gulf of Thailand. Percentage values refer to the total associations. Minimum and maximum values are plotted at the corresponding stations.

The patterns displayed by values of the diversity indices (figs. 6D and E) are similar to the frequency patterns of *Florisphaera profunda.* The values of the diversity indices vary between those calculated for samples from open marine environments and the highest value calculated for samples from the semi-confined seas around Japan (figs. 5 and 6).

Species composition in surface sediments of the Arafura Sea and the Gulf of Carpentaria

Twenty-three surface sediment samples were studied, which contained a total number of fourteen species. The list of species closely resembles that reported for the Gulf of Thailand; it differs by the absence of four species (*Acanthoica* sp., *Neosphaera coccolithomorpha*, *Umbellosphaera irregularis* and *U. tenuis*), and by the occasional presence of *Braarudosphaera bigelowii*.

Gephyrocapsa oceanica and *Emiliania huxleyi* are the most important taxa in the Arafura Sea/Gulf of Carpentaria (figs. 7A and B). The distribution patterns of these two species and the diversity indices (figs. 7C and D) indicate the presence of more open sea type environments in the western part of the area studied. In contrast to the tendency in the Gulf of Thailand the

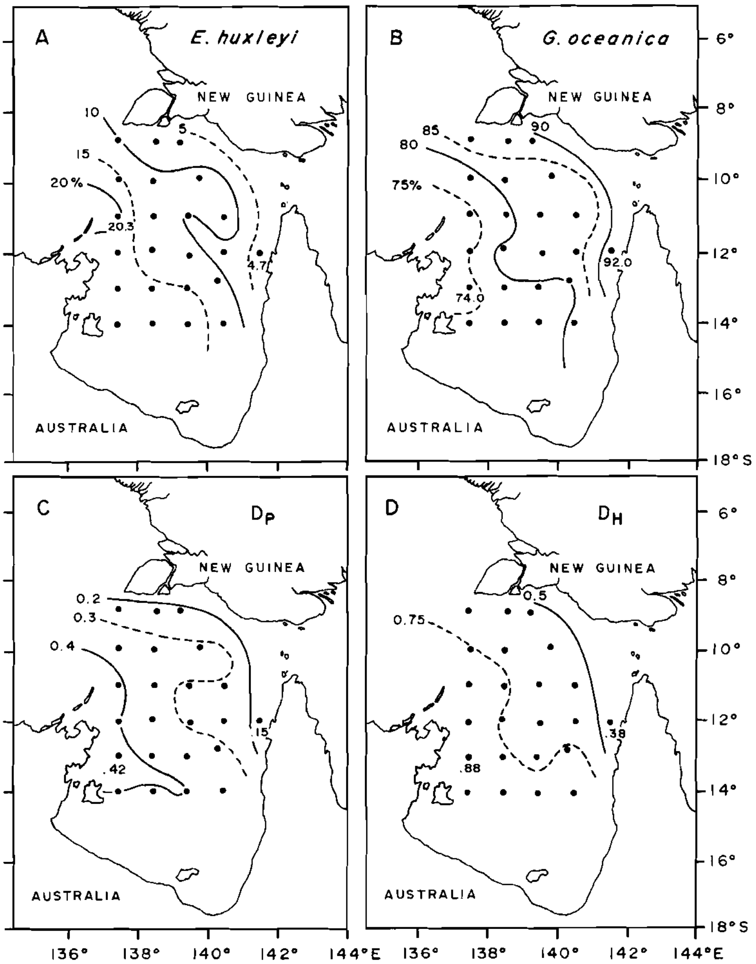


Fig. 7 Distribution patterns of two major species (*Emiliania huxleyi, Gephyrocapsa oceanica*) and of the values of two diversity indices in surface sediment samples from the Arafura Sea/Gulf of Carpentaria. Values are presented in the same way as in fig. 6.

contour lines of percentage values and of diversity indices do not run roughly parallel to the coast lines. This difference may be due to the limited freshwater input into the Gulf of Carpentaria.

Florisphaera profunda is rare in the samples of all stations. In associations from 11 stations in the Gulf of Thailand covering about the same depth-range (49–74 m) as the stations in the Arafura Sea/Gulf of Carpentaria (40–68 m), however, *F. profunda* may reach values of more than 10% of the total associations. This suggests that depth alone does not account for the differences in relative numbers of *F. profunda* between the Gulf of Thailand and the Arafura Sea/Gulf of Carpentaria.

DISCUSSION

Combining all data discussed in the preceding paragraphs, the following conclusions may be drawn concerning the distribution of calcareous nannofossils in surface sediments from low and mid-latitude areas of the western Pacific Ocean:

1. The relative abundance of *Florisphaera profunda* shows a positive correlation with depth in open marine environments ranging from the lower continental shelf to abyssal depths. *F. profunda* dominates the associations in the deep basins.

2. *Gephyrocapsa oceanica* predominates in associations from shallow marginal seas; the species may even monopolize the associations in samples from very shallow and semi-confined seas.

It is attempted to illustrate the relations between species abundances and environmental settings in a triangular co-ordinate diagram. In this diagram *Florisphaera profunda*, *Gephyrocapsa oceanica* and the group of all other species together were chosen as the end members (fig. 8). The diagram illustrates the provincialism of calcareous nannofossils; the composition of the associations in the groups of samples studied reflects the effects of different environmental settings, i.e., marginal sea, open sea, neritic, and open sea bathypelagic to abyssopelagic. Since the numbers of data are limited, however, the "phase boundaries" in figure 8 can only be tentative and need to be reexamined by plotting more data.

The distribution patterns of both *Florisphaera profunda* and *Gephyrocapsa oceanica* are geographically controlled: these species are found in high relative numbers in low to mid-latitude waters and they are not common at high latitudes. Therefore, the diagram can be useful only for warm regions, and the limits of its applicability have to be checked by incorporating data from other seas and oceans.

The values of the two diversity indices calculated for the associations discussed in this paper are independent of the relative frequencies of any particular species. The utilization of these indices as one or two component members of the diagram may widen the applicability of this method for paleoenvironmental analysis.

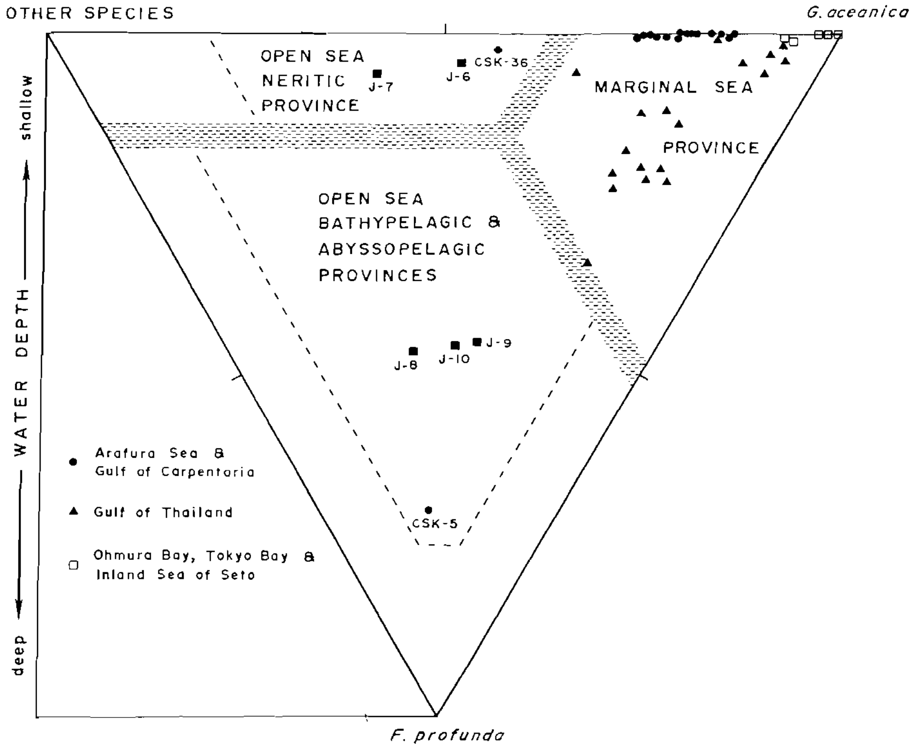


Fig. 8 Triangular co-ordinate diagram showing the relations between species composition of nannoplankton associations in surface sediment samples and depositional environments. Samples are plotted by using percentage values of the total associations for each component.

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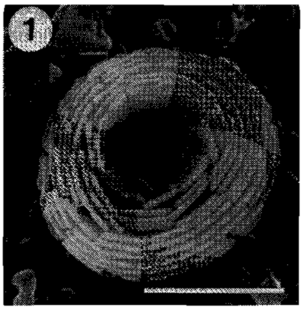
Dr. K. Matsuoka, Nagasaki University, Dr. M. Anraku, Nansei Regional Fisheries Research Laboratory, Dr. M. Okamura, Khochi University and Dr. E. Matsumoto, Geological Survey of Japan, collected samples from the Ohmura Bay and a nearby coastal station (J1 and 6), from the western part of the Inland Sea of Seto (J2 and 3), from the eastern station of the Inland Sea (J4) and from the Tokyo Bay (J5), respectively. Mr. Y. Kinoshita and

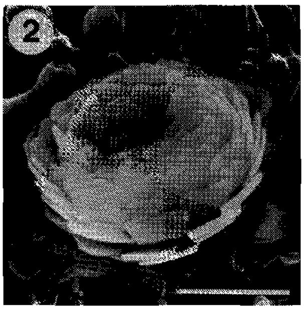
Plate 1

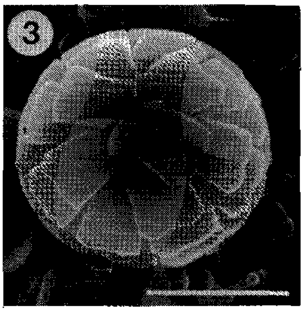
Florisphaera profunda as living coccospheres in plankton samples (figs. 1–9) and as nannofossils in marine sediments (figs. 10, 11). Scale bars = 3 μm.

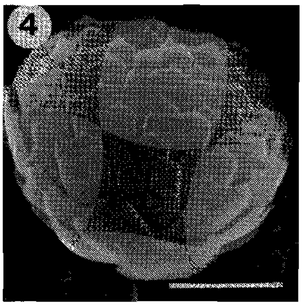
Figs. 1–4	Scanning electron micrographs of *F.* ***profunda*** var. ***profunda.*** 1, top view, 2, oblique top view, 3, bottom view, 4, oblique bottom view. All specimens recovered from the 150 m level of the Equatorial Central Pacific.
Figs. 5, 6	Scanning electron micrographs of *F.* ***profunda*** var. ***elongata.*** 5, bottom view, 6, oblique top view, Specimens recovered from the 175 m level of the Equatorial Central Pacific.
Fig. 7	Scanning electron micrograph showing *F.* ***profunda*** var. ***profunda*** (coccosphere) and desintegrated coccoliths of *F.* ***profunda*** var. ***elongata.*** Specimens derived from the same level as those illustrated in figures 1–4.
Fig. 8	Transmission electron micrograph of unnamed variety of *F.* ***profunda.*** Specimen recovered from the 125 m level of the Equatorial Central Pacific.
Fig. 9	Transmission electron micrograph of unusual *F.* ***profunda*** showing zig-zag patterns in its configuration of coccoliths. Specimen recovered from the 125 m level of the Central Red Sea.
Fig. 10	Transmission electron micrograph showing a small form of *F.* ***profunda*** var. ***elongata*** from the Western North Atlantic (DSDP 386-1-1-130 cm).
Fig. 11	Light micrograph showing Pleistocene nannofossil association from the Philippine Sea (DSDP 445-1-6-75 cm). Large arrow: *F.* ***profunda*** var. ***elongata***; small arrows: *F.* ***profunda*** var. ***elongata,*** a coccolith marked "G", and *Gephyrocapsa oceanica.*

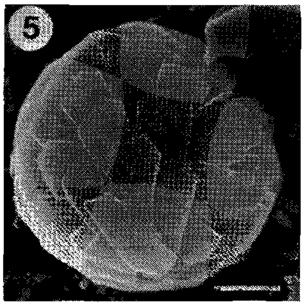
Plate 1

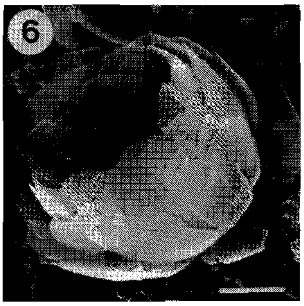


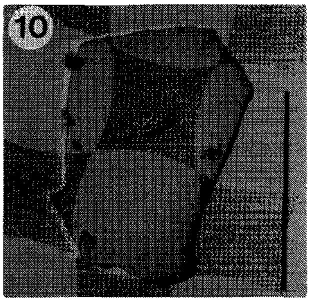


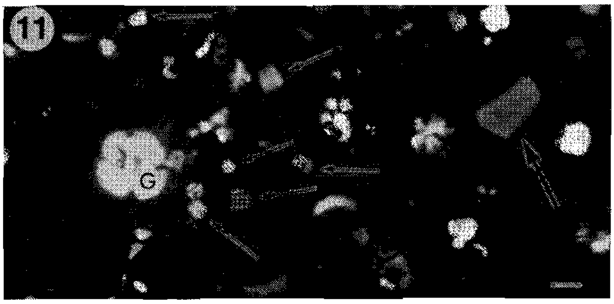












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STABLE ISOTOPES IN CALCAREOUS NANNOFOSSILS: POTENTIAL APPLICATION TO DEEP-SEA PALEOENVIRONMENTAL RECONSTRUCTIONS DURING THE QUATERNARY

THOMAS F. ANDERSON and JOHN C. STEINMETZ

ABSTRACT

While calcareous nannofossils offer some important advantages in stable isotope studies of past oceanic conditions, they are seldom used because of the very fine grain size and polyspecific nature of the assemblages. We report here a study of the isotopic and taxonomic changes in a late Quaternary core from the Caribbean to illustrate the potential applicability of nannofossils in marine paleoenvironmental reconstructions. Oxygen isotope variations in the 3–25 μm fraction, which is dominated by gephyrocapsids throughout, clearly define glacial-interglacial cycles. Globally-synchronous coccolith datums occur at the predicted levels in our $\delta^{18}O$ values and have a much higher amplitude than the record of a shallow-dwelling planktonic foraminifer. The available evidence suggests that the $\delta^{18}O$ record of the nannofossils is the more reliable indicator of surface water changes during climatic cycles. Both the weight fraction and number of species of nannofossils in the 3–25 μm fraction are higher during glacial epochs than interglacials. A change in the relationship of $\delta^{13}C$ in nannofossils to climate may indicate a change in the pattern of vertical circulation at this site over the past 160,000 years.

INTRODUCTION

The stable isotope record of calcareous microfossils in deep-sea sediments have provided a wealth of information on past oceanic environments. Oxygen isotopic variations are indicators of changes in oceanic temperature and salinity and the extent of continental glaciers (see Savin, 1977; Savin and Yeh, 1981; Shackleton, 1982). Carbon isotopic data can, in principle, be interpreted in terms of changes in fertility, circulation patterns, and the global exogenic cycle of carbon (see Shackleton, 1977; Bender and Keigwin, 1979; Scholle and Arthur, 1980; Savin et al., 1981; Broecker, 1982). Emiliani (1954, 1955) was the first to describe and interpret the record of oxygen isotopic variations in Quaternary deep-sea sediments from the analyses of planktonic foraminifera. Shackleton and Opdyke (1973) demonstrated that these fluctuations primarily reflect changes in the volume of glacial ice, and hence in the $^{18}O/^{16}O$ ratio of sea water.

Monospecific assemblages of planktonic and benthic foraminifera are the most widely used groups in isotope paleoenvironmental studies. Foraminiferal tests are large enough to be identified taxonomically and examined for signs of secondary alteration (overgrowths, dissolution) under a low-power microscope. Foraminifera secrete their tests at or reasonably close to oxygen isotopic equilibrium with ambient seawater (for review, see Savin, 1977). Deviations from oxygen isotopic equilibrium for planktonic and benthic foraminifera are generally constant for a given species. Therefore, comparison of isotopic data between locations requires that analyses be conducted on taxonomically limited (i.e., monospecific) assemblages in order to compensate for small (but often unknown) "vital" isotope effects.

The oxygen isotopic composition of planktonic foraminiferal assemblages in sediments can be influenced by other variables as well, the most important of which are changes in the mean depth (hence temperature) of test secretion and selective dissolution of the more fragile tests during sedimentation (Emiliani, 1971; Savin and Douglas, 1973; Berger and Gardner, 1975). Both influences tend to increase the $^{18}O/^{16}O$ ratio of sediment assemblages relative to living assemblages and probably contribute to the observed differences in oxygen isotopic compositions of some planktonic foraminifera in surface sediments relative to plankton tows (for example, Van Donk, 1970; Shackleton et al., 1973; Vergnaud-Grazzini, 1976; Kahn, 1977; Duplessy et al., 1981). Thus, the exact relationship of oxygen isotopic fluctuations in planktonic foraminifera to changes in sea-surface conditions is difficult to establish with certainty.

Calcareous phytoplankton remains (dominantly coccoliths) offer some potential advantages over planktonic foraminifera in isotopic paleoceanographic studies. Because the organisms are photosynthetic, their depth habitat is restricted to the upper 150 meters of the water column (Okada and Honjo, 1973). Coccoliths are more resistant to dissolution than planktonic foraminifera (McIntyre and McIntyre, 1971; Schneidermann, 1973; Roth and Berger, 1975). In principle, therefore, the oxygen isotope record of calcareous nannofossils should reflect more accurately the paleoenvironmental conditions at the sea surface and should be less influenced by selective dissolution. Furthermore, nannofossils comprise about half of the $CaCO_3$ in Quaternary deep-sea sediments and are more abundant in Tertiary and Cretaceous sediments (Bramlette, 1958; Berger, 1976).

Despite these apparently advantageous properties, calcareous nannofossils have been little used in isotopic studies of deep-sea sediments except in detailed stratigraphic investigations in sections where planktonic foraminifera are lacking (i.e., Douglas and Savin, 1975; Thierstein and Berger, 1978; Scholle and Arthur, 1980). The reluctance to use nannofossils in isotopic studies is directly related to their very small grain size: Taxonomic identification and preservational characterization in polyspecific coccolith assemblages require high-resolution microscopy and can be tedious. In addition, because of the probable existence of species-dependent vital isotope effects (recently confirmed by Dudley et al., 1980, and discussed below), variations in the species composition of coccolith assemblages may obscure the paleoenvironmental significance of their isotopic signal. Several studies have compared the isotopic trends of nannofossils and foraminifera in sediments ranging in age from late Cretaceous to Holocene (for example, Anderson and Cole, 1975; Margolis et al., 1975; Kroopnick et al., 1977; Berger et al., 1978; Goodney et al., 1980). These results show that isotopic variations in coccolith and foraminiferal assemblages are generally parallel but that coccolith $\delta^{18}O$ values were typically offset from planktonic foraminifera values by up to 2 permil (and often in the direction of ^{18}O enrichment). The interpretation of these differences was enigmatic since it was difficult to distinguish between preservational (Douglas and Savin, 1975) and vital isotope effects (Anderson and Cole, 1975). Moreover, the parallelism of oxygen isotope trends in nannofossils and monospecific planktonic foraminifera implied that little new paleoenvironmental information would be obtained from nannofossils.

An important contribution to our understanding of the stable isotope record of nannofossils was the results of Dudley et al. (1980) on oxygen isotopic fractionation in coccolithophores grown in culture. These experiments revealed two distinct groups of non-equilibrium (but temperature-dependent) fractionations in coccolith precipitation: ^{18}O-rich (+1 permil relative to equilibrium calcite) and ^{18}O-depleted (−2 to −3 permil relative to equilibrium calcite). These data suggest that the direction and extent of offsets of coccoliths relative to foraminiferal assemblages may be due solely to variations in species composition. In addition, these exciting results hold out the promise for quantitative interpretations of the oxygen isotope ratio in well-preserved coccolith assemblages in terms of the temperature and oxygen isotopic composition of paleo-surface seawater.

Although this experimental fractionation evidence is very important, our present understanding of the factors and processes which control the stable isotopic composition of nannofossil assemblages is rudimentary. More data are needed on effects such as surface productivity, taxonomic variations, dissolution and preservation changes, and benthic mixing processes. Our approach has been to focus on isotopic and taxonomic changes in nannofossil assemblages from Quaternary sediments where climatically-induced oxygen isotope fluctuations in monospecific foraminifera are well established. We recently reported our initial results on one core from the central Caribbean (Anderson and Steinmetz, 1981). The purpose of the present paper is to describe these results, together with some additional data and refined interpretations as a well-documented illustration of the potential significance (and important unresolved problems) of stable isotope variations in nannofossils for paleoenvironmental reconstructions.

Our initial results have been obtained on the 3–25 µm fraction of the central Caribbean core P6304-4 (15°27'N, 70°43'W; 4,136 m; 1,070 cm deep) from the University of Miami collection. It is one of four long piston cores taken in the same area on which Emiliani (1966, 1972) has measured oxygen isotope ratios on the planktonic foraminifer *Globigerinoides sacculifer.* Emiliani's data provided a reference for interpreting the oxygen isotope signal in the nannofossils.

Detailed taxonomic studies on nannoplankton remains were done on the 3–25 µm fractions and on bulk sediment samples (Steinmetz and Anderson, in prep.). The carbonate portion of the fine (3–25 µm) fraction consists almost entirely of well-preserved coccoliths dominated by the genus *Gephyrocapsa.*

The pattern of oxygen isotope fluctuations for the nannofossil assemblage from this core (fig. 1) is remarkably similar in several features to the composite foraminiferal record for the Caribbean and equatorial Atlantic (Emiliani, 1978). Maximum and minimum $\delta^{18}O$ excursions are generally

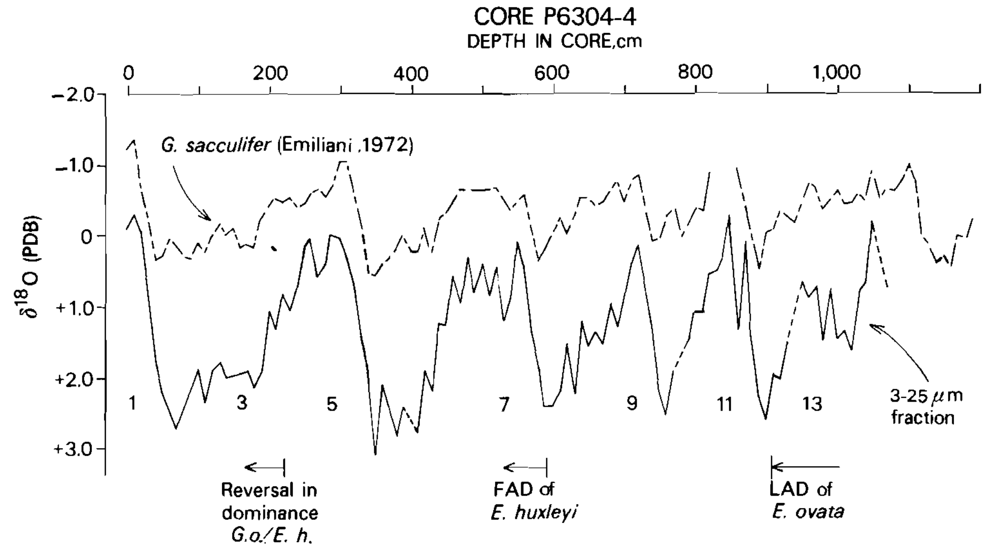

Fig. 1 The oxygen isotope results on the 3–25 µm fraction (nannofossils) of core P6304-4. The numbers beneath the curve indicate the interglacial isotope stages of Emiliani (1966). The isotopic results on *Globigerinoides sacculifer* from Emiliani (1972) are also shown. The Quaternary coccolith datum levels of Thierstein et al. (1977) are indicated at the bottom of the diagram. *G.o.* = *Gephyrocapsa oceanica; E.h.* = *Emiliania huxleyi;* FAD = first appearance datum; LAD = last appearance datum. Modified from Anderson and Steinmetz (1981).

confined to < ∓ 0.4 permil of their average values (+2.4 and +0.1 permil, respectively). Glacial and interglacial isotope stages (Emiliani, 1966) are readily identified, and the "saw-toothed" shape of the curve (indicative of rapid deglaciation, see Broecker and Van Donk, 1970) is apparent. The sharp deglaciation transitions are well defined and occur about 10 cm lower (earlier) than in the isotope record of G. *sacculifer* (Emiliani, 1972). It is unlikely that this apparent nannofossil isotope "lead" is significant because the distance is close to our sampling resolution (10 cm) and because foraminiferal and nannofossil assemblages were sampled from different bulk sediment splits.

Our taxonomic studies on the fine fractions showed that thirty-two nannoplankton species are present. Relative species abundances were determined by the method originally proposed by Hay (1970), in which the order of magnitude of species frequency per field of view under high magnification is recorded. Although individual species counts would insure greater precision, the time required for such counting would be prohibitive considering the large number of samples and species under study. Moreover, Sancetta (1979) has shown that semi-quantitative microfossil data collected in this manner are statistically equivalent to those collected quantitatively, and hence can be used with reasonable accuracy. The results of our species census indicate that gephyrocapsids are the dominant taxon both in terms of numbers of individual coccoliths and volume of carbonate in all of the samples. There are no obvious correlations between the relative abundance of gephyrocapsids and oxygen isotope stages. This is true on both the generic and specific level (i.e., for *Gephyrocapsa* as well as for the most abundant species: *G. caribbeanica, G. oceanica, G. aperta,* and *G. doronicoides*). While there are trends or "preferences" for interglacial or glacial stages among some of the lesser abundant taxa (Steinmetz and Anderson, in prep.), the volume of calcium carbonate involved is not sufficient to influence the oxygen isotope signal. Therefore, the amplitudes of $\delta^{18}O$ change in the nannofossil assemblages in this core are not significantly affected by species-dependent vital effects.

From a detailed analysis of Quaternary cores from the Atlantic, Pacific, and Indian Oceans, Thierstein et al. (1977) demonstrated the global synchroneity of two coccolith datum levels in the Pleistocene. The extinction of *Emiliania ovata (= Pseudoemiliania lacunosa)* in the middle of oxygen isotope stage 12 (458,000 y BP from the chronology of Shackleton and Opdyke, 1973) and the first appearance of *Emiliania huxleyi* in oxygen isotope stage 8 (268,000 y BP from the same chronology). A third event, the reversal in dominance between *Gephyrocapsa caribbeanica* and *E. huxleyi* was found to be time-transgressive from transitional waters to sub-tropical and tropical waters. All three datum events were identified in core P6304-4 by examination of unprocessed splits of the bulk sediment samples (we had to use bulk samples because the small coccolith *E. huxleyi* was not retained in the 3–25 μm fraction). Relative to the nannofossil isotope stratigraphy, the location of these events in P6304-4 are in almost exact agreement with their globally synchronous placement by Thierstein et al. (1977) (fig. 1). This correlation is important for several reasons. First, it substantiates the results of Thierstein et al. for Carribbean deep-sea sediments; it is the first data of this type on this basin. Moreover, since Thierstein et al. used planktonic foraminifera to determine isotope stages, the oxygen stratigraphy of nannofossils in P6304-4 is now closely tied to the late Quaternary chronostratigraphic framework. Our results demonstrate for the first time that the oxygen isotope record of Quaternary nannofossil assemblages can yield reliable and precise stratigraphic information.

OFFSET AND AMPLITUDE DIFFERENCES BETWEEN FORAMINIFERAL AND NANNOFOSSIL OXYGEN ISOTOPE RECORDS

The nannofossil $\delta^{18}O$ curve is displaced in a positive direction with respect to the *G. sacculifer* curve (fig. 1). The displacements vary systematically down-core: +1.0 to +1.1 permil during maximum interglacial stages, +2.0 to +2.4 permil during maximum glacial stages. As noted earlier, a positive offset of nannofossil $\delta^{18}O$ values has been reported previously but could not be unambiguously interpreted (for example, see Anderson and Cole, 1975, on earlier work in the Caribbean). In core P6304-4, we are confident that the offset is due to differences in oxygen isotope fractionation in the precipitation of foraminiferal and coccolith calcite. Although there has been considerable debate on the issue, it is adequate for our purposes to note that *G. sacculifer* probably deposits its test with an oxygen isotope composition in the range from predicted equilibrium calcite to 1–2 permil depleted relative to equilibrium. Nannofossils in the 3–25 μm fraction are essentially a monogeneric gephyrocapsid assemblage. The experimental work of Dudley et al. (1980) showed that one important species of this genus, *Gephyrocapsa oceanica*, secretes coccoliths which are enriched in ^{18}O with respect to equilibrium calcite. If this isotopic behaviour is representative of other gephyrocapsids (as seems likely), then the offset between nannofossils (^{18}O-rich) and *G. sacculifer* (equilibrium to ^{18}O-depleted) is reconciled. Preservational effects in nannofossils, namely the precipitation of isotopically-enriched secondary calcite from cold bottom waters, cannot be an impor-

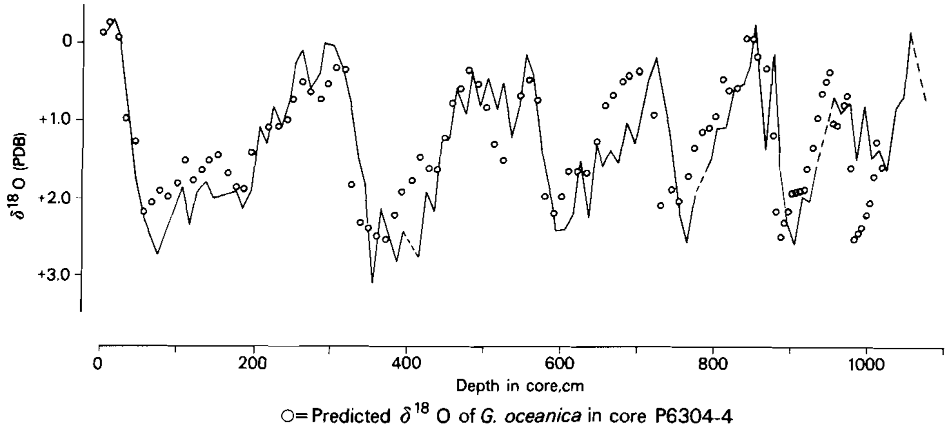

Fig. 2 The open circles show the predicted oxygen isotope composition of *Gephyrocapsa oceanica* from the results of Imbrie et al. (1973) and Dudley et al. (1980). The curve is the observed nannofossil data from figure 1.

tant contributor to the offset because the nannofossil assemblages show no evidence for this type of post-depositional alteration.

The systematic variation in the nannofossil – foraminiferal offset is more interesting but more difficult to explain. This difference means that the amplitude of glacial-interglacial $\delta^{18}O$ fluctuations for nannofossils (average 2.4 permil) was significantly higher than that for *G. sacculifer* (average 1.2 permil). Since both curves cannot be records of temperature and $\delta^{18}O$ in the same part of the water column, which is the more reliable indicator of changes in near-surface Caribbean seawater during Pleistocene climatic cycles? Our choice is the nannofossil record for several reasons. As discussed previously, the depth habitat of nannoplankton could not have changed much between glacial and interglacial epochs. This restriction does not necessarily apply to planktonic foraminifera (i.e., Emiliani, 1971; Savin and Douglas, 1973; Berger et al., 1978). A restricted depth habitat also means that selective dissolution of nannofossils (for which there is no evidence in our samples) would not result in a bias towards an ^{18}O-enriched sediment assemblage as it often does in shallow-dwelling planktonic foraminifera (for example, Savin and Douglas, 1973; Berger and Killingley, 1977; Berger and Gardner, 1975; Duplessy et al., 1981).

In an attempt to determine whether the foraminiferal record from core P6304-4 had been truncated, we examined the isotopic data on *G. sacculifer* from other Caribbean cores (Emiliani, 1955, 1966, 1972; Imbrie et al., 1973; Van Donk, 1970). An interesting pattern was observed. The amplitudes of the $\delta^{18}O$ signal in cores from water depth > 3,900 m, including P6304-4, were smaller than the amplitudes in cores from < 3,000 m (Anderson and Steinmetz, 1981, table 1). Droxler et al. (1983) recently reported on the ^{18}O stratigraphy of *G. ruber*, another shallow-dwelling planktonic foraminifer, from an aragonite-rich core taken at 1,935 m in an interbank trough on the Bahama Platform; the average $\delta^{18}O$ amplitude from this shallow core is also 1.9 permil (A. M. Droxler, personal communication, 1983). The smaller amplitudes in the deeper cores are due mostly to less negative $\delta^{18}O$ values during interglacials than in the shallower cores.

We have checked the compatibility of the nannofossil $\delta^{18}O$ record in core P6304-4 with the foraminiferal record in one of the shallower cores, V12-122 (2,800 m). Variations in the oxygen isotopic composition of surface seawater were calculated from down-core variations in the $\delta^{18}O$ of *G. ruber* and the average sea-surface temperature determined by quantitative faunal methods (Imbrie et al., 1973). Our procedure and results were essentially the same as those of Van Donk (1976, p. 157–160, fig. 7). The isotopic composition of nannofossils was calculated from our estimate of the temperature-dependent fractionation curve for *Gephyrocapsa oceanica* (Dudley et al., 1980; W. C. Dudley, personal communication, 1981) and the temperature and $\delta^{18}O$ of seawater. Correlation between V12-122 and P6304-4 was done at each of the prominent glacial-interglacial transitions. The comparison between the predicted nannofossil $\delta^{18}O$ values for P6304-4 and the observed curve is remarkably good (fig. 2). The mismatch below 950 cm may be due to a missing section of sediments near this interval in V12-122 (Imbrie et al., 1973). Nonetheless, the excellent fit between prediction and observation argues strongly that: (1) the assumption made in calculating the temperature and $\delta^{18}O$ changes in seawater was appropriate, (2) Dudley's experimental results are valid for gephyrocapsid-dominated nannofossil assemblages, and (3) the isotopic record of nannofossils in P6304-4 more closely follows the foraminiferal results from a shallower core than from P6304-4 itself.

But what accounts for the difference in $\delta^{18}O$ between the foraminiferal and nannofossil records in core P6304-4? The most logical explanation for this difference, as well as for the pattern of decreasing $\delta^{18}O$ amplitudes for *G. sacculifer* with increasing depth, is more intense selective dissolution of planktonic foraminifera during interglacial epochs. This would result in ^{18}O enrichment in the foraminiferal sediment assemblage relative to their living counterparts. However, extensive selective dissolution during interglacials appears to be contradictory to other lines of evidence. For example, selective dissolution sufficient to cause a significant increase in the $\delta^{18}O$ of *G. sacculifer* should also have been obvious in the state of preservation of nannofossils. As noted earlier, the nannofossil fractions were almost always well preserved. The only exceptions were samples at 840 and 850 cm, where fragile specimens were either broken, reduced in number, or missing. Interestingly, these samples were from the peak of *interglacial* stage 11. In this same interval, the > 62 μm fraction (foraminifera) is at its maximum value in the core, and there were evidently too few well-preserved *G. sacculifer* tests for an isotopic analysis (Emiliani, 1972). In addition, extensive carbonate dissolution during interglacials is not supported by the poor preservation of foraminiferal assemblages, low bulk calcium carbonate abundance, and low coarse fraction abundance during *glacial* stages in a number of Quaternary Caribbean, and eastern and western equatorial Atlantic cores (Berger, 1968; Ruddiman, 1971; Gardner, 1975; Bé et al., 1976). On the other hand, the low carbonate content during glacial stages in Caribbean basins is primarily the result of terrigenous influx from surrounding continental margins (Prell, 1978 and references cited therein), and we are not aware of any published studies of planktonic foraminiferal preservation on cores from the central Caribbean in the vicinity of P6304-4.

An increase in the mean depth of test secretion during interglacials would also result in a high ^{18}O content in shallow-dwelling foraminiferal assemblages. However, this influence should have been common to all of the cores from this same general area and not solely to those from greater depth. The same argument can be applied against differences in the seasonality of foraminiferal test secretion between glacial (mostly summer) and interglacial (mostly winter) epochs. A seasonality effect on nannofossil precipitation during Pleistocene climatic cycles is difficult to evaluate reliably. From estimates of winter and summer faunal temperatures in the Caribbean (Imbrie et al., 1973; Prell et al., 1976; Prell and Hays, 1976), the maximum seasonality effect, i.e., precipitation during glacial winters and interglacial summers, on the $\delta^{18}O$ range of nannofossils would be +0.4 to +0.6 permil. Although the actual seasonality effect was probably much smaller, this effect might account for the fact that nannofossil $\delta^{18}O$ values predicted from *faunal* estimates of temperature and $\delta^{18}O$ of surface seawater do not quite reach the maximum extremes of the observed curve (fig. 2).

We cannot offer a completely satisfactory explanation at this time for the difference in glacial-interglacial $\delta^{18}O$ changes between nannofossils and *G. sacculifer* in core P6304-4. The excellent agreement between the nannofossil data and the results on foraminiferal assemblages from shallower, and presumably better preserved cores suggests strongly (but certainly does not prove) that the nannofossil variations are a better record of the climate-induced fluctuations in the temperature and isotopic composition of Caribbean surface seawater.

The offset and amplitude differences we observed in nannofossil and foraminiferal isotopic records in the Caribbean are not representative of results from the western Pacific by Berger et al. (1978), Schiffelbein and Thierstein (1981) and unpublished data from our laboratory. These studies show no major amplitude difference between nannofossil and foraminiferal $\delta^{18}O$ signals. In addition, average $\delta^{18}O$ values of nannofossils and G. *sacculifer* were similar, i.e., there was no offset. Anderson and Cole (1975) reported a negative nannofossil – foraminiferal offset in eastern equatorial Pacific sediments. We suspect that this difference in offset relative to the Caribbean is due to a higher proportion of ^{18}O-depleted nannofossils, such as *Cyclococcolithus leptoporus* (Dudley et al., 1980) in the nannofossil assemblages from the equatorial Pacific (Geitzenauer et al., 1976; Roth and Berger, 1975) rather than to any basin-to-basin difference in vital isotope effects among taxonomically equivalent assemblages. Schiffelbein and Thierstein (1981) noted a shift of about 0.8 permil toward more negative $\delta^{18}O$ values at about isotope stage 8, corresponding to a globally documented decrease in the abundance of the previously dominant *Gephyrocapsa caribbeanica.* This shift almost certainly represents a change in the species composition of the Pacific assemblages; it was not observed in our Caribbean study.

SPECIES DIVERSITY, CARBONATE CONTENT, AND $\delta^{13}C$ IN NANNOFOSSIL ASSEMBLAGES

The total number of nannofossil species in the 3–25 μm fraction varies from 7 to 20 down-core (fig. 3). The variations are not random but are roughly correlated to oxygen isotope stages (fig. 4). During peak glacial stages the total number of species in a sample is generally between 15 and 18, with an average of 16.2. During peak interglacials the average total number of species is 13.5, and the distribution is bimodal with peaks at 11–12 and 17–18. The greater diversity of nannofossil species during glacial stages agrees with taxonomic data on other Caribbean cores (Cohen, 1964; Gartner, 1972). Further details on species diversity and variation with climate are discussed in Steinmetz and Anderson (in prep.).

The $CaCO_3$ (i.e., nannofossil) content in the 3–25 μm fraction ranges from 10 to 50%. There is no obvious systematic relationship between carbonate content and climatic stage (fig. 3). However, when the data are

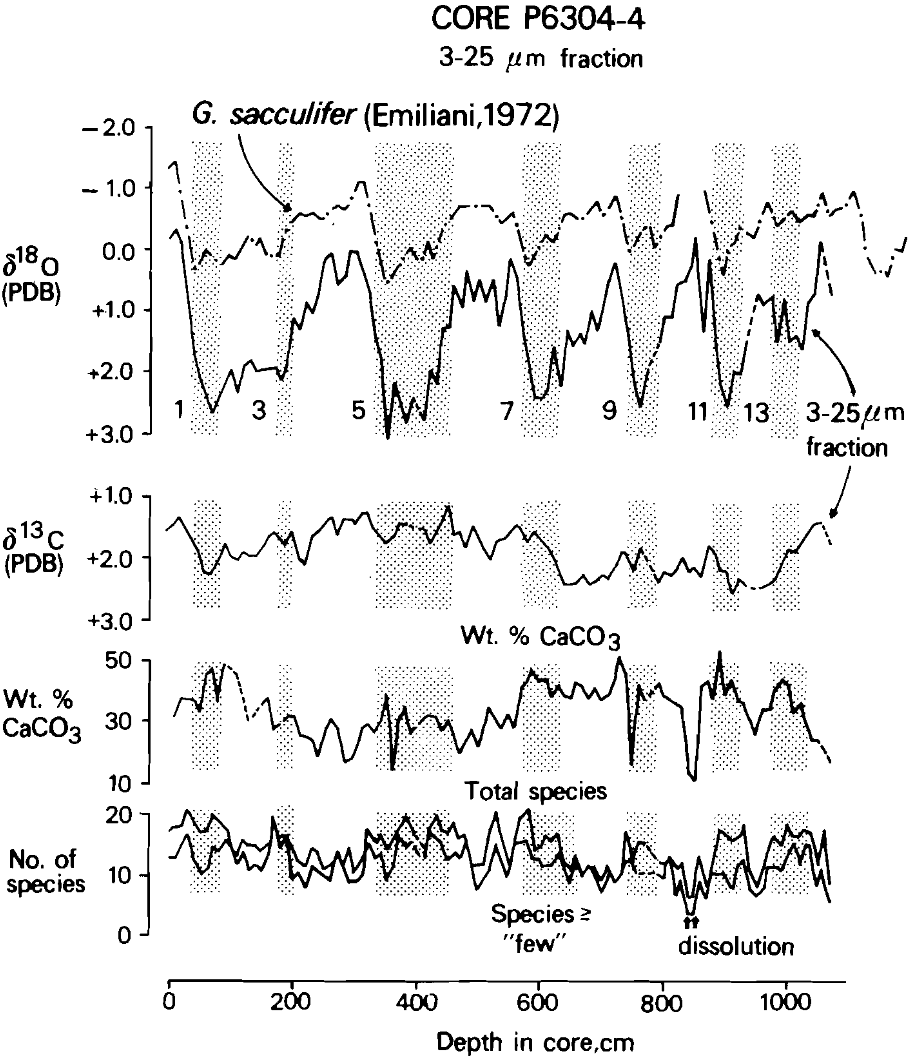

Fig. 3 Oxygen and carbon isotope results, weight percent $CaCO_3$, and species abundance for the 3–25 μm fraction. The shaded areas are glacial stages.

plotted in histogram form, a tendency for higher $CaCO_3$ to occur in glacial stages becomes apparent (fig. 4). This relationship is exactly opposite to the well-documented association of high $CaCO_3$ with interglacial stages in bulk sediment samples in other Caribbean and equatorial Atlantic cores (see Prell, 1978). The generally-accepted explanation for this association is greater terrigenous input during glacial low sea-level stands (Broecker, 1971). This makes our results on P6304-4 even more surprising since terrigenous input should be especially apparent in the fine silt and clay-sized fractions. Consequently, our results may represent the first indication in the Carribbean for greater nannofossil production and sedimentation during glacial stages. It will be interesting to see whether this speculation is supported by similar analyses on other Caribbean cores.

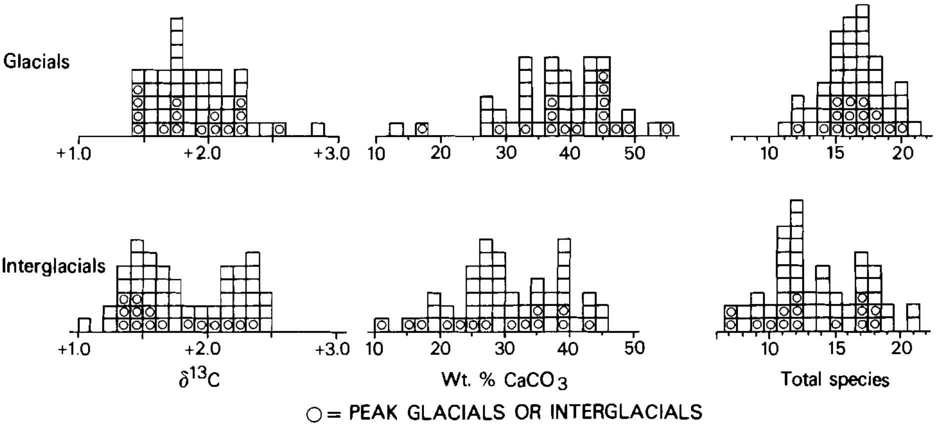

Fig. 4 Histograms of $\delta^{13}C$, weight percent $CaCO_3$, and species abundance for glacial and interglacial stages. The open circles are data from peak glacial or interglacial stages.

The carbon isotope composition of nannofossils range from +1.1 to +2.6 permil. There appears to be no obvious relationship between $\delta^{13}C$ and climate from the data presented in figures 3 and 4. Several major shifts are suggested in the down-core $\delta^{13}C$ record (fig. 3): a positive shift of 1.0 permil at 950–1040 cm (stage 14), and a negative shift of 0.9 permil at 590–640 cm (stage 8). Schiffelbein and Thierstein (1981) reported a similar carbon isotope shift at stage 8 in several Pacific cores. The possibility of global $\delta^{13}C$ shift in nannofossil assemblages at this time is consistent with our results.

In order to check more carefully for possible covariance between $\delta^{13}C$ and $\delta^{18}O$, we plotted a scatter diagram for these two variables. The results were somewhat surprising (fig. 5). In the lower two-thirds of the core (stages 6–15) there is no significant correlation between $\delta^{13}C$ and $\delta^{18}O$ ($r = 0.03$). This pattern is consistent with Broecker's (1982) prediction that $\delta^{13}C$ of surface ocean water did not change during glacial-interglacial cycles (even though the $\delta^{13}C$ of mean ocean water changed by 0.7 permil; see Shackleton, 1977).

The data from stages 1–6 show a quite different and unexpected trend: $\delta^{13}C$ correlates with $\delta^{18}O$ ($r = 0.72$). In other words, the $\delta^{13}C$ of nannofossils was higher during glacial stages than interglacial stages. Does this change in

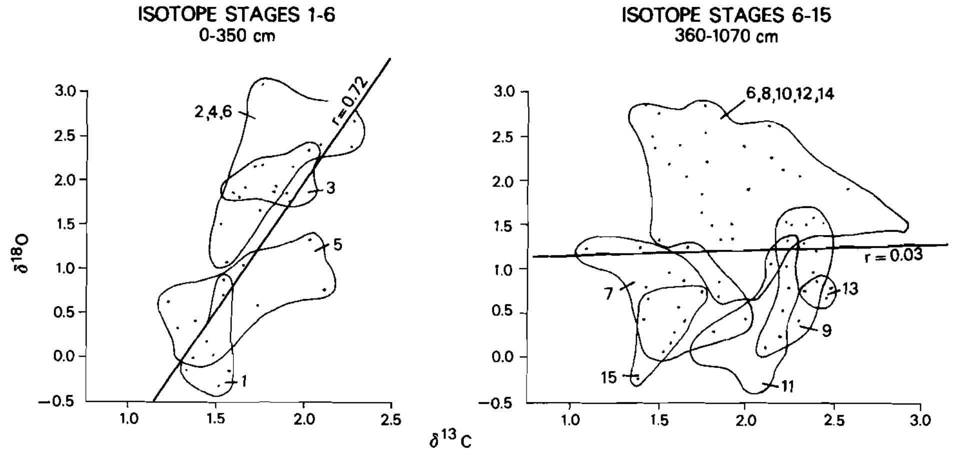

Fig. 5 A scatter diagram for $\delta^{18}O$ vs. $\delta^{13}C$ from the nannofossil assemblages. The enclosed areas define the limits of the data for each stage.

the carbon isotope record of nannofossils have implications for the paleoceanography of the central Carribbean? This depends upon the extent to which $\delta^{13}C$ in nannofossils reflects $\delta^{13}C$ in surface ocean water, and we have only begun to investigate that relationship. Based on results obtained from Cretaceous and Cenozoic DSDP cores, Kroopnick et al. (1977) concluded provisionally that nannofossil $\delta^{13}C$ values are a better indicator of surface seawater than planktonic foraminiferal values. However, Goodney et al. (1980) showed that $\delta^{13}C$ variations in nannofossils from Recent deep-sea sediments are often difficult to interpret and suggest that they may be influenced by complex interrelationships between carbon isotope fractionation during nannoplankton photosynthesis and vital carbon isotope effects in nannoplankton calcite secretion which vary with the rate of photosynthesis.

If the nannofossil assemblage in core P6304-4 does follow past changes in the carbon isotopic composition of surface seawater, then the $\delta^{13}C$–$\delta^{18}O$ covariance might indicate enhanced local upwelling of ^{12}C- and nutrient-enriched waters during interglacial stages 1 and 5. Some support for this interpretation is provided by the fact that Van Donk's (1970) data on planktonic foraminifera from V12-122 show a similar $\delta^{13}C$–$\delta^{18}O$ trend in the same time interval, but not over the entire core (Broecker, 1982). Until more confirming evidence of this type is obtained, detailed interpretations of nannofossil $\delta^{13}C$ records will remain speculative.

CONCLUDING REMARKS

The application of stable isotope measurements on calcareous nannofossils to paleoceanographic reconstructions has evolved rapidly over the past several years. An important contribution of these initial studies has been to show that the isotopic record of nannofossils is not redundant with that of planktonic foraminiferal assemblages and that new and important information can be obtained. Although isotopic analysis of nannofossils offers some distinct advantages, we caution that particular care must be taken in sample preparation and characterization in order for the isotopic results to be meaningful. As in any developing technique, there are still large gaps in our understanding of the stable isotope geochemistry of nannofossils. For example, there are very little data on the relationship between isotopic composition of nannofossils in surface sediments and the physical and chemical properties of overlying surface seawater. Several other groups besides us are actively involved in nannofossil isotope research. We are optimistic that, as new results become available, stable isotope studies on nannofossils will become an important tool in marine paleoenvironmental reconstructions.

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PRESERVATION AND DISSOLUTION OF FORAMINIFERAL CARBONATE IN AN ANOXIC SLOPE ENVIRONMENT, SOUTHERN GULF OF CALIFORNIA

HANS SCHRADER, GUANGFEN CHENG AND RICHARD MAHOOD

ABSTRACT

Seven cores, retrieved from the slopes (between 500 to 800 meters water depth) of the central Gulf of California, were analyzed for their carbonate content. Sedimentation rates of the varved sediments are around 100 cm/10^3 years, TOC and carbonate values range from 4.0 to 5.1% TOC and 0.83 to 6.7% carbonate, respectively. Most carbonate is biogenic and consists of autochthonous benthic foraminifera (*Bolivina seminuda, B. subadvena, Buliminella tenuda, Cassidulina subcarinata, C. tumida, Suggrunda eckisi* a.o.). Foraminiferal accumulation rates are highly variable (0 to 200 individuals/cm^2/year). Foram accumulation rates increase over those intervals which show lower sedimentation rates, show an increased presence of Pacific and California Current waters, and have less distinctly well developed lamination.

We postulate that during times of increased biogenic productivity in the surface waters the rain ratio of C_{org} to carbonate approaches infinity and that enough dissolved oxygen occurs in the bottom water so that biogenic carbonate is dissolved. Conversely, the rain ratio of C_{org} to carbonate is greatly reduced during episodes with decreased primary productivity, and because the bottom waters are without dissolved oxygen, due to sluggish circulation of intermediate waters, foraminifera tests are preserved. The generalized assumption that carbonate preservation is enhanced under anoxic bottom water conditions is not unconditionally applicable to the anoxic slope depositional environment of the Gulf of California.

INTRODUCTION

Laminated-varved marine sediments are commonly found in Pacific (Ingle, 1981), Indic (von Stackelberg, 1972), and Atlantic Tertiary and Quaternary (Soutar et al., 1981) sediment sections. With the development of corers which recover undisturbed deep-sea sediments (Hydraulic Piston Cores of the Deep Sea Drilling Project, modified Box- and Kasten-corers) it became evident that the areal and temporal distribution of varved marine sediment is more widespread than thought a few years ago. The Mediterranean area also has a number of sections with laminated and possibly varved sediments exposed on land (Gersonde, 1980, a.o.) and on the sea floor (Hsü et al., 1978: Sites 375 and 376).

Marine varved sediments are associated with past and present high productivity in surface waters, with a strong and sharp seasonality in the supply of biogenic and terrigenous sediment particles, and with bottom waters depleted of dissolved oxygen, which prevents mixing of sediments by bottom infauna. These sediments are natural recording systems of temporal changes of climatic-oceanic parameters and they provide seasonal resolution over long time periods; besides tree-rings, no other records are available to construct long-time series beyond the instrumental and historical records available.

Cores collected in the Gulf of California south of the Tiburon, Angel de la Guardia, San Lorenzo island chain, and from within the oxygen minimum zone (around 400 to 800 meters water depth) contain large numbers of

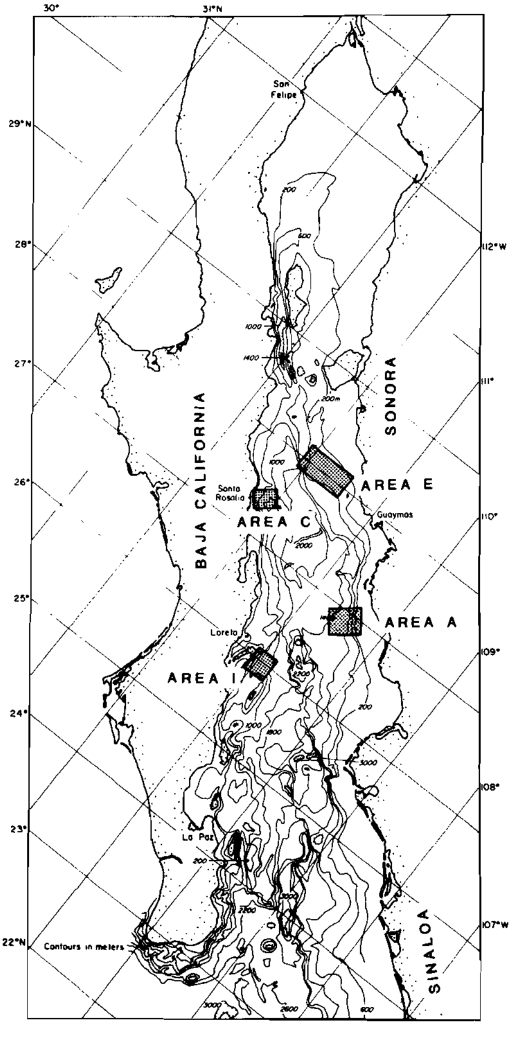

Fig. 1 Generalized bathymetry (contours in meters) of the Gulf of California and location of coring areas E, C, A, and I.

benthic and planktonic foraminifera in surficial sediments. Further downcore, some cores were barren in foraminiferal carbonate, whereas others contained selected horizons with increased abundances of foraminifera. According to Berger and Soutar (1970), sediments deposited under anoxic conditions in the Santa Barbara Basin off Santa Barbara, California contained better preserved calcareous microfossil shells compared to nearby sediments deposited under oxic conditions.

The first objective of this paper is to test if anoxic sediments in the Gulf of California reveal similar preservational patterns.

Ingle (1967a) stated that "it is apparent that a significant percentage of benthonic foraminiferal specimens found in the deep basins of the Gulf of California have been displaced." Bandy (1961) came to a similar conclusion: his text-figure 7 (l.c.) shows a high proportion of displaced shallow water forams deposited within the anoxic sediment facies; unfortunately, this interval was not closely sampled and conclusions were based on only very few samples. Bandy (1961) and Ingle (1981) found that a significant increase in population densities along a cross-section over the Guaymas Basin was related to the anoxic slope environment on both sides of the Gulf.

Our second objective is to investigate the areal distribution of foraminifera in "young sediments" and to relate these numbers to oceanographic parameters.

The varying abundance and preservation of benthic and planktonic foraminifera downcore (over the last 2000 years), their accumulation rates, and the relationship to paleoclimatic and/or paleoceanographic alterations is our last objective. We want to know whether or not a causal relation exists between variations in water masses, in primary productivity, and in temporal variations of dissolved oxygen in bottom waters, and the accumulation of forams.

MATERIALS AND METHODS

Seven cores were selected for this study; they were collected during two cruises of the H-1 Matamoros into the Gulf of California in 1979 and 1980. These cores were chosen because they cover a broad geographic area, they are representative of cores with "good" surface recovery from the west and the east coast, and because physical and isotopic data are available. The logistics of the cores are given in table 1.

Cores I-39, I-42, and C-22 were collected from the Baja California slope and cores A-2, A-5, E-9, and E-17 were collected from the mainland side

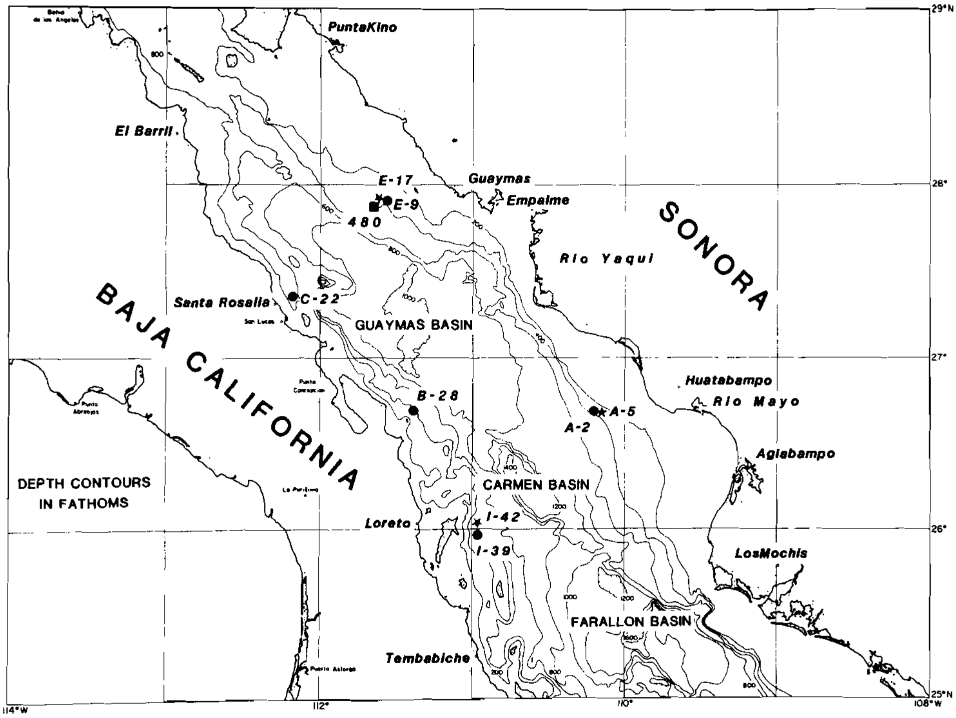

Fig. 2 Location of the seven cores studied in the central Gulf of California. For further information on the cores, see table 1 (closed circles are Box cores, asterisks are Kasten cores).

(figs. 1, 2). All cores were laminated from top to bottom; only core C-22 had bioturbated sections overlying laminated sediments (detailed structural and lithological information is presented in figure 3; see also Schrader and Baumgartner, 1983). Bulk densities were determined for cores E-17, I-39, and I-42 from freshly collected cores. Values for core A-5 were determined in 1983 from collected material kept under refrigerated conditions in sealed plastic bags. The water content values for core A-5 seem to be lower than those from other cores, which is probably due to water loss during storage. This is the reason why we used interpolated values from other cores for core A-5. The interpretation of other bulk density values was based on the assumption that the values of these cores are similar to those from neighbouring cores.

Samples for foraminiferal and silicoflagellate counts were taken by scraping perpendicular to the axis of the core and parallel to the bedding planes, thus collecting around 5 g of sediment. We tried to sample separately intervals with a different color, "gray layers", and intervals which showed some

Core number	Date collected	Type of core	Latitude N	Longitude W	Water depth (in meters)	Total length of core (in cm)	Interval studied in this paper	Water content Bulk density measurement	^{14}C dates	Silicoflagellates
BAV 79 A-5	09/18/79	Kasten	26° 43.4′	110° 07.0′	705	185.0	0–184 cm	Yes	Yes	Yes
BAV 79 A-2	09/18/79	Box	26° 43.4′	110° 08.6′	710	∿ 35	0– 30 cm	No	No	No
BAV 79 E-9	09/19/79	Kasten	27° 53.2′	111° 37.2′	660	192.0	0– 30 cm	No	Yes	Yes
BAM 80 E-17	11/06/80	Kasten	27° 55.2′	111° 36.6′	620	449.5	0– 40 cm 75– 90 cm	Yes	Yes	Yes
BAM 80 I-39	11/15/80	Box	25° 57.4′	111° 00.0′	768	36.0	0– 30 cm	Yes	No	Yes
BAM 80 I-42	11/15/80	Kasten	26° 00.5′	110° 59.0′	745	237.0	0– 30 cm	Yes	Yes	Yes
BAV 79 C-22	09/24/79	Box	27° 24.2′	112° 11.5′	576	53	0– 30 cm	No	No	Yes

TABLE 1 Logistics of cores studied.

coarse grains at their lower base. Slides for silicoflagellate analysis were prepared from uncleaned material (see Schrader and Baumgartner, 1983). Silicoflagellate parameters were calculated using the definitions listed in table 2.

$$(1)\quad \mathrm{EQP} = \frac{\textit{D. calida} + \textit{D. spec. A}}{\textit{D. calida} + \textit{D. spec. A.} + \textit{D. spec. B.} + \textit{O. pulchra}}$$

[EQP = Equatorial Pacific]

$$(2)\quad \mathrm{CC} = \frac{\textit{D. speculum} + \textit{D. epiodon}}{\textit{D. speculum} + \textit{D. epiodon} + \textit{O. pulchra} + \textit{D. spec. B}}$$

[CC = California Current]

$$(3)\quad \mathrm{GP} = \frac{\textit{O. pulchra}}{\textit{O. pulchra} + \textit{D. messanensis} + \textit{D. spec. B.} + \textit{D. epiodon} + \textit{D. calida} + \textit{D. spec. A.}}$$

[GP = Gulf Productivity]

$$(4)\quad \mathrm{G/O} = \frac{\textit{O. pulchra} + \textit{D. spec. B.} + \textit{D. messanensis}}{\textit{O. pulchra} + \textit{D. spec. B.} + \textit{D. messanensis} + \textit{D. epiodon} + \textit{D. calida} + \textit{D. spec. A.} + \textit{D. speculum}}$$

[G/O = Character Gulf/Non-Gulf]

TABLE 2 Definition of Silicoflagellate parameters used to interpret past oceanic fluctuations.

Foram samples were freeze-dried and weighted, and chemically and mechanically treated to concentrate foraminifera. In order to remove opal, samples were gently boiled for two to three hours in a 0.8 molar solution of sodium-carbonate (85 g/L Na_2CO_3). To remove the remaining fine debris, the samples were gently wet-sieved over a 63 μm sieve. Fecal material and other organic sheeting was removed by adding an equal volume of buffered concentrated hydrogen peroxide, leaving the samples at room temperature until all organic material was disintegrated. Samples were then gently wet-sieved again over 63 μm, dried and transferred into standard foraminiferal counting trays. The coarse fraction (> 63 μm) was analyzed and notations made regarding major components. The taxonomy followed Uchio (1960), Bandy (1961), Harman (1964), Phleger (1964), Ingle (1967a) and Matoba and Yamaguchi (1982). Preservation was defined as poor when most individuals were broken and as good when most forams showed no, or very little, breakage and fragmentation of their last chambers.

Individual laminae were counted downcore in 2 cm wide increments using

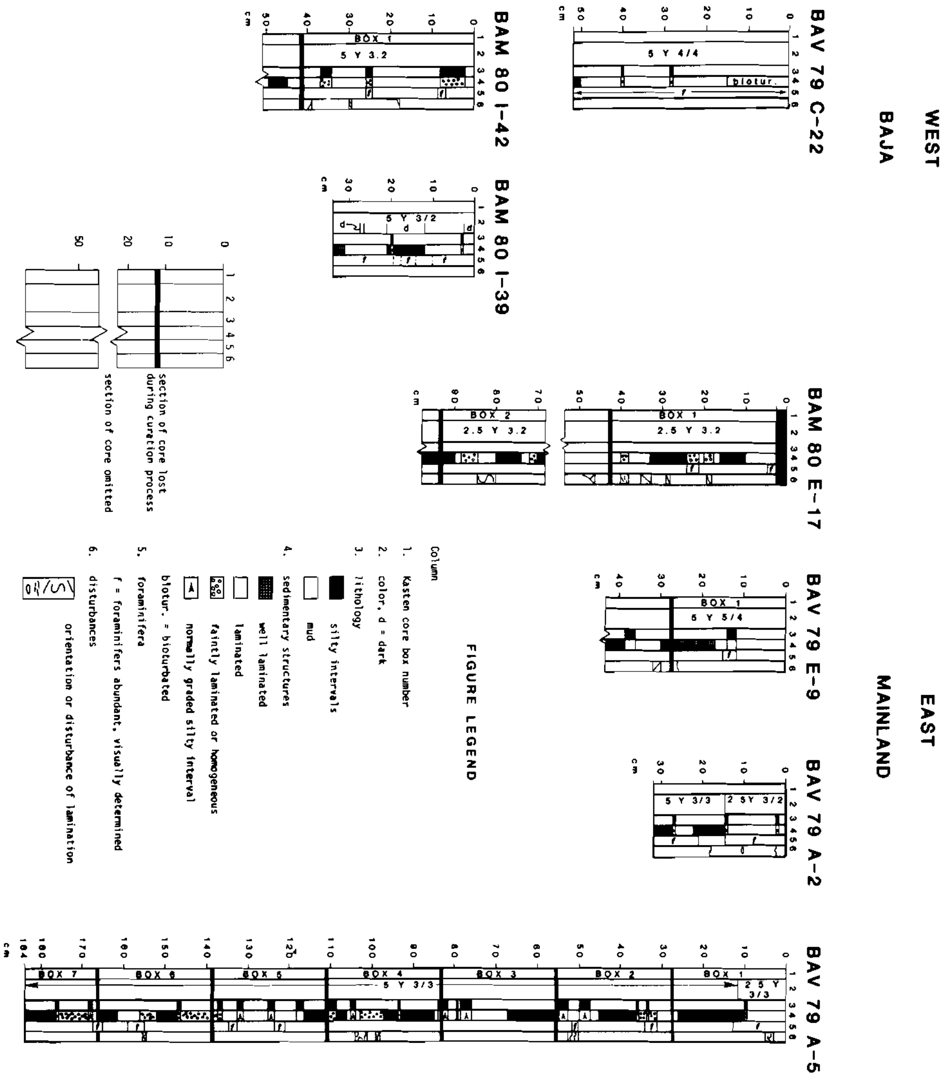

Fig. 3 Generalized lithologies of cores; depth scale in cm. Columns 1–6 refer to: 1) Kasten core subsampling tray number; 2) color, Munsell color chart; 3) lithology (black intervals: silty, white intervals: clayey); 4) sedimentary structures (open circles: homogeneous and/or very faintly laminated, cross-hatched: laminated; black arrows point to graded silty/sandy intervals); 5) f: occurrence of benthic foraminifera; 6) occurrences of disturbances; offset of laminae, overturn of laminae, interruption a.o. Note that top 15 cm of core C-22 are strongly bioturbated and not laminated.

a 5-time magnifying lens. Portions which were lost during the curation process (the thick black lines between joining boxes) were interpolated using averaged laminae numbers above and below that interval. These laminae counts were used to establish a laminae-varve chronology. The O-horizon and/or locking horizon of 1910 (see Schrader and Baumgartner, 1983) was utilized to establish a downcore reference horizon independent of loss of surface material. Average sedimentation rates are listed on table 3.

Core	Interval (cm)	Sedimentation rate in cm/yr
BAV 79 A-5	0–180	0.11
BAV 79 E-9	0–120	0.10
BAM 80 E-17	0–120	0.10
BAM 80 I-42	0–237	0.08

TABLE 3 Average sedimentation rates of Kasten cores studied, based on lithostratigraphy, varve chronology, and ^{14}C dates.

Individual sedimentation rates determined by varve counts and a few ^{14}C dates were used to calculate accumulation rates using the following formula (Dymond and Veeh, 1975):

$A = N \cdot S \cdot \rho\ (100 - W)$, in which

A = accumulation rate in number/cm^2/yr

N = number forams/gram dry sample

ρ = wet bulk density in g/cm^3

W = water content in %

S = sedimentation rate in cm/year

(values are not salt corrected)

Abundance of sand-sized terrigenous grains (mostly quartz, feldspar, and mica) was determined by counting the number of grains on one of the sixty grid areas of the slide, after the grains were evenly distributed over the slide surface. The number of grains per grid was multiplied by 60 to estimate the total number of grains on the entire slide. The estimated total was then divided by the dry weight of the original sample. We used this number to determine possible downslope transport by either turbidity currents or major flooding events of the type described by Gorsline and Emery (1959) and Soutar and Grill (1977) from the Santa Barbara Basin.

Silicoflagellates

Silicoflagellates were counted in all cores from continuous, slightly overlapping channel samples. They are used in this paper to define the stratigraphy and the correlation of cores, and to record surface parameters and their changes through time. Floral characteristics and ratios (table 2) are defined in order to interpret past changes in productivity and in ocean conditions through time. The procedure is based on results documented in Schrader and Baumgartner (1983), Juillet et al. (1983), and Murray and Schrader (1983). Changes in productivity in all cores for the last 300 years are described in figure 4. Figure 5 illustrates changes in three cores over time intervals of 2000 years (for definition of parameters, see table 2; note changes in definition from previously published papers).

Silicoflagellate productivity ratios are interpreted to reflect "real" changes in total primary productivity as determined by studying a large collection of

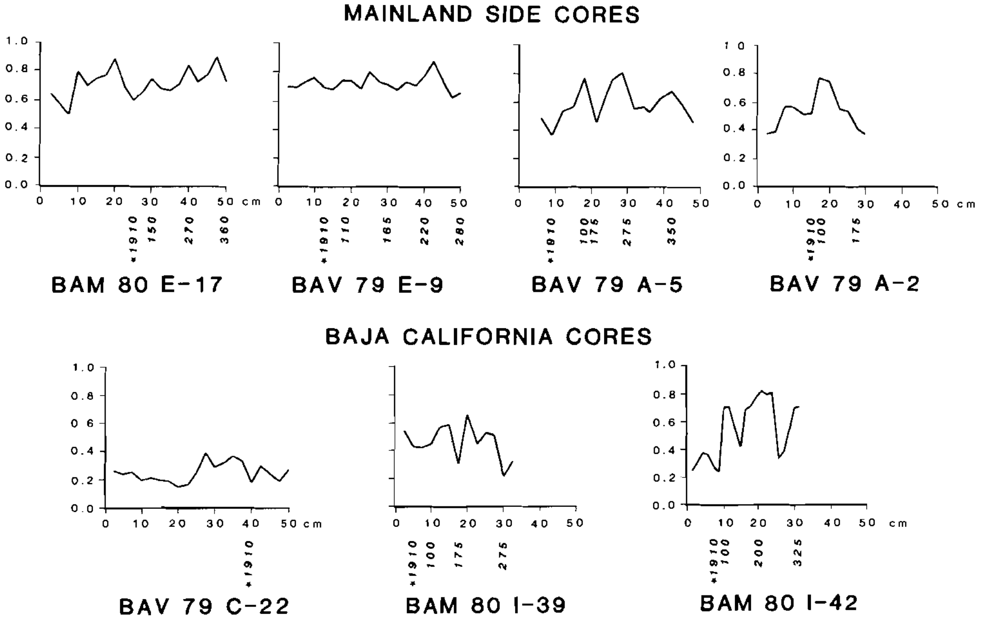

Fig. 4 Silicoflagellate Productivity Ratio in the upper 50 to 30 cm of the seven cores studied. Position of "locking" horizon 1910 (= 70 years) determined by varve counting, cross-correlation, and floral evidence. Values in italics are years before 1980 and give relative age of specific horizons.

phytoplankton samples during two seasons. Highest average values over the last 300 years are found in Area E (average 0.7), followed by Area A (average 0.6), Area I (average 0.5), and Area C (average 0.3).

Primary productivity in the southern Gulf is high (Zeitzschel, 1969) with values of 0.53 g C/m^2/day for the areas bounding the Guaymas Basin, measured during December. Based on our data, averaged productivity values over 10–25 years should be highest on the mainland side, with a decreasing gradient from North to South.

Changes over the last 2000 years are plotted in figure 5; to the left, a tentative age scale is presented with 70 being the 1910 horizon. Major fluctuations can be traced from one core to the next; the tentative time scales based on lamina-varve chronology, ^{14}C averaged sedimentation rates, and distinct lithologic changes correspond very well. The lows in the curves of figure 5 represent times when more surface Pacific and/or California Current waters entered the Gulf, which periods coincided with a decrease in primary productivity. During such periods sedimentation rates decreased, which is expressed by an increase in the number of laminae per core length (see fig. 3).

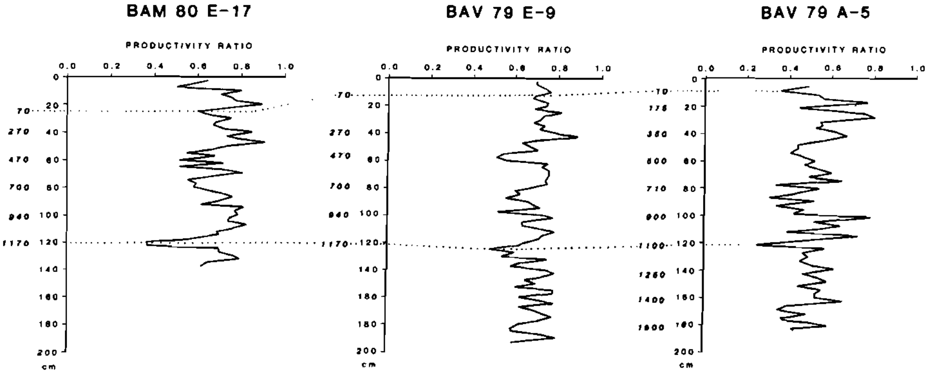

Fig. 5 Silicoflagellate Productivity Ratio in the upper 100 cm of cores from the mainland side. Position of "locking" horizon 1910 (= 70 years) determined by varve counting, cross-correlation, and floral evidence. Values in italics in front of depth scale are years before 1980 and are relative ages of horizons. Note the good correlation of horizon 1170 with a pronounced low ratio.

Abundance of Foraminifera

Foraminifera generally occur in low numbers in the well laminated sections of IPOD-DSDP Leg 64, Site 480 (fig. 2); they are abundant over those sections showing mottling and bioturbated sediments (Crawford and Schrader, 1982). A similar pattern is found in recent sediments (fig. 6). The bioturbated topsection in core C-22 has very high numbers. Cores I-39 and I-42 contain high numbers at the top; a drastic drop can be observed at around 20 cm depth, which is followed by a steady increase further downcore. Cores from area E have high numbers in near-surface sediments; numbers drop to zero below 30 cm. Cores from area A start with high surface values, the values decrease to zero around 20 cm and then increase below.

Visually determined horizons with higher numbers of foraminifera (fig. 3) from cleaned, untreated core surfaces can be used to determine general abundance fluctuations. These horizons are mostly full of benthic and planktonic forams with numbers as high as 50,959 individuals per gram dry sediment (Core I-39). Except for the near-surface layers, such horizons have distinct lithologies: they consist of indistinctly, mostly very finely laminated, and partially homogeneous sediments.

Exceptions on this general pattern are due to the problems in recovery by either Box or Kasten coring of near-surface material, i.e., the top 5 cm (Core E-9, fig. 6, is a good example).

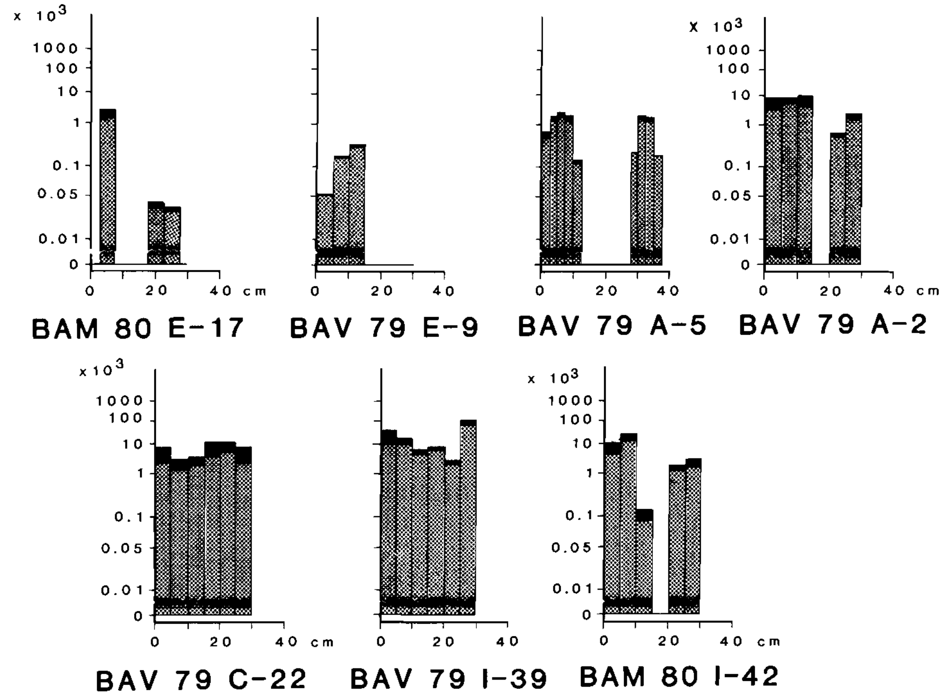

Fig. 6 Abundances of benthic plus planktonic foraminifera in the top 30—40 cm of the seven cores studied. Note abundance scale in log X 10^3.

SAMPLES																	
DEPTH IN CM VARIABLES	0 2.5	2.5 5.0	5.5 7.5	7.5 10.0	10.0 12.5	28.5 30.5	30.5 33.0	33.0 35.5	35.5 38.0	45.5 47.0	47.0 50.0	50.0 53.0	72.0 74.5	74.5 77.0	84.5 87.0	87.0 89.5	89.5 92.0
Dry weight of sample (g)	1.0	1.0	2.2	1.8	1.6	1.6	1.7	1.5	1.2	1.4	3.4	2.1	2.2	2.1	1.7	1.7	2.0
Number of Benthic Forams/g/Dry sample	732	2448	2681	2085	200	438	2693	2508	345	271	925	172	97	1228	254	1384	39
Number of Planktonic Forams/g/Dry sample	166	434	313	725	8	0	81	172	5	3	75	7	1	0	0	0	0
Abundance of Sand Sized Terrigenus	2640	900	109	533	188	188	280	40	1650	6000	∞	8475	2000	∞	1500	1200	1700
Preservation of Forams	3	3	2-3	2-1	2-3	3	2	1	3	3	2	2-3	2	1-2	3	2-3	2-3
Ratio of Planktonic/Benthic Forams	0.227	0.177	0.117	0.270	0.040	x	0.030	0.069	0.014	0.011	0.081	0.041	0.010	x	x	x	x
Abundance of Major Benthic Forams:																	
Bolivina seminuda	+++	++	++	+	++	+	++	-	++	++	+	-	+	-	-	-	-
Bolivina subadvena	++	-	+	+	+	+++	+	+	++	+++	-	++	+++	++	+++	++	+++
Buliminella Tenuata	++	++	++	++	+++	+++	+++	++	+++	+++	-	+++	++	+++	+++	+++	+++
Pseudoparrella sp. A	-	+++	+++	+++	+++	-	+++	+++	+++	+	+++	+	-	+++	++	+++	0
Cassidulina subcarinata	-	+	++	-	+	0	+	-	-	-	0	-	0	-	0	-	0
Cassidulina tumida	+	-	+	-	-	0	-	+	0	0	-	+++	-	+	0	0	0
"Islandiella" cushmani	+	-	++	-	+	-	+	-	0	+	-	+	-	++	0	-	0
Suggrunda eckisi	-	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0
Nonionella stella	-	-	0	-	0	0	-	-	0	0	-	0	0	-	0	0	0
Brisalina argentea	+	-	-	-	-	0	-	-	-	0	-	0	0	0	0	0	0
Brizalina interjuncta	-	-	-	-	0	0	0	-	0	0	0	0	0	0	0	0	0
Abundance of Major Planktonic Forams:																	
Globigerina bulloides	++	++	+	+++	-	0	+	+	-	-	++	-	-	0	0	0	0
Globigerina falconensis	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0
Globigerina quinqueloba	-	-	-	-	0	0	-	-	0	0	-	0	0	0	0	0	0
Globorotalia fimbriata & G. Cultrata	-	+	-	-	0	0	-	0	0	0	-	-	0	0	0	0	0
Pulleniatina obliquiloculata	-	-	-	-	0	0	0	-	-	-	-	-	-	-	-	-	-
Globigerinoides ruber elongatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

SAMPLES	BAV-79 A-2					BAV-79 E-9			BAV-79 E-17			BAM-80 I-39		
DEPTH IN CM VARIABLES	0 5.0	5.0 10.0	10.0 15.0	20.0 25.0	25.0 30.0	0 5.0	5 18.0	10.0 15.0	2.5- 7.5	17.5- 22.5	22.5- 27.5	0 5.0	5.0 10.0	10.0 15.0
Dry weight of sample (g)	1.5	2.0	1.7	1.4	1.8	0.6	0.4	0.4	0.6	1.0	0.6	1.0	0.4	0.4
Number of Benthic Forams/g/Dry sample	6392	7158	6268	804	3044	67	313	438	2786	44	567	29018	18580	8060
Number of Planktonic Forams/g/Dry sample	1528	930	2929	26	467	0	0	3	2767	1	7	27141	11595	120
Abundance of Sand Sized Terrigenus	5500	900	4300	343	770	0	0	0	0	0	0	0	24000	1400
Preservation of Forams	1-2	1-2	1	2-3	3	2	2	3	1	3	1-2	1	2-3	2-3
Ratio of Planktonic/Benthic Forams	0.239	0.130	0.467	0.032	0.153	x	x	0.007	0.993	0.023	0.012	0.910	0.624	0.015
Abundance of Major Benthic Forams:														
Bolivina seminuda	+++	++	+++	++	+++	++	++	++	+++	+	++	++	+++	++
Bolivina subadvena	++	++	+++	++	++	+	++	+	+++	-	++	+++	++	++
Buliminella Tenuata	++	+++	++	++	+++	-	++	+	+++	++	+++	+++	+++	++
Pseudoparrella sp. A	++	++	++	+++	+	-	0	++	+	-	0	++	++	+++
Cassidulina subcarinata	+	+	++	+	-	-	0	-	+	0	0	++	+	+
Cassidulina tumida	++	++	++	+	+	0	0	-	++	0	-	++	+	+
"Islandiella" cushmani	0	0	0	0	0	0	0	0	-	0	0	0	-	0
Suggrunda eckisi	0	-	-	0	0	0	0	0	-	0	0	-	-	0
Nonionella stella	0	-	0	0	-	0	0	0	0	0	0	0	-	0
Brisalina argentea	+	-	-	-	0	0	0	0	+	0	0	+	+	-
Brisalina interjuncta	+	-	0	+	0	0	0	0	+	0	0	+	-	0
Abundance of Major Planktonic Forams:														
Globigerina bulloides	+++	++	+++	+	++	0	0	-	+++	-	0	+++	+++	+
Globigerina falconensis	+	+	-	0	0	0	0	0	+	0	0	-	+	0
Globigerina quinqueloba	-	+	-	-	0	0	0	0	-	0	0	+	-	-
Globorotalia fimbriata & G. Cultrata	-	-	+	-	0	0	0	0	-	0	-	+	-	0
Pulleniatina obliquiloculata	-	-	+	0	-	0	0	0	-	0	0	+	-	0
Globigerinoides ruber elongatus	0	-	-	0	-	0	0	0	-	0	0	-	-	0

TABLE 4 Data of all cores and samples studied.

BAV-79
A-5

108.5 110.5	118.5 121.0	121.0 123.5	123.5 124.5	124.5 125.5	125.5 128.0	128.0 130.5	130.5 131.5	131.5 132.5	132.5 135.5	135.0 137.5	137.5 140.0	140.0 142.5	142.5 145.0	145.0 146.5	147.5 150.0	150.0 152.5	152.5 155.0	155.0 157.5	157.5 160.0	160.0 162.5	162.5 165.0	165.0 167.5	167.5 168.5	168.5 169.5	172.0 174.5	174.5 177.0
1.8	2.0	1.9	1.4		1.5	1.7	1.0	1.2	1.9	1.9	1.7	1.6	1.8	0.8	1.7	1.6	1.6	1.6	1.7	1.5	1.6	1.5	0.7	0.5	1.2	1.4
227	2160	2023	96	855	37	1311	2870	737	3301	408	750	621	1478	261	485	986	918	1210	2824	3064	1123	2602	1271	230	243	80
0	6	93	19	0	0	5	5	0	118	5	0	0	0	0	1	1	0	0	89	5	0	99	89	14	0	0
12 000	2000	790	600	17 000	19 000	1100	180	∞	∞	19 000	1400	525	1000	1350	1024	2700	1200	850	6800	680	3300	2000	8000	6600	1600	3500
2-3	1	2	1-2	1-2	3	1	1-2	2	2	2	2	2	1	1-2	2	2	2	1-2	1-2	2	2-3	2	2-3	2-3	3	3
x	0.003	0.046	0.198	x	x	0.004	0.002	x	0.036	0.012	x	x	x	x	0.002	0.001	x	x	0.032	0.002	x	0.038	0.070	0.061	x	x
++	+++	+++	+	++	+++	+++	++	+++	++	++	+	++	+++	++	+	+	+++	++	++	++	+	++	++	+++	+	0
++	++	++	+		++	+	+	+	-	+	+++	++	++	++	+++	+++	+++	++	++	+	+	-	-	-	++	+
+++	++	++	+	++	0	+++	+++	++	++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	++	++	++	++	+	+++	+++
++	+++	++	0	+	0	+++	+++	++	+++	+++	++	++	++	++	-		-	++	++	+++	+++	+++	+++	++	0	0
0	-	+	+++	++	0	-	-	0	-	-	0	-	-	-	0	-	0	-	-	-	-	+	++	++	0	0
-	-	+	+++	-	0	+	0	-	+	+	0	-		-	0	-	-	+	++	++	-	+	+	+	0	0
+++	+	++	++	++	0	+	++	-	++	++	-	+	+	+	-	-	+	+	+	+	+	++	+++	+	0	+
0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	-	0		0	-	+	-	+	-	-	-	-	0	0	-	-	-	+		-	-	-	-	0	0
0	-	-	-	-	0	0	-	-	-	-	0	-	-	0	0	0	0	-	+	0			-		0	0
0	0	0	0	-	0	0	0	-	-	-	0	0	-	-	0	-	0	-	-	-	-	-	-	-	0	-
0	0	+	-	0	0	0	0	0	+	0	0	0	0	0	0	0	0	-	-	-	0	+	+	-	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	-	0	0	-	-	0	+	-	0	0	0	0	-	-	0	-	-		0	-	-	-	0	0
-	-	-	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0
0	0	0	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

BAV-79
8C-22

BAM-80
1-42

15.0 20.0	20.0 25.0	25.0 30.0	0 5.0	5.0 10.0	10.0 15.0	15.0 20.0	20.0 25.0	25.0 30.0	0 5.0	5.0 10.0	10.0 15.0	20.0 25.0	25.0 30.0
0.6	0.7	0.4	1.1	1.1	1.2	1.2	1.5	1.9	0.7	1.0	0.5	0.8	0.7
9740	4126	12300	4745	2538	3747	6810	7216	4850	8354	24283	148	2015	3120
20	74	4780	4852	1861	1953	7420	6552	3556	6102	13296	224	30	94
1800	500	0	6900	11000	18000	40000	35000	41000	14000	2400	5160	900	1460
3	2	1-2	1-2	1-2	3	2	2	2	1-2	1-2	2-3	1-2	2-3
0.002	0.018	0.389	1.023	0.733	0.521	1.040	0.908	0.733	0.730	0.547	1.514	0.015	0.030
++	++	++	+++	++	++	++	++	+	+++	++	+	++	++
++	++	++	+++	+++	++	+	+	+	++	+	+	++	++
+++	++	+++	++	++	++	+++	++	+++	+++	++	+	++	++
+++	-	++	+++	+++	0	+++	+++	+++	+++	+++	++	++	+++
+	++	++	+	+	+	++	0	-	++	++	0	+	0
+	-	+	-	+	-	-	0	0	++	+	0	-	-
0	0	0	0	0	0	-	-	0	-	-	0	0	0
0	-	0	-	-	-	0	-	-	-	-	0	0	0
0	0	-	-	0	0	-	0	-	0	0	0	0	0
0	-	-	+	-	+	+	-	-	+	+	0	0	-
0	0	-	+	-	-	+	+	+	-	-	0	0	-
+	-	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	-	
0	0	-	+	++	+	+	+	+	+	+	-	0	0
-	-	+	++	+	+	++	+	-	+	++	+	-	-
0	0	-	+	+	-	++	++	++	-	-	-	0	0
0	0	-	+	+	-	++	++	++	-	-	-	0	-
0	0	0	0	-	0	-	-	0	0	0	-	0	0

Note: Sample with less than 30 foraminiferal specimens per gram dry sample weight are not included into this listing.

Ratio of Planktonic/Benthic Foraminifera:

X = not calculated

Abundance of Forams found:

+++	> 20%	abundant
++	10-20	common
+	10-4	frequent
-	< 4	few
0		absent

Preservation

1	well preserved
2	moderately preserved
3	poorly preserved

Foraminifera

General faunal trends are documented in table 4; except for Core A-5, we used a semiquantitative approach to calculate abundances. Planktonic foraminifera never exceed abundances of benthic forams. The planktonic/benthic foram ratios never exceed values over 0.27 (Core I-42). The planktonic associations are dominated by the following species: *Globigerina bulloides, G. falconensis, G. quinqueloba, Pulleniatina obliquiloculata,* and *Globigerinoides ruber.* The planktonic forams are most abundant in cores from the Baja side. Here, a mixture of cold and warm water species was observed, whereas the fauna on the mainland side is dominated by cold water species. The mixture of cold and warm water species might be the result of the seasonal character of upwelling and of the more pronounced oceanic character on the Baja side, or it may be defined by a stronger influence of Pacific Ocean waters penetrating along the Baja side into the Gulf.

A large number of planktonic samples revealed only a few foraminiferal specimens, which indicates that there is, in general, a low standing stock in the neritic – nearshore environments of the Gulf. Apparently the Gulf does not support a large standing stock of planktonic forams.

Most specimens recovered from sediments are highly fractionated; planktonic specimens are only abundant over those intervals where benthic foraminifera are common. Bandy (1961) argues that planktonic species are stenohaline and would not be able to compete successfully in an area with marked salinity and temperature variations.

The benthic foraminiferal fauna is characterized (compare table 4) by low diversity and by the predominance of a few species preferentially florishing under low oxygen conditions: *Nonionella stella, Bolivina seminuda, Suggrunda eckisi, Brizalina argentea, B. interjuncta, B. tenuata, Cassidulina tumida,* and *C. subcarinata* (Matoba and Yamaguchi, 1982). All cores lack major changes in the general composition downcore. Core C-22 with its bioturbated top section contains larger individuals as compared with the other cores, but it does not show differences in the general composition. The majority of the species are interpreted to be autochthonous; we found only traces of displaced shallow shelf, upper slope individuals (e.g., *Buliminella elegantissima*) in layers with graded sediments which might represent turbidites. The discrepancy concerning the depth distribution of *Nonionella stella* (Phleger, 1965) cannot be solved in this paper; we followed the broader interpretation of Matoba and Yamaguchi (1982), who listed a depth range of 10 to > 1000 meters. Differences in species composition between west and east cores are very small and we were unable to discover any major trends.

Accumulation Rates

Accumulation rates were calculated for two time horizons: 1910 and 1705. These horizons were selected because they might have been deposited under very similar oceanographic conditions, marked by a high influence of open Pacific and/or California Current surface water penetrating into the southern Gulf; they were also selected because their downcore position was relatively easy to determine by litho and biostratigraphy. Wet bulk densities of 1.1 g/cm^3 and water contents of 84% were used for those cores for which no physical data were collected (values were taken from Donegan and Schrader, 1982). Sedimentation rates were determined individually only for the sampling interval covering the 1910 and 1705 horizons. These differ from averaged values, since sedimentation rates vary strongly over short periods of time (see Schrader and Baumgartner, 1983).

Core	% water	Wet Bulk Density (g/cm^3)	Sedimentat. rate (cm/year)	Accumul. rate "1910"	Accumul. rate "1705"
C – 22	84*	1.1*	0.58	1022	–
I – 39	79	1.2	0.11	1999	599
I – 42	83	1.1	0.09	707	82
E – 17	84	1.1	0.14	17	0
E – 9	84*	1.1*	0.18	17	0
A – 2	84*	1.1*	0.15	288	–
A – 5	84*	1.1*	0.23	263	120

* values interpolated, see Donegan and Schrader, 1982.
(–) values not available, core younger than 280 years.

TABLE 5 Accumulation rates of foraminifera at two chronostratigraphic horizons, "1910" and "1705".

Table 5 demonstrates the dramatic drop in accumulation rates from near-surface sediments, i.e., the 1910 horizon, to older horizons, in this case only around 20 cm below the previous. No values are available for the 1705 horizon from cores C-22 and A-2, since this level was either not analyzed for foraminifera, or was not recovered.

In cores from area E the values drop from low numbers to zero; in cores I-39 a 23%, in core I-42 a 10%, and in core A-5 a 31% decrease is observable. Rates are highest in cores from area I, followed by Area C, Area A, and Area E.

Accumulation rates downcore in core A-5 were similarly determined; bulk densities and water contents might be slightly off, due to evaporation of samples during storage, and late determinations. We assume that, if water loss did occur, this should have influenced all samples equally. Maximum rates of around 300 foram individuals per cm^2 per year were found near the surface of the core; further downcore, maximum numbers were only around 200, a drop of almost 40% (fig. 7).

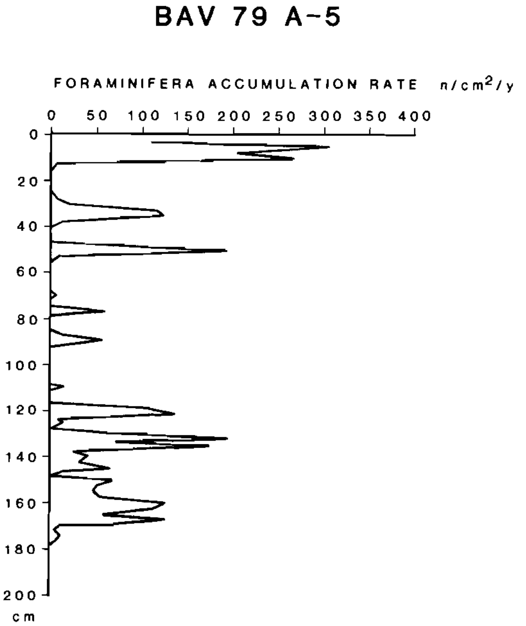

Fig. 7 Accumulation rates of n (planktonic and benthic foraminifera) per cm^2 per year in core A-5.

This general pattern is documented also in cores from Area I, and Area C, whereas cores from Area E are barren in foraminiferal carbonate from below the top 30 cm down to around 400 cm (about 3000 years old).

An almost identical pattern was detected by studying a core from Area B, an area west of Punta Concepcion (26° 42.5′ N–111° 24.5′ W; for core location and lithology, see Schrader and Baumgartner, 1983). This core, B-28, has high foraminiferal (and also high calcareous nannoplankton) abundances over horizons that are time-correlative to horizons with abundant calcareous microfossils in cores from Areas A and I. Thus, the accumulation rates of foraminiferal tests in the Gulf are time-bound and must, therefore, be related to major oceanographic changes.

Carbon-Carbonate Analysis

Dark laminae seem to be enriched in diffuse, opaque, and brownish aggregates of organic matter. Near-surface values for organic matter and carbonate are tabulated in table 6.

Generally, subsurface sediments are rich in organic carbon in the central Gulf, with values of up to 5% for Area E, 4.9% for Area B, 4% for Area A, and 4.4% for Area C.

Downcore values as determined for one core from Area E (E-7) and for one from Area B (B-26) show little variation in C_{org}, but a gradual decrease in carbonate (B-26) from 11% in sample 0–5 to 2% in sample 26.7–28.1 cm.

Core	$\%C_{total}$	$\%C_{CO_3}$	$\%C_{org}$	$\%CaCO_3$
A–5 (0–5 cm)	4.1	0.1	4.0	0.83
B–30 (0–5 cm)	5.7	0.8	4.9	6.67
C–25 (0–5 cm)	4.7	0.3	4.4	2.50
E–10 (0–2 cm)	5.2	0.1	5.1	0.83

TABLE 6 Subsurface composite samples: carbon-carbonate analysis in dry weight percent.

Accumulation Rates and Relation to Oceanographic Parameters

Accumulation rates of benthic and planktonic foraminifera in all cores (except from Area E) reveal a very similar pattern. Horizons with high rates are time-equivalent and they occur over widely-separated areas in the southern

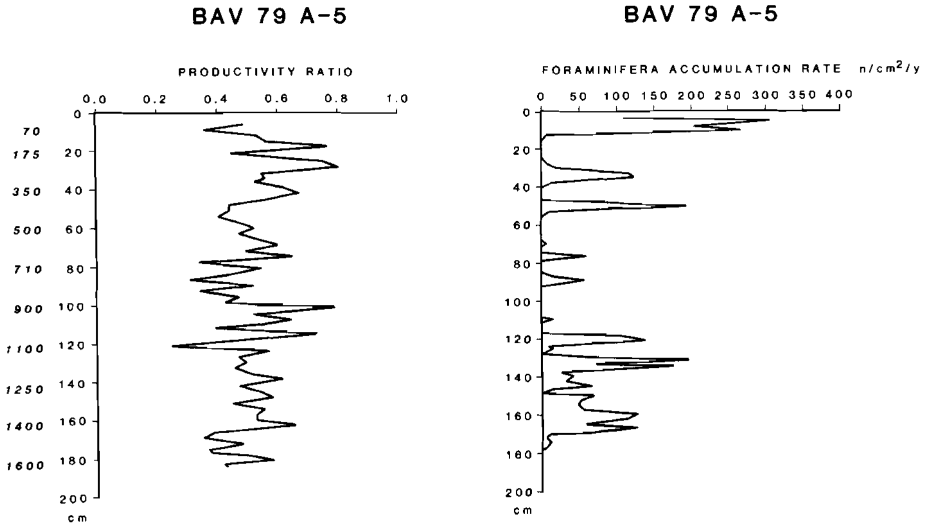

Fig. 8 Accumulation rates of foraminifera and Silicoflagellate Productivity Ratio in core A-5. Letters in italics represent a tentative age scale in years before 1979. Note inverse relationship between the two curves.

Gulf; the same is true for horizons which have low rates. Silicoflagellate analysis indicates that surface water productivity was relatively low during periods marked by high foraminiferal accumulation rates (fig. 8). Intervals which indicate increased surface water productivity by a high silicoflagellate ratio (over 0.6), by very distinctly laminated intervals, and by high sedimentation rates, in core A-5, do not have noticeable foraminiferal carbonate. A general drop of around 30% in the number of foram tests can be observed from near-surface sediments to comparable and older sediments further downcore. All other cores, except those from Area E, show a similar pattern (compare figs. 4 and 6). High values of the silicoflagellate parameter, used to define presence of Pacific / California Current surface water in the central Gulf (table 2), correspond to higher values of the accumulation rates of both benthic and planktonic foram tests. Cores which have, in general, high surface productivity parameter values (over 0.6) are devoid of foraminiferal carbonate below 30 cm.

DISCUSSION AND CONCLUSION

Marine laminated/varved, hemipelagic sediments can be characterized by their high (siliceous) biogenic and terrigenous components, deposited alternately as a result of seasonal input. The biogenic component is primarily opal from diatom tests and only a small fraction is composed of carbonate from foraminifera and calcareous nannoplankton. The carbonate fraction, as we have demonstrated in this paper, can be altered substantially. Some cores contain over their total length carbonate in varying proportions, others have only distinct intervals showing some carbonate, and others are completely devoid of carbonate. Sediments of the latter type are common in the Monterey Formation and in some areas of the Gulf of California.

Results from our study in the Gulf indicate that a strong postburial dissolution process can completely dissolve carbonate present at, or near, the sediment-water interface, even under strong anaerobic conditions. We do not believe that carbonate-free sections, as seen in cores from Area E, were initially without large standing stocks of benthic foraminifera at the sediment-water interface. Standing stocks reported in the literature compare very well with standing stocks that we found. In the Santa Barbara Basin, Phleger and Soutar (1973) found 752 live and dead benthic foraminifera per cm^2; in the Gulf we found, on the average, 620 (average value from 7 core tops). Planktonic foraminifera are poorly preserved in older sediments. Phleger and Soutar (1973), Berger and Soutar (1970), and others state that "fossil benthic assemblages of foraminifera in low oxygen environments induced by high surface production should be characterized by good preservation, abundance of small, thin-shelled tests, and dominance by a few species". This statement should not be accepted without reservation; it is applicable only to a few sections. In his classical paper on the Monterey Formation, Bramlette (1946) states: "calcium carbonate is almost entirely lacking from the thick diatomaceous deposits at Lompoc, and no foraminifera are found there". In further discussing the preservation and dissolution of carbonate tests, we will first discuss surface parameters and keep these separated from the downcore study.

Benthic foraminiferal faunas living under depleted dissolved oxygen conditions (< 2.0 mL O_2/L) can be characterized by their low diversity, by the dominance of only a few species, and by generally thin-shelled, delicate, and small tests (Bandy, 1961; Harman, 1964; Streeter, 1972; Phleger and Soutar, 1973; Douglas and Heitman, 1979; Gorean and Garrison, 1981). Conversely, the relative number of individuals per area is minor. The faunas are very similar in species composition, independent of geographical position. Species best adapted to live under these conditions in the Gulf are: *Bolivina seminuda, Suggrunda eckisi, Nonionella stella, Bolivina subadvena*, and *Buliminella tenuata.* Many of these recent species have homeomorphic equivalents in the Miocene Monterey Formation and elsewhere (Harman, 1964). The preservation of these delicate tests in the upper 5 cm (of undisturbed cores) is mostly excellent, whereas planktonic foraminifera are already etched, broken, and show signs of dissolution.

Downcore, a dramatic change occurs: we observed an overall decrease in the number of benthonic foraminifera in all cases studied. This decrease shows that under dysaerobic bottom water conditions, dissolution of carbonate takes place. This dissolution attacks the total foram population equally, even to the extent that no foram tests are preserved. This contradicts reports from other areas, such as from the California borderland (Douglas and Heitman, 1979). There, selective dissolution effectively removed only some species.

Carbonate preservation in the Gulf is inversely related to primary productivity in the surface waters. The higher the primary productivity rates, the higher the carbonate dissolution. Intervals deposited under such conditions also exhibit the highest sedimentation rates and their (siliceous) biogenic component is dominant. Dunbar (1983) documented significant variations in the amount of carbonate in the Santa Barbara Basin and found a positive correlation between laminae thickness and carbonate accumulation. Parameters similar to those we have used to interpret productivity variations in the past were not applied by Dunbar to the Santa Barbara cores. A general downcore increase of dissolution as observed by us was also found by Dunbar (1983).

LeClaire and Kelts (1982), studying calcium carbonate variation downcore Site 480, retrieved within our Area E, compared their carbonate data with coarse fraction data presented by Crawford and Schrader (1982). They found a general decrease in carbonate content over distinctly laminated intervals, whereas values increased over intervals which were bioturbated. The authors also offered an explanation for carbonate dissolution under oxygen minimum conditions. If the overlying water is completely anoxic, anaerobic sulfate reduction will tend to preserve carbonate (Berner et al., 1970; Dunbar and Berger, 1981). All of our cores from cruise BAM 80 in the central Gulf show bacterial sulfate reduction. Sulfate maxima are found near to the sediment-water interface with values of 28.6 mM/L at 1–5 cm and 29.3 mM/L at 5–8 cm. Values steadily decrease below 10 cm (Hans Brumsack, personal communication, 1983). The few dissolved oxygen values available from the literature indicate seasonal values at 500 m water depth of 0.15 in April, of 0.15 in October, and of 0.10 mL O_2/L in November, 1974 (data from table 1 in Soutar et al., 1981). In case bottom waters are not completely anoxic, the model of carbonate preservation and/or dissolution proposed by Emerson and Bender (1981) might be applied where the rain ratio of organic carbon to carbonate controls this cycling. In the Gulf, carbonate production in the water column and at the sediment-water interface is relatively low. On the other hand the flux of organic matter is extremely high, due to upwelling phenomena, thus providing enough organic matter to actually dissolve all carbonate. The only requirement for this reaction is the availability of oxygen. The differences we see in the Gulf and in our downcore studies might be explained by the availability and/or non-availability of dissolved oxygen. We speculate that areas in the Gulf with very high levels of productivity, which is primarily related to wind-driven processes experience some internal mixing by which oxygen depleted bottom waters are replaced by slightly oxygenated waters. This process does not apply to areas where lower productivity prevails, less intense and long wind periods are absent, and bottom waters are more stagnant. Oxygen minimum depositional environments on slopes should be more frequently and easily affected by this exchange phenomenon than basinal oxygen minimum areas. Part of the carbonate variability (Dunbar, 1983) in the Santa Barbara Basin might be due to the periodic flushing of the basin floor with oxygenated waters (Sholkovitz and Gieskes, 1971). Very similar results are reported by von Stackelberg (1978) for the West Indian coast. He found a drop in carbonate content in his "Bänderschlick" and poorer preservation in comparison to deeper cores.

In conclusion, carbonate derived from foraminifera and calcareous nannoplankton can be occasionally better preserved in oxygen depleted depositional environments. In most cases, complex mechanisms control the dissolution of carbonate in these environments. These mechanisms are related to primary productivity levels, occasional replacement of oxygen depleted water with slightly non-oxygenated waters, and the flux volume of carbonate and organic matter.

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SEASONAL VARIATION OF STABLE ISOTOPES IN *AMPHISORUS* FROM THE GULF OF AQABA (ELAT), RED SEA

B. LUZ, Z. REISS and T. ZOHARY-SEGEV

ABSTRACT

Oxygen isotope ratios in *Amphisorus hemprichii* follow the seasonal temperature cycle and correspond very closely to expected equilibrium values. Carbon isotope ratios are related mainly to seasonal changes in photosynthetic rates of the plant-substrate and possibly also to seasonality in nature and availability of food.

INTRODUCTION

Seasonal variation of stable isotope composition in shells of large porcelaneous, tropical shallow water, symbiont-bearing foraminifera has been shown by analysis of ontogenetic stages of the same specimen by Wefer and Berger (1980) and by Wefer et al. (1981). The latter authors demonstrate that $\delta^{18}O$ in these foraminifera is indicative of the annual temperature cycle despite the fact that they do not form their calcitic shells in isotopic equilibrium with the water. Variations in $\delta^{13}C$ were attributed to "vital effects" considered to be related to symbiont-activity, growth rates and increased metabolism during reproduction.

The present paper reports isotopic results derived from whole specimens of *Amphisorus hemprichii* populations, which were sampled throughout the entire growth cycle. The important parameters for isotopic fractionation have been monitored.

POPULATION DYNAMICS

The specimens analyzed originate from the collections used for a population-dynamics study by Zohary et al. (1980). Information on present-day general conditions in the Gulf of Aqaba is summarized among others by Reiss (1977) and on those at the sampling site (*Halophila* meadows, Wadi Taba, 4 m depth) of *Amphisorus* during the population study, by Zohary et al. (op. cit.). The taxonomy and distribution of *Amphisorus* in the Gulf of Aqaba have been discussed by Hottinger (1977).

The annual growth cycle of *A. hemprichii*, expressed by temporal changes in mean diameter, is shown in figure 1.

The weight per individual (megalospheric) is given in table 1. Test weight is added gradually with age and can be expressed by a regression equation (1) with a correlation coefficient of .998.

$$W_t = 5.97 \times 10^{-8}t^3 + 3.202 \times 10^{-5}t^2 - 1.469 \times 10^{-3}t + 6.44 \times 10^{-2} \qquad (1)$$

where W_t is the estimated weight of an individual t days after start of the generation. As shown in figure 1 and table 1, there is no record for the beginning of generation I. In order to use the results of this generation in deriving equation (1), it is assumed that its beginning stages were identical to those of generation II. The simple growth pattern of *A. hemprichii* makes it an ideal species for modeling and for comparison of the expected equilibrium isotopic composition with actual measurements.

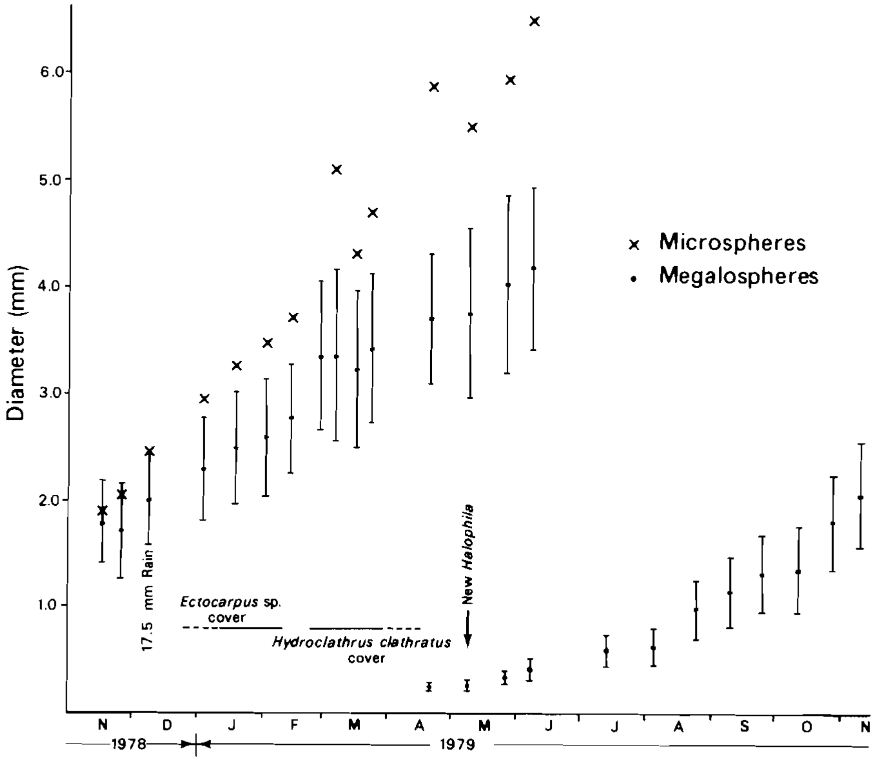

Fig. 1 Annual growth cycle of megalospheric and microspheric *A. hemprichii* generations, expressed by temporal changes in mean diameter (standard deviations of microspheric forms' mean diameter are not included, because of their low frequency in the population). Seasonal algal cover over the *Halophila* meadow is indicated (from Zohary et al., 1980).

Generation	Sampling date (d-m-yr)	Water temp. (°C)	Average specimen weight (mg)
I	16–11–78	25.0	.849
	8–12–78	23.0	1.059
	3– 1–79	22.5	1.500
	18– 1–79	21.7	1.850
	1– 2–79	21.6	1.896
	13– 2–79	21.8	2.360
	27– 2–79	21.4	2.597
	6– 3–79	21.3	2.740
	23– 3–79	21.8	3.310
	21– 4–79	22.0	4.500
	8– 5–79	23.1	4.670
	26– 5–79	23.6	5.620
II	26– 5–79	23.6	.067
	13– 7–79	25.7	.103
	4– 8–79	26.0	.100
	24– 8–79	26.2	.266
	9– 9–79	26.0	.360
	24– 9–79	25.9	.360
	11–10–79	25.7	.567
	9–11–79	25.3	1.042

Table 1. Water temperature and weight of living *Amphisorus hemprichii* (megalospheric)

EXPERIMENTAL PROCEDURE

Specimens for the present study were randomly collected from a 4 m deep sea-grass (*Halophila*) meadow. The samples for isotopic analyses were washed in water and dried at room temperature. *A. hemprichii* was separated and sieved into different size fractions. Subsamples of 1–5 individuals were crushed under methanol, vacuum-roasted at 450°C for 30 minutes, then reacted with purified H_3PO_4 at 50°C. The evolved CO_2 gas was analysed for isotopic composition on a Micromass 602C mass-spectrometer. The details of this procedure are described by Shackleton (1974). Conversion to PDB was made by calibration of the machine reference-gas with the Cal-Tech PDB-IV standard.

In addition to shell isotopic composition, a few analyses of $\delta^{18}O$ of the seawater and of the dissolved bicarbonate were run by following the procedures of Craig and Gordon (1965) and of Kroopnick (1974). The measurements were made with respect to the same machine reference as used for carbonates. In this manner possible problems due to inaccurate interlaboratory calibrations are avoided. The $\delta^{18}O$ of the seawater was found to be very stable, viz. 1.9‰ (vs. SMOW) on the average. The $\delta^{13}C$ values of the dissolved bicarbonate range between 1.3–2‰ PDB. A few samples of *A. hemprichii* were analyzed by an atomic absorption spectrophotometer in order to determine the $MgCO_3$-content of the shells, which is 12.65 mole %.

Equilibrium composition of Mg-calcite can be calculated by equations (2) and (3) by substitution of the appropriate $\delta^{18}O$ for the water, and $\delta^{13}C$ for dissolved bicarbonate, and the water temperature (table 1). Equation (2) is based on Craig (1965) and on Tarutani et al. (1969). Equation (3) is from Emrich and others (1970).

$$\delta^{18}O_{eq}\ (‰\ \text{PDB}) = \delta^{18}O_{water}\ (‰\ \text{SMOW}) + 15.93 - (130.95 + 7.69T)^{\frac{1}{2}} + 0.06M \qquad (2)$$

$$\delta^{13}C_{eq}\ (‰\ \text{PDB}) = \delta^{13}C_{bicarbonate}\ (‰\ \text{PDB}) + 1.15 + 0.035T \qquad (3)$$

where T is the temperature in °C and M is $MgCO_3$-content in mole percent.

RESULTS

The results are listed in table 2, and plotted in figure 2. Separate measurements of different size classes, of microspheric and of megalospheric forms, all seem to fall within the same range, and all do not seem to deviate from equilibrium composition. The only exception to this is the isotopic composition of embryonic stages, which fall well below the equilibrium range (table 2). The weight of the embryonic stages (on the order of a few μg) is rather small and thus contributes very little to the average composition of even small specimens. The only indication of the effect of the embryonal composition is found in very young specimens collected on May 16, 1979 (table 2). In two analyses from this date the carbon isotopic composition seems lighter than normal.

DISCUSSION

Oxygen isotopes

The age of the specimens analyzed is on the order of months, and thus the data represent an integration of changing environmental conditions. In order to account for this integration in comparing the isotopic observations with expected values, a model of isotopic composition is used (eq. 4).

Sampling date (d-m-yr)	Amerage specimen diameter (mm)	$\delta^{18}O\,^0/_{00}$ vs. PDB	$\delta^{13}C\,^0/_{00}$ vs. PDB		Generation
16–11–78	1.3	.45	4.06		
	1.8	.68	3.84		
	2.6	.40	3.42		
8–12–76		.78	3.69		
		.36	3.83		
18– 1–79	1.8	.93	3.83		
	3.1	.65	3.39		
	4.0	.91	3.37	M	
	5.2	.65	3.34	M	
1– 2–79		.65	3.45		
		.80	3.38	M	
13– 2–79	1.6	.86	3.94		
	2.3	.74	3.73		
	2.3	1.03	3.58		I
	3.1	.59	3.35		
	3.7	.91	3.20		
	3.7	1.00	3.30	M	
6– 3–79	2.3	.48	3.33		
	3.1	.94	3.41		
	4.4	1.04	3.45		
	6.1	.82	3.45	M	
21– 4–79	2.6	.97	3.25	M	
	4.4	.80	3.57	M	
26– 5–79	4.4	1.02	3.58		
	5.2	1.02	3.51		
	4.4	.87	3.51	M	
21– 4–79	0.2	–3.04	–0.08	P	
26– 5–79	0.6	.77	2.67		
	0.6	.63	2.74		
13– 7–79	0.8	.68	3.82		
4– 8–79	0.4	.64	4.29		
	0.7	.51	4.35		
	0.9	.68	4.53		
	1.1	.70	4.46		
	1.3	.62	4.14		
24– 8–79	0.9	.51	4.18		
	1.2	.78	4.23		
	1.6	.64	4.08		
9– 9–79	0.5	.47	4.03		II
	0.7	.56	3.99		
	1.3	.61	4.33		
	1.6	.43	4.43		
	3.1	.36	4.03		
24– 9–79	0.9	.53	4.54		
	1.3	.54	4.50		
11–10–79	0.7	.68	4.21		
	1.6	.42	4.56		
	1.8	.43	4.22		
4–11–79	1.6	.44	4.17		
27–11–79	1.6	.36	3.90		
17– 4–80	2.6	.95	3.80		

M – microspheric form, P – embryonic stage

Table 2. Shell size and isotopic composition of living *Amphisorus hemprichii*

$$\delta_t = \frac{\delta_{t'} \times W_{t'} + \delta_T\ (W_t - W_{t'})}{W_t} \tag{4}$$

where δ_t is the integrated equilibrium $\delta^{18}O$, t days after start of the generation, δ_T is the $\delta^{18}O$ of equilibrium calcite formed at temperature T (calculated with eq. 2), W_t and $W_{t'}$ are estimates of individual-weight (eq. 1), t and t' days after start of the generation, where t' corresponds to the immediately preceding sampling period.

When plotting the $\delta^{18}O$ data along with the model-curve (fig. 2b) there is a remarkable good fit (with the exception of juveniles which are clearly not in equilibrium). At least part of the deviation from the model-curve can be explained by non-uniform individual growth rates (figs. 1,2b). *A. hemprichii* forms its shell in oxygen isotopic equilibrium.

The fact that certain porcelaneous foraminifera form shells in equilibrium has been first noted by Vinot-Bertouille and Duplessy (1973), and more recent studies indicate that they are at equilibrium or closer to it than lamellar, perforated foraminifera (Erez, 1978; Wefer and Berger, 1980; Wefer et al., 1981), possibly because of different models of shell-formation (Luz and Reiss, this volume). Moreover, the very low photosynthetic rates of symbionts associated with porcelaneous foraminifera seem to have little influence on stable isotopic ratios of the host-shell (Erez, op. cit.). However, there are important cases in which large porcelaneous species are in disequilibrium. It seems that the tendency for disequilibrium depends on the local ecological conditions, e.g. specimens from Elat and from Bermuda are in equilibrium, while those from the Philippines are depleted in ^{18}O. The latter sampling site is located in the tropical region where productivity is higher than in either Bermuda or Elat. This might suggest that enhanced metabolism at higher productivity causes deviation from equilibrium.

Carbon Isotopes

Most of the results (table 2, fig. 2c) fall within the expected equilibrium range (3.2–4.1$^0/_{00}$) or above it. The only exception are embryonic stages which are about 4$^0/_{00}$ lighter than equilibrium calcite. All the specimens analyzed were sampled before reproduction took place and thus cannot be compared with the results of Wefer et al. (1981) for reproductive chambers. The $\delta^{13}C$ values of the "laminate" (nepionic-neanic-ephebic) stage of *A. hemprichii* show the same trend as those of *Cyclorbiculina compressa* from Bermuda, i.e., lower $\delta^{13}C$ during the colder season and in older specimens. The fact that *Marginopora vertebralis* from the Philippines shows an opposite trend, with lower $\delta^{13}C$ in summer, but not towards the end of the laminate

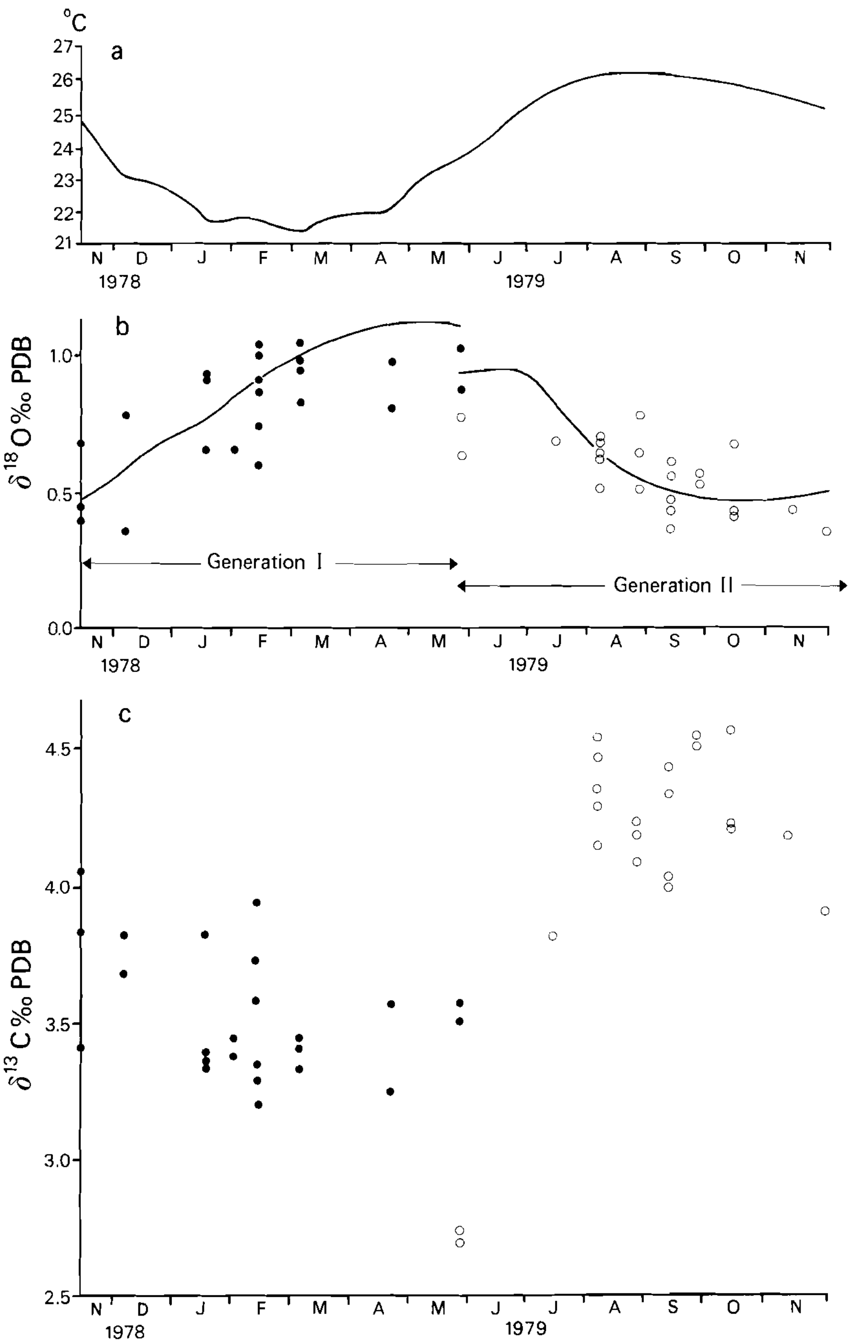

Fig. 2 (a) Water temperature during the sampling period.

(b) δ^{18}O of *A. hemprichii.* Closed circles: generation I; open circles: generation II. The solid curve is a model-derived equilibrium-δ^{18}O.

(c) δ^{13}C of *A. hemprichii.* Closed circles: generation I; open circles: generation II. The equilibrium range is 3.2–4.1‰.

stage (Wefer and Berger, 1980), seems to indicate that the variations depend on the seasonal change in environmental conditions and less so on ontogenetic age.

In the case of the present study it is possible that changes in the microenvironment control part of the $\delta^{13}C$ variations. During spring and summer the substrate-*Halophila* is blooming, and there is good reason to believe that near the leaves to which *Amphisorus* specimens are attached (see Zohary et al., 1980, fig. 2), ^{13}C is enriched in the dissolved HCO_3^- due to preferential ^{12}C consumption for photosynthesis. This can explain the higher than equilibrium values recorded in this period. In contrast to this, $\delta^{13}C$ is within equilibrium range in winter, when thick filamentous algal mats cover the meadow and light penetration is restricted. It is important to note in this respect that growth rates slow down at the same time.

Another possibility is that availability of food, and perhaps $\delta^{13}C$ of the food, changes seasonally (diatoms become very abundant in winter). The rate of metabolism and thus $\delta^{13}C$ of metabolic CO_2 incorporated, may change and affect the carbon isotope ratio of the shell.

The role of microenvironment of *Amphisorus*, *Sorites* and *Peneroplis* on their shell-$\delta^{13}C$ has been demonstrated by Noy (1982). Specimens of these genera are enriched in ^{13}C when living attached to *Halophila* leaves, but depleted (up to $1^0/_{00}$) when attached to stems. Again, photosynthetic uptake of ^{12}C may be suggested as the reason for the leaf-stem difference. On the other hand, the role of availability of different food-sources on the two substrates cannot be excluded.

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PROCESSES DETERMINING THE DISTRIBUTION OF LARGER FORAMINIFERA IN SPACE AND TIME

LUKAS HOTTINGER

RÉSUMÉ

Les grands foraminifères sont 1. liés étroitement aux faciès des dépôts néritiques, 2. restreints à des provinces biogéographiques, et 3. remplacés périodiquement de manière synchrone. Les trois ensembles de processus déterminant ces caractères généraux de leur distribution sont largement indépendants. Des associations d'espèces sont échelonnées selon le gradient de la profondeur et souvent distinctes sur substrat solide ou meuble. Les associations récentes caractérisées par l'habitus de leur coquille sont comparables aux associations fossiles composées de taxons différents. La notion gradient de profondeur cache plusieurs facteurs plus ou moins parallèles qui ont des effets différents sur la vie des foraminifères: lumière (par son effet sur la symbiose et sur la calcification), énergie de l'eau (par son effet sur le substrat et la nourriture), maturation des peuplements et degré de coordination du cycle reproducteur avec le cycle saisonnier. Le provincialisme des grands foraminifères implique des processus de colonisation pendant de longues périodes de temps et le remplacement simultané de nombreuses espèces au cours de l'histoire géologique reflète leur dépendance de la stabilité du milieu.

INTRODUCTION

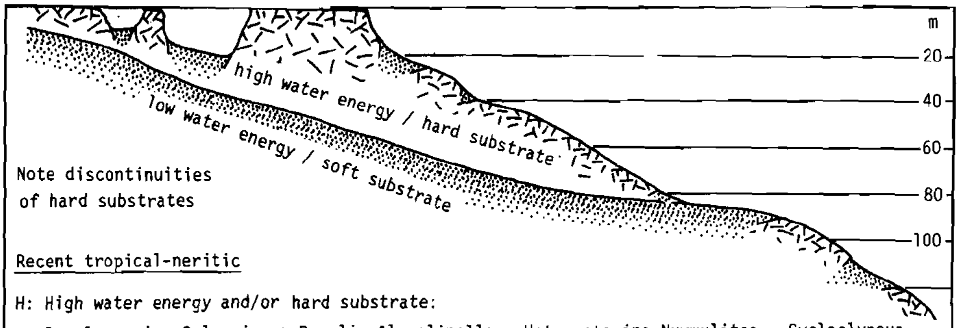
Larger foraminifera are abundant and cover a wide range of neritic environments. They are the best documented of the very few classes of fossils which can be identified at generic level in random sections of hard rocks. Therefore they are most important for rough dating and as indicators of the environment of their deposition. Their well documented, rapid evolution at species level is widely used for detailed biostratigraphic work. In contrast to pelagic foraminifera, their distribution in space and time is narrowly restricted. What are the factors and/or processes determining their distribution? "Facies specificity", "biogeographic limitations" and "frequent synchronous replacement" during earth history characterize in general their complex distribution pattern. These reflect three different and largely independent sets of processes which are roughly outlined here in a somewhat speculative way because precise, quantified knowledge is currently available only on a very limited number of relevant issues.

FACIES SPECIFICITY

Experience from studying the distribution of larger foraminifera in sedimentary rocks teaches us about narrow dependences between facies types and particular associations of genera. Many such facies types were called after the predominant larger foraminifera ("alveolina-" or "nummulites-limestones", "operculina-" or "discocyclina-marls", etc.). In sequences of rocks, the succession of facies-types with its associated genera is often similar. Particular successions in rock sequences interpreted as transgressive may be reversed in contemporaneous regressive series. Repetition of transgressive cycles after shorter or longer time intervals produces repetition of sequences of the associated larger foraminifera, in which equivalents from different time levels may not be represented by identical genera but by foraminifera with a comparable type of shell morphology (Hottinger and Drobne, 1980). From shallow to deeper environments we find conical-agglutinated > discoidal porcelaneous > fusiform porcelaneous > thickly lenticular-perforate > flat lenticular- or discoidal-perforate types (fig. 1).

Similar sequences of associations of larger foraminifera are observed in recent sediments of tropical seas when collected along the depth gradient (Reiss et al., 1977). Light and water energy (Hottinger, 1981) seem to be the most important single factors determining the distribution of the foraminifera with depth. At extreme values, temperature and salinity are limiting factors for all larger foraminifera whereas at intermediate values they have no obvious selective effect. Short-lived extreme values as observed in tidal pools often produce irregularities in shell growth such as the supplementary half disc perpendicular to the original one in discoidal porcelaneous forms.

Mapping the distribution of larger foraminifera in the Gulf of Aqaba revealed a second primary parameter, the nature of substrate, governing the distribution of some groups of larger foraminifera whereas others with relatively smaller shells (*Borelis, Amphistegina*) are indifferent to this factor (Hottinger, 1977). The solid or soft nature of the substrate produces at comparable depth two fundamentally different biota. On solid substrate, bottom covering communities of sessile organisms are dominated by long-lived stony corals in the euphotic zone, and by bryozoans at greater depth (Hottinger and Fricke, in press). On soft substrate, perennial vegetation covers are found to 70 m depth, seasonal covers to 90 m depth. Under the general conditions of the gulf characterized by very low nutrient concentrations in the water column (Klinker et al., 1978) the two main biota have to adopt particular strategies to recycle the nutrients. On hard substrate in the euphotic zone, most organisms have symbionts as means of recycling (Muscatine and Porter, 1977), on soft substrate the organic material produced by the plant cover is recycled by the burrowing community turning over the topmost sediment within a few days (Hottinger, 1977). The distribution of hard and soft substrates depends on an antagonistic system where an advancing front of early diagenetic crystallisation in the subsurface is balanced



Recent tropical-neritic

H: High water energy and/or hard substrate:
Baculogypsina,Calcarina → Borelis,Alveolinella → Heterostegina,Nummulites → Cycloclypeus

L: Low water energy and/or soft substrate. In the deepest section, the H/L difference may be inconspicuous or irrelevant.
Sorites,Amphisorus,Marginopora → Borelis,Alveolinella → Operculina → Heterocyclina

Miocene

H: Baculogypsina → Heterostegina (inv.) → Flosculinella → Nummulites → Cycloclypeus

L: "Archaias",Sorites → Borelis,Flosculinella → Operculina,Planoperculina

Oligocene

H: "Pararotalia" viennoti → Borelis → Nummulites → Heterostegina (inv.) → Spiroclypeus

L: Praerhapydionina → Borelis,Bullalveolina → Nummulites → Heterostegina (ev.) → Operculina

Late Eocene

H: Baculogypsinoides,Fabiania → Borelis → Nummulites,Heterostegina (inv.) → Spiroclypeus
Pellatispira (inv.)

L: Fallotella?,Orbitolites → Borelis → Nummulites → Operculina gr. gomezi & gr. alpina
Biplanispira,Pellatispira(ev.) → Bullalveolina

(inv.)=involute
(ev.) =evolute

Middle Eocene

H: Calcarina?,Fabiania,Dictyoconoides → Alveolina → Nummulites

L: Coskinolina,Dictyoconus → Orbitolites,Fabularia → Alveolina → Nummulites → Operculina s.l.

Early Eocene

H: Lockhartia,Dictyoconoides → Alveolina → Nummulites

L: Coskinolina,Dictyoconus → Orbitolites,Somalina,Fabularia → Alveolina → Nummulites → Operc.

Middle-Late Paleocene

H: Miscellanea, Daviesina (ornate),Kathina → Alveolina → Nummulites

L: Fallotella,Coskinon,Glomalveolina → Alveolina → Nummulites,Ranikothalia → Operculina
Broeckinella,Saudia Daviesina (compressed)

Upper Cretaceous

H: Siderolites,Daviesina,Sulcoperculina → Lacazina compressa → Pseudosiderolites

L: Calveziconus,Montsechiana → Periloculina,Subalveolina → Lacazina elongata - Meandropsinids
Ilerdorbis,Dicyclina

Fig. 1 Succession according to depth and substrate of selected genera of larger foraminifera. Ranges are largely overlapping. Amphisteginid and orbitoid species form similar parallel successions.

by sedimentation of freshly produced grains (Hottinger, 1982, in press). The sedimentation rate depends on local sediment production by shelled organisms, on trapping in permanent bottom covering communities, on bioerosion and exposure to water movement carrying away the finest fractions of the sediment by winnowing. The growth of sessile communities on hard substrate changes the relief of the sea bottom, the local regime of water movement and with this the rate of sedimentation. Therefore, the two main bottom facies types migrate slowly. Where the diagenetic front advances at very low angles in respect to the bottom surface, the rate of migration was observed to reach several metres per year in depths between 10 and 20 m.

Where the nature of the substrate changes with time, processes of maturation determine the composition of the community. So far, the slow migration of the biota have not revealed any effect on the composition of the fauna of larger foraminifera. However, where the base level for sand reaches greater depths during the winter storms, larger grains covered by encrusting pioneer organisms are periodically turned over and form macroids. Burrowing might help in places to destabilize the macroids. The latter represent a short-lived hard-bottom substrate on which the pioneer community is kept permanently in a stage of maturing according to the turnover-time of the substrate (Hottinger, 1983). The composition of the community depends on the result of competition for space on the substrate after the given turnover period under the specific conditions of depth. In the Gulf of Aqaba, the periodicity of macroid turnover is most probably related to the yearly seasonal cycle for macroids forming belts between 40 and 60 m depth. One of the largest living foraminifera, the encrusting *Acervulina inhaerens* capable of covering patches of substrate with a diameter up to 8 cm, is the main constituent of the macroids successful in competition with coralline algae, encrusting *Sorites* and bryozoans. Analogous foraminiferal macroids are known in particular from Eocene deposits (Hagn and Wellnhofer, 1967). The same foraminifer is the most important agent cementing loose coral rubble on the coral carpets between 40 and 90 m depth (Hottinger and Levinson, 1978). Its unusual success in the Gulf of Aqaba may be due to the extremely low nutrient concentration hampering the growth of coralline algae whereas its limitation to the euphotic zone must be due to the diatoms representing part of its food source.

The arborescent larger foraminifera *Miniacina* and *Homotrema* are the first larger pioneers settling on hard substrate. In the photic zone they occur sporadically in dark cavities below corals or algae. Below the photic zone, they cover in dense formations fresh, solid substrate irrespective of its exposure, before it is overgrown by bryozoans.

Thus, different substrates at comparable depth zones produce different biosystems inhabited by different genera or species of larger foraminifera. Why do we recognize in the fossil record mainly the depth gradient whereas on recent sea bottoms the distribution according to depth and substrate is equally well documented? There are several reasons for this bias in the fossil record. The most important one is the difference in methodology for investigating recent and fossil sediments in the field. On a recent sea-bottom we see and map contemporaneous surfaces large enough to identify the elements of a detailed mosaic of different communities. In fossil sediments, erosion usually uncovers sections of rocks in which only a single line of restricted length along a bedding plane represents an approximately isochronous element for study. Measurements along such short lines crossing a mosaic of environments in an undetermined angle to the ancient depth gradient must produce irregular signals impossible to interpret whereas the signals from long time-sequences in sections of transgressive or regressive sediments are systematic and repeatable in parallel sections. They are easily identified as meaningful by their systematic trend. A systematic distinction of hard bottom ("high energy") and soft bottom ("low energy") depth sequences based on the shell morphology in larger foraminifera would considerably enhance the resolution power of the paleobathymetric interpretation of neritic sediments (fig. 1).

Depth dependence in larger foraminifera has several different reasons. We have to consider separately the sequential distribution of species along the depth gradient and the intraspecific variation of a particular species over its depth range. Strikingly enough, there are parallel trends in sequential distribution of species and in intraspecific variation. As a rule, the shapes of discoidal or lenticular shells get more compressed in deeper habitats. In porcelaneous forms (archaiasinids, soritids) the thickness of the shell is reduced by narrowing the lateral extension of the median, endoskeletal zone (compare Hottinger, 1978). In lamellar, perforated shells, the reduction of the shortest shell diameter results either from a reduction of the thickness of the lamellae forming the lateral chamber walls (Hallock and Hansen, 1979) or from a change in chamber proportions reflected often by looser coiling (Hottinger, 1977a, b). Often, both morphologic changes are combined. Whereas the lamellae in the lateral shell walls of all nummulitid genera are getting thinner, ornamental pillars generated by lamellar thickening are forming strong reliefs on the lateral chamber walls. Such pillars are suspected to function as light lenses but the optical properties of the shells and their ornaments have not yet been adequately studied.

Both depth-dependent morphologic trends in shells of perforated-lamellar forms are supposed to be related to the symbionts owing to their light requirements or their effect on calcification rates. However, larger foraminifera bearing no symbionts show similar trends (*Planorbulinella*, Thomas, 1977). Therefore, the simple functional relationship between enlarged lateral shell surfaces as a response to weaker light intensities is questionable.

The requirements of the symbionts concerning light intensity and colour depend on the chromatophores with their specific pigments. The symbiont-host relationship is a specific one (Leutenegger, 1983a, b): porcelaneous-

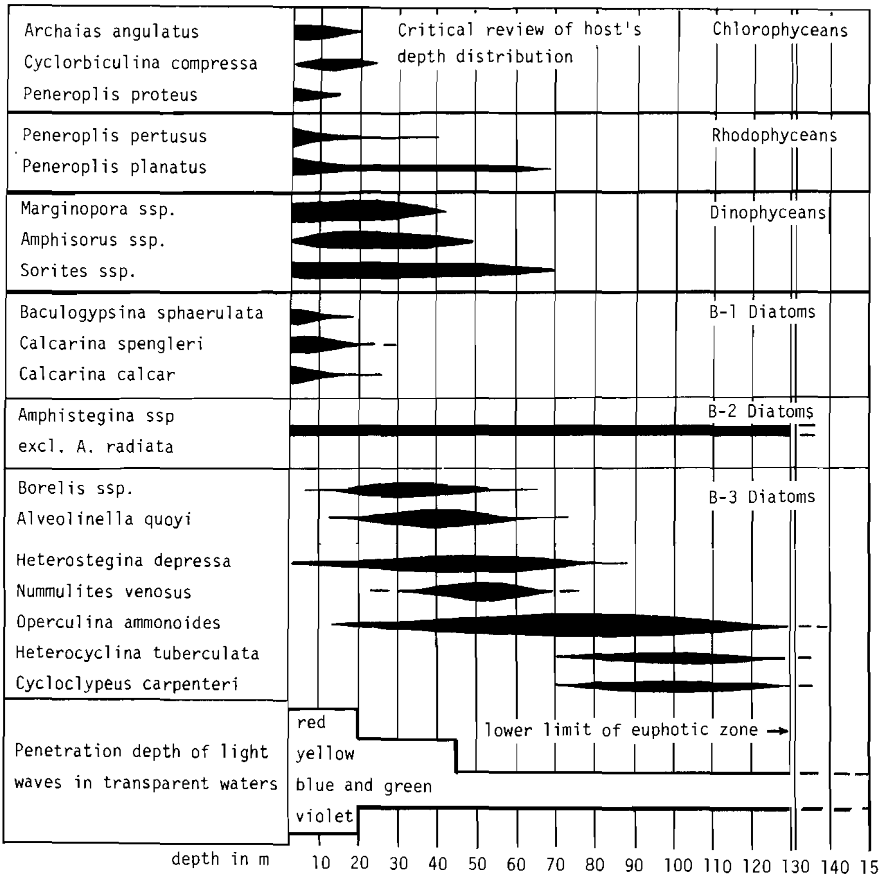


Fig. 2 Depth distribution of recent larger foraminifera grouped according to ultrastructural chloroplast types of symbionts and compared to penetration depth of light with different wave lengths. Chlorophycean symbionts might need red, rhodophycean and dinophycean symbionts yellow light, while diatoms may use green and blue light. Note the behaviour of hosts of B-1-diatom symbionts living probably in the sandy bottom of high energy substrates. Data after Leutenegger, 1983b, simplified.

discoidal larger foraminifera have chlorophycean or dinophycean, porcelaneous-fusiform and many perforated-lamellar species have diatomacean symbionts (fig. 2). Light intensity and quality may therefore be a factor limiting the distribution of the host species at the lower end of its depth range, while the upper end of the range is determined by additional factors. In the presence of too intensive irradiation by sunlight, the behaviour of symbionts and host may avoid or reduce photoinhibition. In *Sorites, Amphisorus* and *Marginopora* associated with dinoflagellates, the symbionts have short flagellae and move by themselves to the shaded side of the shell through the lacunar system of the protoplasm (Leutenegger, 1977b). In addition, the substrate selected by the host is dark so that the light regulation mechanism may not be hampered by the reflection of the substrate. In alveolinids, the symbiotic diatoms are retracted with the host protoplasm in the inner whorls of the shell. At lest *Alveolinella* may also disappear below the first layers of coarse sand grains thus finding a protection against too strong irradiation (Hottinger, 1981). Amphisteginids show negative phototaxis (Zmiri et al., 1974) hiding in the shade of boulders, plants or corals. *Heterostegina depressa* lives in shaded pools or reef front overhangs at very shallow depth (Röttger, 1976; Hottinger, 1981) but in the Gulf of Aqaba its distribution is limited to greater depths because the small fringing reefs seem to provide shaded environments which are not large enough.

The lower limit of all symbiont bearing organisms in the Gulf of Aqaba was observed to be located at 130 m by visual control from the submersible GEO. The illumination at this depth corresponds to 0.5% of the surface light intensity (Fricke and Schuhmacher, in press).

Depth distribution of intraspecific morphological variants may also be related to properties of the reproduction cycles. In shallow water, the asexual reproduction cycles of *Amphisorus* and *Sorites* are synchronous and closely linked with the seasonal cycle (Zohary et al., 1980). On a particular bottom surface, the population of *Amphisorus hemprichii* consisted during one year of high numbers of megalospheric forms with comparably small embryos and some microspheric specimens, the next year exclusively of megalospheric forms with larger embryos; not a single microspheric form was found. If we exclude the migration of microspheric forms in and out of the system (for which no indication was found so far) we must interpret this cycle as a paratrimorphic one (Leutenegger, 1977a), coordinated with the seasonal cycle over two successive years (fig. 3). If the coordination with the seasonal cycle gets weaker or lost in deeper waters (for which qualitative observations in situ provide support) the mixture of megalospheric schizonts and gamonts in the population will change. Trends in average values of megalosphere diameter observed along the depth gradient (Fermont, 1977) might therefore reflect changes in coordination of reproduction cycles with the seasonal cycle and should be verified by sampling over long time intervals with methods avoiding the effects of mixture by bioturbation and taking into account the patchiness of the distribution of living populations.

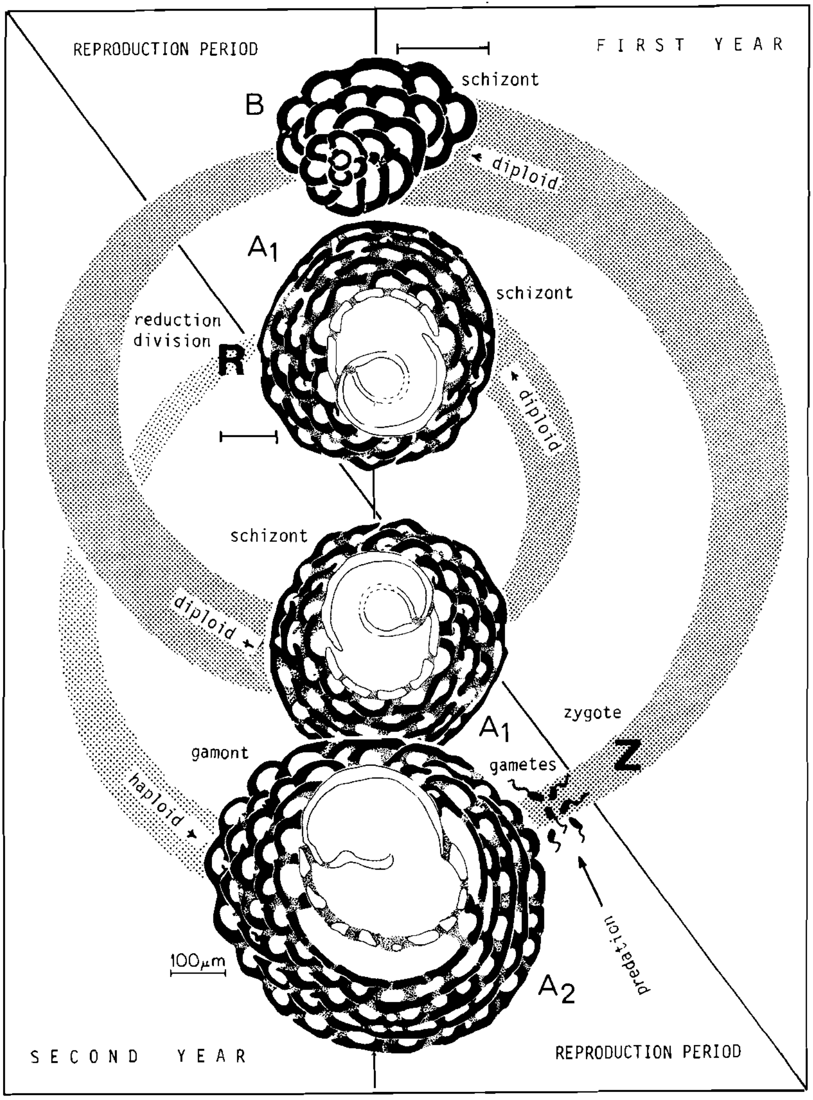


Fig. 3 Reproduction cycle of *Amphisorus hemprichii* reinterpreted as paratrimorphic and coordinated with the seasonal cycles of two successive years. Data from Zohari et al., 1980.

BIOGEOGRAPHIC DISTRIBUTION

Biogeographic distribution of larger foraminifera is measured by the presence or the absence of single species or genera in a particular region. In order to differentiate whether the absence of a taxon is due to the absence of its favourite biotope or to other reasons, all biotopes of the investigated region must be surveyed. Negative, "absence" data from the literature based on haphazard collections are of very limited use in this respect. It would be wise to operate with presence data only by restricting geographical distribution studies to groups of larger foraminifera known to substitute each other in the same kind of environment as for instance *Amphisorus* and *Archaias* as epiphytic dwellers in shallow tropical seas. The shallowest faunas of larger foraminifera provide further advantages for biogeographic study: they provide the densest "presence" data in the literature from collections of beach sands and they are likely to react most clearly to sealevel changes and to give the best answers to the unsolved questions of true endemism on isolated island groups.

As Adams (1967, 1983) pointed out, three major biogeographic provinces, namely the caribbean, the mediterranean and the indopacific provinces, may be defined by latitudinal and by longitudinal limits. The latitudinal ones are doubtlessly reflecting climatic barriers such as limiting temperatures, the longitudinal limits are representing some kind of barrier for the propagation of the species as for instance a large open ocean. If we consider the distribution of species and take into account the species diversity of particular regions, the picture gets obscured. Some examples may illustrate the complexity of the question.

During maximum species diversity of larger foraminifera during Early and Middle Eocene, low diversity subprovinces developed in marginal position with respect to the region of highest diversity, namely along the southern eurasian continental margin (Helvetic Alps and their eastern equivalents and forelands), in epicontinental basins of western Europe (Paris basin s.l.), along the north african and west african coast lines, etc. (fig. 4). In the pyrenean basin opening into the atlantic, diversity is notably higher while the highest diversity occurs in the central tethyan (alpine) sea from Northern Italy to Turkey (compare Schaub, 1981). Some species from such different groups as orbitolitids, alveolinids, nummulitids and discocyclinids are common to all provinces permitting biostratigraphic correlation and showing exchange between the subprovinces. Mechanisms other than barriers for propagation must play some role in the system the more so because different contemporaneous associations of species characterize different low-diversity marginal provinces. During times of general, low-diversity as for instance during the

Late Eocene Priabonian Age, no marginal provinces can be recognized. In early times of phylogenetic cycles (see below) such as the Late Paleocene *Alveolina primaeva* Zone, the communities of larger foraminifera are usually uniform over more than one major bioprovince (Drobne, pers. comm.). Thus the generation of bioprovinces must be linked to some kind of historical process.

The situation of today's Red Sea may provide some additional insight into the significance of bioprovinces. This particular low-diversity marginal province is characterized by three soritid species, one alveolinid and three nummulitids, whereas on the Maledivan Islands studied with comparable methods and by the same investigator, five soritid species, three alveolinids and five nummulitids occur (Hottinger, 1981). One nummulitid species, *Heterocyclina tuberculata*, substitutes in the marginal Red Sea *Cycloclypeus carpenteri* from the open Indopacific. The substitute in the marginal community shows morphological characteristics of the nepiont corresponding to the early stages of the *Cycloclypeus* lineage in Oligocene times (Meulenkamp, 1977). It may therefore represent a newly evolved species derived from the *Heterostegina operculinoides* stock (Hottinger, 1977b) present in the main province and immigrated into the niche of *Cycloclypeus* left vacant in the marginal province. *Planorbulinella elatensis* might be a similar case (Thomas, 1977).

The inverse relationship between diversity of species and intraspecific variation is particularly striking. Although extensive quantitative studies have not yet been carried out, the counting of specimens from many samples revealed clear differences in the range of elongation in *Borelis* species. In the monospecific *Borelis* communities of the marginal province, variation is very high whereas each of the two maledivan species is strikingly uniform. Where the two species occur in the same sample their range of variation is the same as in samples where they occur separately. We do not yet know whether the coexistence of species belonging to closely related genera such as *Marginopora* and *Amphisorus* has the same effect as the association of congeneric species. Unusually wide ranges of intraspecific variability are known also in Eocene *Nummulites planulatus, N. laevigatus,* etc. (Schaub, 1981) and in *Alveolina rütimeyeri, elliptica, elongata* or *fusiformis* (Hottinger, 1960).

The information so far available from samples and from literature data verified from figured specimens, indicates that the limit of the Red Sea marginal province is not positioned in the straits but extends longitudinally through the open Indian Ocean hitting the asian continent on the coast of Pakistan (fig. 4). The only barrier likely to hamper free propagation of species in this region is the very low oxygen content of the water column

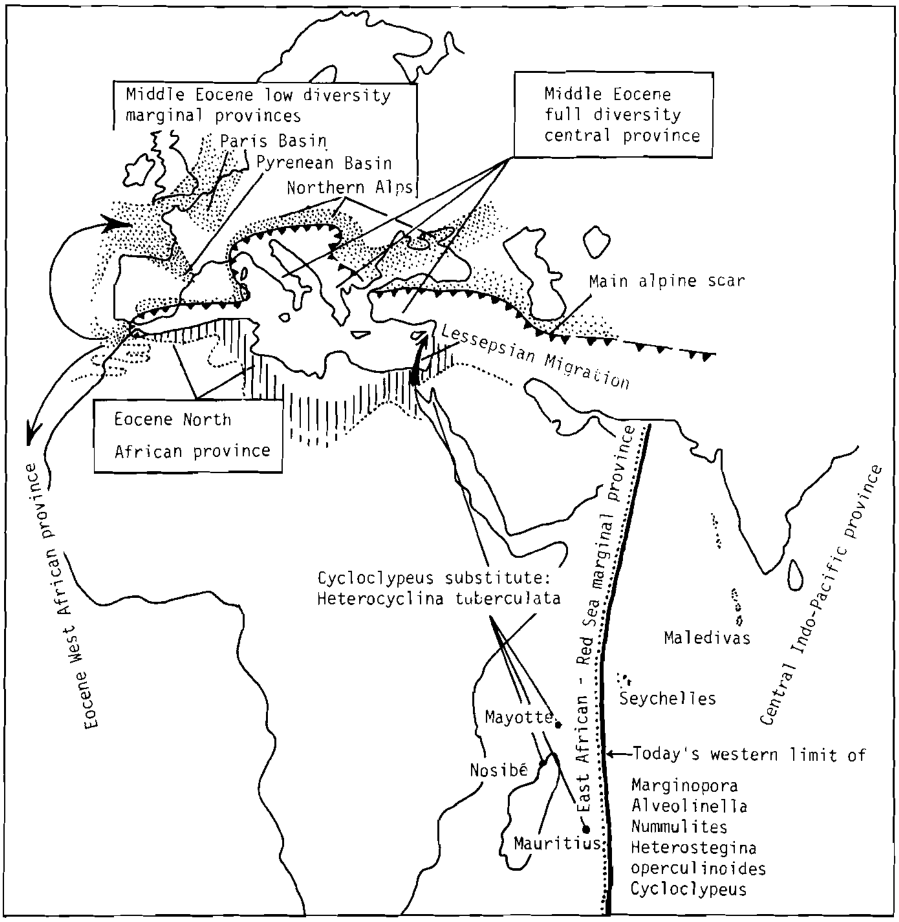


Fig. 4 Tentative sketch of Eocene bioprovinces based on diversity estimates of larger foraminifera as compared to the recent low diversity marginal province comprising the East African Shelf, the Red Sea and the Persian Gulf.

extending from the open ocean over the shelf into shallow water (Düing, 1967; Schott et al., 1970; v. Stackelberg, 1972).

Lessepsian migration (Por, 1978) is the most important model showing the effects of a barrier on propagation. In 100 years, about 140 taxa (including *Heterostegina depressa*) migrated against current and salinity barriers through the narrow Suez Canal and spread northwards over 1000 km along the mediterranean coast. Mode of locomotion and of reproduction had no effect on this process. This demonstrates that the driving force for propagation of species might not be the free communication between marine basins but the availability of empty ecological niches or successful competition for such niches. If the barriers have little effect on propagation, the provincial diversities must be the result of some kind of gigantic maturation process involving many biota and their interaction over whole provinces during long time intervals. In such a system, the barriers would not act as simple bottlenecks for propagation of species but as boundaries canalising parallel equilibrated maturing processes with different historical background and duration on their evolutionary path. The question remains open whether the documents of earth history have enough resolution power in space and time to verify such a hypothesis.

PERIODICAL AND SYNCHRONOUS REPLACEMENT OF SPECIES

In the course of earth history, larger foraminifera are replaced frequently. In particular, associations of foraminifera characterizing particular shallow facies types are dying out and are replaced after a certain time interval by new associations with the same structure of shell morphology, emerging from a new evolutionary process of adaptation. From Middle Cretaceous to recent times discoidal-porcelaneous series of analogous genera, *Cycledomia* > *Larrazetia* > *"Taberina" danieli* > *Orbitolites* > *"Archaias" kirkukensis* (Hottinger, 1982) > *Marginopora* (compare Hamaoui, 1979) reflect such a periodical replacement. Alveolinids (Reichel, 1937; Caus, 1981), Orbitoids, larger Rotaliids and foraminifera with enveloping canal system (*Siderolites,* Wannier, 1980 to *Calcarina,* Hottinger and Leutenegger, 1980) show similar trends. Biostratigraphic ranges of species demonstrate best the synchronous disappearance of representatives of different biota as for instance during the terminal Middle Eocene event. Sometimes, the state of classification in larger foraminifera obscures the general trend, particularly in nummulitids where the genus concept is still uncomfortably large (Schaub, 1981; Hottinger, 1977b). In the main bioprovinces, the large evolutionary cycles are not always synchronous (replacement *Discocyclina-Lepidocyclina*). This might also be some kind of artefact produced by inappropriate classification (Caudri, 1972). However, the history of biostratigraphic classification of shallow water deposits from Mid-Cretaceous to Late Eocene clearly illustrates relationships between larger sedimentary cycles reflecting changes of sealevel and climate (Berger and Vincent, 1981) with synchronous extinction of numerous species and/or evolutionary cycles.

Some of the main biological characteristics of larger foraminifera are 1. their long life cycles reaching two years in *Marginopora* (Wefer and Berger, 1980) and implying an extensive ontogeny during which complex shell structures are built and exceptionally large body sizes are reached, 2. their refined reproduction cycles linked to seasonal cycles and their juveniles with particularly structured shells often protected by brood chambers, 3. their symbiosis protected by shells, 4. their permanent differentiation of protoplasm in canaliferous foraminifera (Hottinger and Dreher, 1974) and 5. their abundance and diversity in regions of low primary productivity. These permit to single out the larger foraminifera amongst all other unicellular animals as extreme K-strategists (Hottinger, 1982a) depending particularly on a long-term stability of the environment. If the stability of the environment breaks down, the most extreme K-strategists are the first to disappear.

The stability of environments with high diversity and low productivity depends on climate and nutrient concentration. Climatic changes thus explain by direct (temperature) or indirect (nutrient-oxygen system) effect the periodical instability of the neritic environments and consequently the replacement of K-strategists. We do not know yet what range of nutrient concentrations permits the main benthic carbonate producers, hermatypic corals and foraminifera, to develop, nor whether there is any direct inverse relationship between nutrient concentration and diversity of K-strategists as inferred from periodical replacement processes. However, the differences in diversity in central-main and marginal bioprovinces discussed above show maturing processes involved in the system. This means that any distribution pattern of larger foraminifera at any given time depends not only on environmental factors of that given time but is also the result of an historical process. Therefore, even today's distribution of larger foraminifera can be fully understood only when the historical background will be adequately elucidated.

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ENVIRONMENTAL GRADIENTS AND EVOLUTIONARY EVENTS IN SOME LARGER FORAMINIFERA

C. W. DROOGER

ABSTRACT

Sudden, large changes in embryon size found to have occurred during the evolution of several, unrelated lineages of larger foraminifera are thought to be linked with a change in depth habitat. These time-bound leaps seem to show a consistent pattern, which is opposite to that of gradual size increase of the embryon, observed in some Recent species along the depth gradient of their habitat range.

THE GENERAL ENVIRONMENT

Larger foraminifera today as well as during the Cretaceous and Tertiary show a general adaptation to various modes of life in the restricted depth range of the photic zone, i.e. the uppermost 100 to 200 metres of bottom habitats. This depth restriction is logical because in one way or another these animals are dependent on living plants. Investigations on Recent forms show that there are several kinds of combinations of certain foraminiferal species and specific floral elements on which the animals feed or which they host in their protoplasm. We have only just begun to speculate on some of such relations.

As soon as we start to deal with larger foraminifera of the fossil record actualistic data are of little importance, particularly because nothing is left of the floral part of the original combinations. Whatever difference we observe between taxa, for instance in relative frequency or in morphology, we are inclined to explain these differences primarily in terms of water depth, because for this environmental gradient the geologist may find some independent evidence from the accompanying sediment. But we know that what is important for the foraminifera is not depth itself, but depth-linked factors, such as light intensity, nutrient distribution, water energy and type of substrate.

The coarse environmental generalizations we conclude from relative abundance patterns of fossil larger foraminifera give us an idea of deeper and shallower, but not of absolute depths in metres.

INTRASPECIFIC CLINES

Another approach that we are currently using to arrive at paleoecological conclusions is to search for morphological clines in separate species, or in groups of closely related species. Understandable regularities in such morphoclines have led us to advance postulates as to the relative positioning of the various morphotypes on the depth-related gradients.

For instance, the relative thickness of the test in certain species has been found to change with depth. It has been fairly well documented for several groups of spiral and orbitoidal species that the test decreases in relative thickness with increasing depth. But the assumption that this change in diameter/thickness ratio is a consequence of differences in water energy is an explanation that has to compete with another one: that the deep-living individuals have changed their shape in order to gain optimum profit from the light quantity for their algal symbionts. Probably both explanations are valid in variable combinations.

Interstitial pillars in the lateral tissue of orbitoidal forms tend to be thicker in shallow forms (fig. 1). This type of shell reinforcement points to mechanical strength under high energy conditions as the ruling ecological factor.

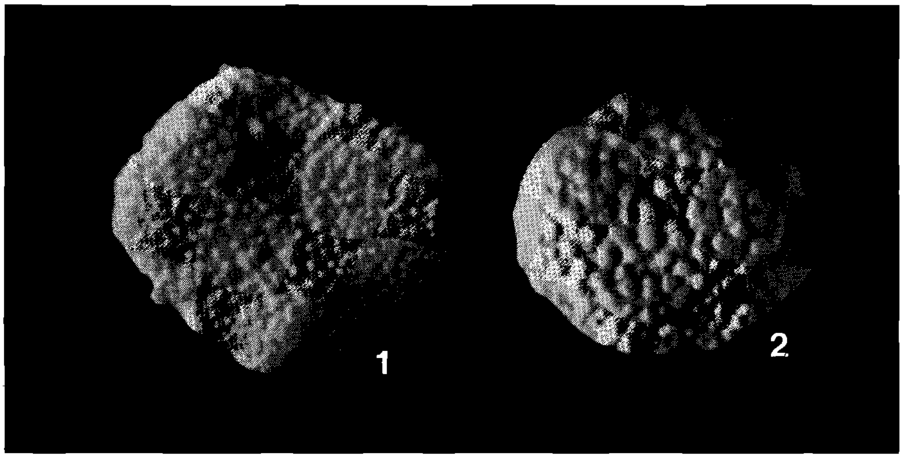

Fig. 1 Two specimens of *Miogypsina globulina* from SW France (coll. Drooger, 1964). Magnification 25 X. The left specimen has a rather flat test with delicate pustules; this type is relatively frequent in the assemblage from Miocene marls near Uzeste (FR 254). The right-hand specimen is very thick with coarse pustules (FR 329, Bazas); such specimens are very common in cross-bedded calcarenites.

At greater depths individuals of certain species often have thinner walls. One of the nicest examples I have encountered is that of *Cycloclypeus* (fig. 2). For the interpretation we again have the choice between the lower energy at greater depths and the better light penetration through the thinner walls for the benefit of the floral symbionts.

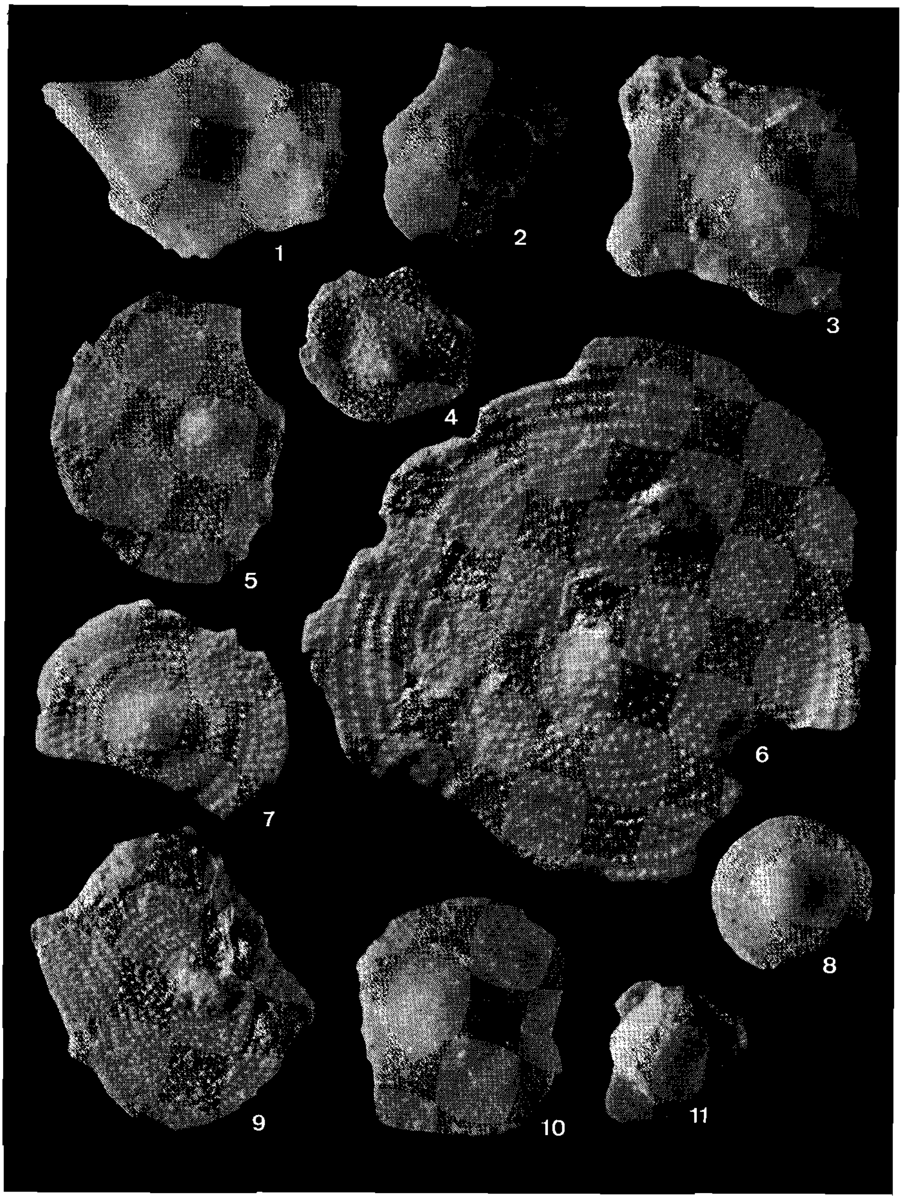

Fig. 2 *Cycloclypeus* specimens, probably washed together from different depths (sample Mo 83, Borneo, see Drooger, 1955). 1—3: thick-walled, opaque individuals, which are usually badly damaged; 4—7: relatively thin-walled specimens with glassy pustules; 8: thin-walled specimen with slight ornamentation; 9—11: regenerated individuals, those of 10 and 11 with a thick central part and a thin flange. Magnification 12 X.

Finally, in *Operculina* and in *Heterostegina* glassy pustules tend to grow on the outer walls at greater depth (Hottinger, 1977), these pustules possibly being some kind of lenses to concentrate the light for the inflora. The ornate forms of our *Cycloclypeus* (fig. 2) example may be explained in a similar way, although the pustules in these specimens have a different position.

These examples show that we recognize, or rather we suspect that there are depth-related clines in outer morphology within individual species of larger foraminifera. These clines are explained best by the influence of a changing light intensity because of the profit for the vegetational part in the life combinations, but in some cases a certain role must be ascribed to the factor of mechanical strength in relation to the amount of water energy.

THE APPLICATION OF NUMERICAL METHODS

In order to obtain a better understanding of evolutionary patterns in larger foraminifera, and especially in several groups of orbitoidal forms, we have done a lot of measuring in Utrecht during the last ten years. We have obtained a large quantity of worthwhile data, which seem to have a distinct bearing on both evolution and paleoecology, but they also raise some questions, to which we have as yet no adequate answers.

We measured two types of items. One has a bearing on chamber arrangement, the other pertains to size.

The chamber arrangement parameters to which we have given various numerical expressions are based on the configuration of the chambers in the early part of the test, which belong to the ontogenetic stages called embryon and nepiont. In these initial stages of the orbitoidal groups we recognize distinct phylogenetic changes towards fewer steps of chamber formation until the individuals attain the ontogenetic stage of radial growth. The main term we use for these evolutionary transformations is nepionic acceleration. In the course of phylogeny all orbitoidal groups changed from a spiral chamber arrangement to a growth habit of functional "all-round-ness'. We are capable of imagining more than one explanation of why the observed trends have an adaptive value, but for the present article there is no need to dwell on these mental constructions.

The second item that we measured is size, not primarily the size of full-grown individuals, but especially that of comparable ontogenetic stages of the animals, for instance the diameter of their protoconch or of their embryon. In the phylogeny of all groups there is a general, but irregular tendency for the size of such primordial chambers to increase.

Actually, this general evolutionary trend is not so easy to explain if one wishes to ascribe an adaptive advantage to the size increase of the embryon. The size of megalospheric embryons depends primarily on the functioning mode of reproduction, in which we may recognize two insufficiently understood variables; the size of the parent individual whether microspheric or megalospheric, and the number of its offspring. If we suppose that the latter remained approximately constant in a certain lineage, an overall phylogenetic increase of "adult" size could have entailed the observed increase in mean embryon size. Along the line of reasoning of Hottinger (1982) such a procedure would be understandable because larger individuals can store larger quantities of food and of symbionts, which they will need for the period of reproduction, or in order to survive prolonged periods of hardship. However, we lack sufficient data to conclude that an overall size increase of the individuals is a valid rule for all lineages. A general trend to giantism (Lee, McEnery, Kahn and Schuster, 1979) is too optimistic an assumption.

Whatever the best explanations for the general trends in embryon size and nepionic configuration may be, the tendencies for both to change in one-way directions make it logical that we find distinct correlations between the mean values calculated for the parameters of the two categories if we consider one orbitoidal group all through its lifetime. We see that irregularities in the succession of means of one category along a stratigraphic column are often accompanied by more or less distinct fluctuations in the other in accordance with the general correlation pattern. This can be understood when we see that in separate populations too embryon size and nepionic configuration tend to show correlation, which may be fairly strong in some lineages, such as *Planolinderina* (fig. 8), but weaker to negligible in others.

As we wish to disentangle the role of evolution as some kind of "autonomous process" and the role of environment we need to consider both types of phylogenetic trend more closely.

We commonly suppose that our configuration parameters were only slightly, if at all, affected directly by short-term environmental changes in the course of time, or by differences along environmental gradients at separate time levels; but this is no more than an assumption because we do not understand how an environmental influence could have affected chamber arrangement. On the other hand we now have several indications that embryon size was not totally independent of environmental gradients.

As a consequence we may surmise that environmental factors had an indirect influence on nepionic configuration via the observed correlations. Within the scope of the symposium we will concentrate on the size parameters, leaving a review of the data on configuration for another presentation.

VERTICAL TRENDS AND HORIZONTAL CLINES IN EMBRYON SIZE

We have advanced already the fairly safe conclusion that the megalospheric embryon shows an irregular overall increase in mean size in all groups of larger foraminifera during the course of their evolution. The explanation for such trends appeared too difficult, but there may be a link with a phylogenetic size increase of the individuals at their ontogenetic stage of reproduction.

In addition, it has been suggested that there are environment-controlled size clines of the megalospheric embryon within single species. Some ten years ago it was postulated (Drooger and Raju, 1973) that *Miogypsina* embryons of a given species were larger at higher latitudes. Although the possible influence of a temperature gradient was not excluded, these authors had some preference for a relation with light intensity. If for the latter reason the embryon size increased with latitude, one would also expect it to increase with greater water depth in one place.

Such a change in embryon size with increasing water depth seems to be confirmed by the investigations of Fermont (1977) on Recent *Operculina* in the Gulf of Elat, and of Röttger and Bor (in preparation) on Recent *Heterostegina* from the waters around Hawaii. Fermont observed an increase of some 40 to 50% in mean linear dimensions of the protoconch from shallow water down to a depth of about 80 metres, followed lower down by a kind of stability (Fermont, 1977) or even by reduction (Fermont, Kreulen and Van der Zwaan, 1983).

Recently, Fermont (1982) suggested a similar cline in mean embryon size for the *Discocyclina varians* group in Eocene deposits of Israel. At the assumedly deepest end of the environmental gradient he found populations of flat individuals with a small embryon (*Discocyclina augustae*) which are morphologically separable from the accompanying *D. varians* with the larger embryon. Nevertheless, Fermont suggests that there must have been a continuous bell-shaped cline in embryon size along the depth gradient for the entire *D. varians-augustae* group, similar to the morphocline concluded for the Recent *Operculina* from the Gulf of Elat (Fermont et al., 1983).

Another unimodal curve along the depth gradient was derived by Fermont et al. (1983) for the frequencies of the *Operculina* individuals per gram of residue, and by Fermont (1982) for the relative frequencies of *Asterocyclina* individuals in the Eocene deposits of Ein Avedat. Fermont linked such bell-shaped frequency curves to productivity.

Even though the increase in embryon size in the morphocline seems to be better documented for the shallow part of the depth gradient than the decrease for the deeper part, the assumed environment-linked connection between high frequencies and a large embryon seems to be logical. If high productivity can be correlated with optimum environmental conditions a larger size of individuals would be understandable.

However logical the connection may seem to be between high productivity, larger adult size and a larger embryon, it cannot answer our basic question of what determines the size of a megalospheric embryon. We need better data to solve the equation with two unknown variables.

Was the number of offspring of separate individuals really constant, or did it perhaps even decrease, during the evolution of a group? And if it was constant, can we explain this phenomenon by arguing that for our larger foraminifera with K-strategy behaviour (Hottinger, 1982) the fitness for competition of the young individuals was of greater importance for the continuation of the species than the creation of larger offspring?

And how are we to explain the lack of any notable change in size of the embryons along the depth gradients for both Recent *Planorbulinella* species in the Gulf of Elat (Thomas, 1977)? Did these species have no optimum depth in their vertical habitat ranges?

MAJOR CHANGES IN EMBRYON SIZE IN PHYLOGENY

The morphoclines we have discussed so far, whether vertical in the course of evolution or horizontal along some environmental gradient, had one feature in common. We suggested that they were continuous. However, if we consider the phylogeny of various orbitoidal lineages we come across several instances of seemingly abrupt changes in mean embryon size. In these cases we are dealing with major changes in average embryon volume, which have an order of magnitude comparable to or larger than, up to some 12 times, the extreme values observed along the depth gradients for the Recent species of *Operculina* and *Heterostegina* (fig. 3).

Although these jumps in mean value seem to be of genetic character rather than ecophenotypic, there is no sharp boundary in the amount of morphological difference between the end member populations of the environment-linked morphoclines and the populations on both sides of the assumedly abrupt changes in the course of phylogeny. It is even possible that the ecophenotypic variation corresponds to or grades into a genetic cline with the possibility of (incipient) isolation at the ends of the range. The above-mentioned *Discocyclina* example of Fermont (1982) seems to be such an ambiguous case with aspects of a gradual morphocline as well as of a breaking up into different species.

The discontinuous phylogenetic changes in the case histories which I am going to enumerate now, may be baptized punctuations of equilibria, to use the jargon of contemporary evolutional theory. There is some doubt, however, whether this term in its original concept (Eldredge and Gould, 1972) is really appropriate. Some of the changes fit in with the overall trends of phyletic size increase, but others do not. Nevertheless, it is feasible that the changes have some relation with environmental gradients and with intraspecific morphoclines, so we will strain our phantasy to link morphology and environment in our case histories.

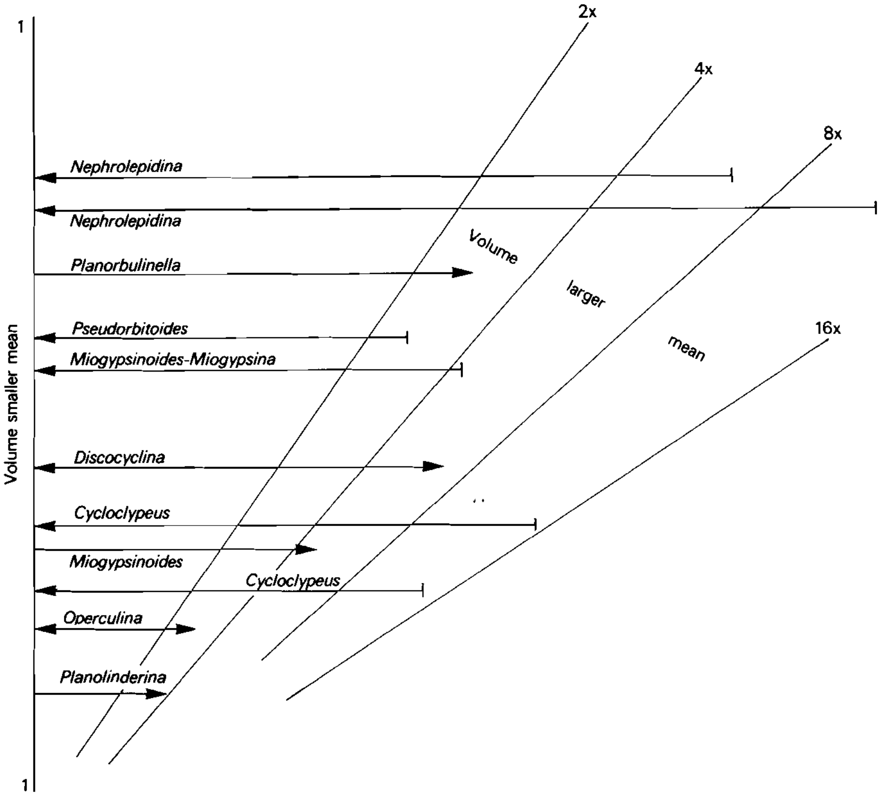

Fig. 3 Relative differences in volume of the embryon (or protoconch) for the discussed examples of environmental morphoclines and phylogenetic leaps.

It should be emphasized that the eight examples dealt with below have not been chosen to prove something; they are simply those best known to me.

1. In the Miogypsinidae the evolutionary change from *Miogypsinoides* to *Miogypsina*, which is based on the introduction of systems of lateral chambers, seems to coincide with a notable reduction in embryon size. The best

documentation has been furnished by representatives from India, which were described by Raju (1974). The general picture shows that the first *Miogypsina* species have much smaller embryons than the accompanying *Miogypsinoides* species. For instance, in the combination of contemporary *Miogypsinoides dehaartii* and *Miogypsina tani,* the latter of which probably originated from the former, we see in Raju's sample G1448 a difference in mean protoconch diameter of 170 μ versus 105 μ. When *Miogypsina* originated, a distinct drop in embryon size evidently was one of the evolutionary changes.

We have no data for a reliable estimate of the possible difference in the habitat of these two Indian species, but recent research by Sikkema (internal report) and Wildenborg (in preparation) on contemporary *Miogypsinoides* and *Miogypsina* in the Miocene of Sicily shows that the individuals of the former genus inhabited higher energy environments than those of *Miogypsina,* and thus probably lived at shallower depths. If we consider the thick outer walls of these *Miogypsinoides* and the relatively thin walls of the lateral chambers in *Miogypsina,* such a difference in habitat seems to be logical as far as the aspect of light penetration on behalf of the symbionts is concerned. The deeper species has to cope with the consequence of weaker light intensity, so thinner walls were welcome.

2. Exactly the same line of reasoning is found to be valid for the sudden change from *Miogypsinoides bermudezi* with a small mean protoconch diameter (70 μ) to *Miogypsinoides complanatus* with a much larger embryon (mean protoconch diameter 115 μ) in successive samples from the Waior section of India (Raju, 1974; Drooger and Raju, 1978); so this time the change goes in the opposite direction from the evolutionary point of view (fig. 4). *M. bermudezi* has relatively thin outer walls and *M. complanatus* very thick walls, so we might be dealing with a habitat change from deeper to shallower. The upper part of the Waior section which contains the *M. complanatus* assemblages seems to contain more calcarenites than the lower part, but a substantiation of the shallowing trend on this basis may well be considered as wishful thinking.

3. The Waior section of Kutch is very instructive because it contains yet another jump in embryon size, this time in the genus *Planolinderina* (Raju and Drooger, 1978), in which in successive samples *P. freudenthali* (mean embryon diameter 45 μ) is replaced by *P. escornebovensis* (mean embryon diameter 70 μ). This leap in embryon size occurs in the section below that of *Miogypsinoides,* but the result is again an increase (fig. 4). If the section really consists of sediments with an overall upward shallowing trend, both genera would have responded in the same way to the environmental change, but at different moments.

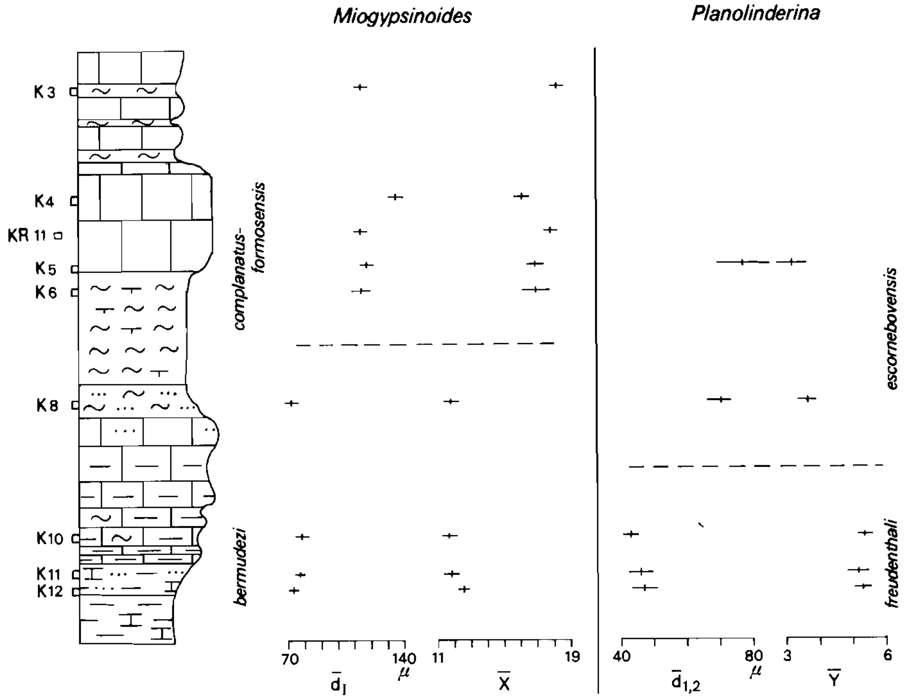

Fig. 4 The section of the Oligocene at Waior, India (after Raju, 1974) with the means ± one SE for parameters of embryon size and nepionic configuration in the assemblages of *Miogypsinoides* and *Planolinderina*.

Three times we have now had suggestions that when there are fairly large changes in the lineages the much smaller embryon size is correlated with the greater depth of the habitat.

4. The nicest example of this type of difference is provided by the Recent *Planorbulinella* in the Gulf of Elat (Thomas, 1977). There appear to be two different species with different depth ranges. *P. larvata* with the larger embryon (mean diameter between 160 and 170 µ) occurs at shallower depths between 15 and 80–90 metres, whereas *P. elatensis* with a mean embryon diameter of about 115 µ was found in the depth range from about 90 to at least 200 metres. If these two species have any phylogenetic relationship with the Miocene Mediterranean *Planorbulinella* lineage (Freudenthal, 1969), it is the deeper *P. elatensis* which is the most logical, direct continuation. The clayey Miocene sediments with *Planorbulinella* in Crete suggest that these supposed ancestors did indeed live at a considerable depth. *P. larvata* thus must be the latest addition to the family tree, with an accommodation to shallower environments. It should be emphasized that the difference in

the embryon size of both Recent species is not accompanied by a similar difference in the size of the full-grown tests; the individuals of both species are of comparable diameter.

I promised eight examples, so there are still another four, for which either the ideas about the possible linkage to environment are less well documented, or for which pertinent data are entirely lacking.

5. From the Caribbean Upper Cretaceous Krijnen (1972) described the *Pseudorbitoides* lineage, in which embryon size shows the well-known overall evolutionary increase. At the end of the lineage Krijnen found two (sub) species, *P. trechmanni trechmanni* with a mean protoconch diameter (∿ 145 μ) answering the increase expectation of the entire group, and *P. trechmanni pectinata* with too small an embryon (mean protoconch diameter ∿ 105 μ). The former taxon Krijnen supposed to have lived in fore-reef environments, whereas the latter he associated with sequences of "shales, marls, sandstones and conglomerates", in which enumeration there is a suggestion of greater depth and/or lower energy. Actually, *P. trechmanni pectinata* is reported to have a relatively flatter test than the other subspecies; this observation may be another point in favour of such a conclusion about the depths of the respective habitats.

6. *Cycloclypeus* furnishes the example longest known in the literature. Tan Sin Hok (1932) found a strong drop in the mean protoconch diameter of his successive Indonesian species *C. oppenoorthi* and *C.eidae* at about the end of the Oligocene. Both species, or rather populations that are morphologically very close, have recently been reported from the Mediterranean Oligocene as well (Drooger and Roelofsen, 1982), the protoconch diameter changing in this area from about 150 μ to some 70 μ. The latter authors suggest a lower energy environment for their *C. eidae* with the smaller embryon, but their evidence is very meagre, to say the least.

7 and 8. Finally I can mention two setbacks in mean embryon size in the course of the development of the Indo-Pacific *Nephrolepidina* lineage; these changes are evident from the monograph of Van Vessem (1978). Van Vessem's oldest Oligocene form seems to belong to the Mediterranean lineage. This *N. praemarginata* with a mean deuteroconch diameter of as much as some 350 μ was followed by *N. isolepidinoides* at a diameter level of about 150 μ. The ensuing irregular increase in deuteroconch diameter up to some 280 μ from *N. isolepidinoides* to *N. sumatrensis* was followed by another strong reduction to about 150 μ in *N. angulosa*, after which there seems to have been a steady increase again up to some 500 μ in the Pliocene representatives of *N. rutteni* (fig. 5). The data on sediment and accompanying fauna are far too scanty to allow us to draw any conclusion about environments that might have changed at the critical points in the morphological sequence.

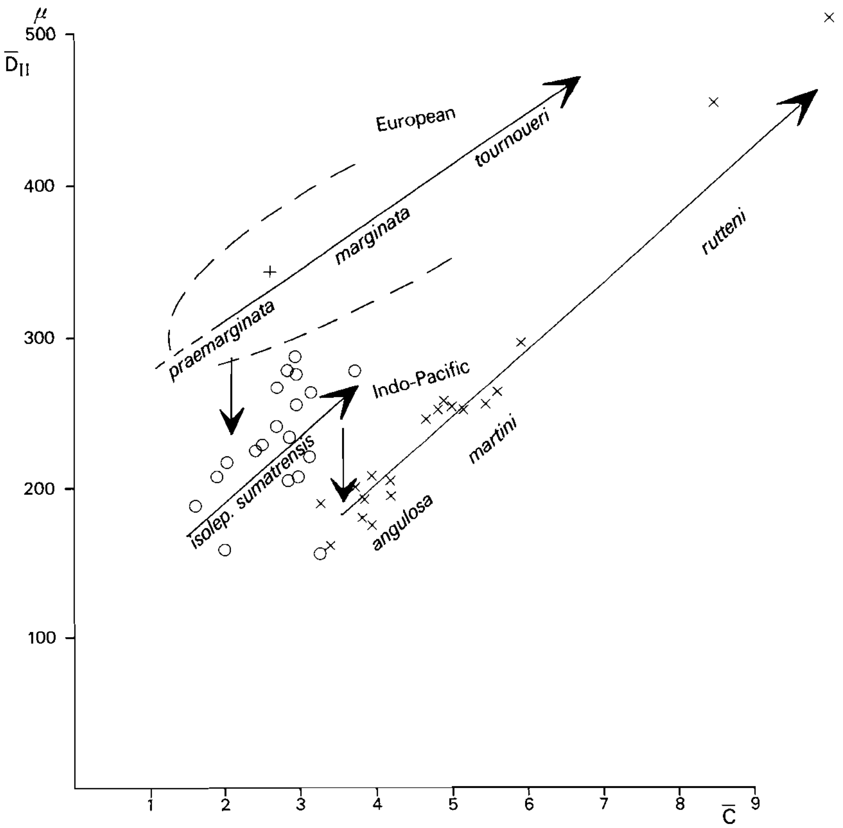

Fig. 5 Scatter diagram of mean deuteroconch diameter versus mean number of accessory auxiliary chambers in the Indo-Pacific assemblages of *Nephrolepidina,* described by Van Vessem (1978).

REGULARITY OR IRREGULARITY OF THE CHANGES

Summarizing these eight case histories we see that there are five examples where the time order of ancestor and descendant corresponds with a strong reduction in embryon size and three in which there is a considerable enlargement. In four of the cases the lineage seems to continue without cladogenesis, the new form simply replacing the older one; in two examples the ancestral line and the descendants are found to have lived on side by side afterwards; for two we do not know the relations. Obviously we cannot recognize any regularity in the results of these changes (fig. 6).

Such a random distribution seems to be absent for the connections we made between the embryon size and the relative depth-light-energy gradients

Type of change in time

to larger embryon size	to smaller embryon size
Planolinderina^{+}	*Pseudorbitoides*
bermudezi → *complanatus*$^{+}$	*Cycloclypeus*
"elatensis" → *larvata*$^{\times}$	*Miogypsinoides* → *Miogypsina*$^{\times}$
	praemarginata → *isolepidinoides*$^{+}$
	sumatrensis → *angulosa*$^{+}$

\+ descendent replacing ancestor

× descendent and ancestor living side by side

Fig. 6 Grouping of the sudden changes relative to the time order.

of the environment. In five out of eight of the examples we feel absolutely to fairly certain that the taxa with the larger embryons are the shallower ones, for the other three examples we have no evidence whatsoever, but there is no indication in any of them for the opposite relation between embryon size and relative depth of the environment (fig. 7).

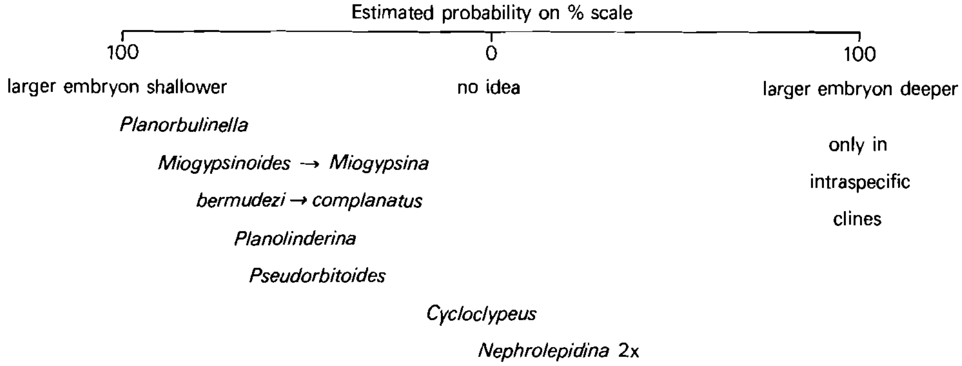

Fig. 7 Grouping of the sudden changes in terms of relative depth.

When we compare for these evident leaps in evolution, the assumed relation between embryon size and relative depth of the habitat with the gradual morphoclines of the embryon size along the depth gradient down to some 80 metres, we see that the two pictures are completely opposite. We seem to be unable to obtain the evolutionary changes by any mechanism in which populations along the shallower part of the depth gradient became separated.

If we want to derive the rapid evolutionary changes by some kind of allopatric speciation we have to rely on the less well documented deeper part of the morphocline – depth gradient combination, which, it was suggested, occurred in Recent *Operculina.* If we suppose that such a clinal size reduction of the embryon below roughly 80 metres is of more general validity, the concept of allopatric speciation may find some additional support from the Recent data. In the Gulf of Elat the sum of the environmental factors seems to change at about this depth contour from variously vegetated substrates to soft bottoms covered by a brown slimy film (Hottinger, 1977). One can imagine that such a rapid light-dependent environmental change might have facilitated genetic isolation in species that expanded their depth range across this limit from one habitat into the other.

Whether such a chain of hypotheses is correct or not, we still do not understand the reason for the regularity of the changes. If we consider the *Planorbulinella* example, it appears that the two Recent species living at different depths consist of individuals of roughly the same adult size. A difference in the size of full-grown specimens at the moment of reproduction thus cannot account for the observed large differences in embryon size.

One might wonder whether anything suddenly went "wrong" in the reproductive processes leading to the megalospheres; such a "phenomenon" could have caused the marked changes in embryon size. And if so, what and why? What is the connection with environment, which caused the regularity?

Unless, of course, our suggestion of regularity in these sudden evolutionary changes is based on wishful thinking, we squeezed out of too few examples. Maybe we are looking for too much regularity in embryon size development. We may well be impressed by the very similar final results of evolution in orbitoidal foraminifera, especially in the overall configuration changes called nepionic acceleration, but in these trends there are also several examples now where the details of the development seem to show random directions (M. M. Drooger, Raju and Doeven, 1979).

In this context we might consider whether the enumerated sudden changes in embryon size coincide with similar leaps in the configuration parameters, and if so whether they conform to the picture expected from the intrapopulational correlation between embryon size and nepionic configuration.

For six of the eight examples the answer is negative; the considerable change in embryon size did not affect the embryonic-nepionic configuration or affected it only slightly. However, in the other two examples it does: in *Planolinderina* and in *Miogypsinoides* from India.

In the populations of *Planolinderina* there is a strong, negative correlation between embryon diameter and spiral length (fig. 8); so it is logical that the considerable increase in the mean of the former parameter will have entailed the opposite change in average spiral length.

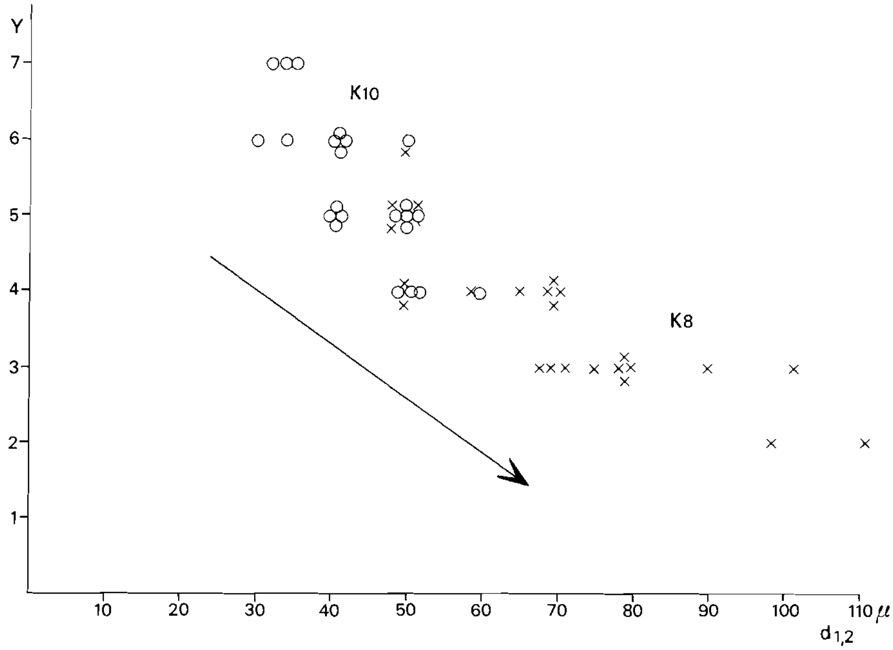

Fig. 8 $d_{1,2}$-Y scatter diagram of the *Planolinderina* individuals in the samples K 10 and K 8 from the Waior section, India. The arrow indicates the direction of change (after Raju and Drooger, 1978).

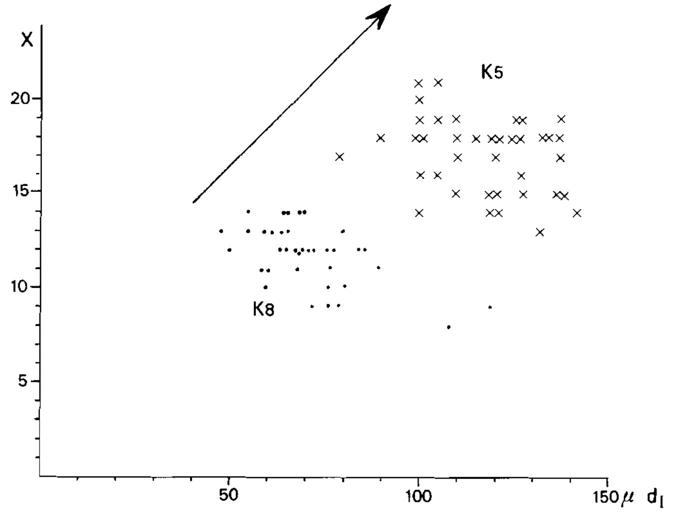

Fig. 9 d_I-X scatter diagram of the *Miogypsinoides* individuals in the samples K 8 and K 5 from the Waior section, India. The arrow indicates the direction of change (after Drooger and Raju, 1978).

In the case of *Miogypsinoides* there is also an intrapopulational negative correlation between protoconch diameter and spiral length, although the correlation is much less intense. However, the direction of evolutionary change from *M. bermudezi* to *M.complanatus* does not follow the direction of this regression (fig. 9). Mean embryon size and mean spiral length are seen to change in the same direction (figs. 4 and 9). Evidently there is not simply a predictable, ecological control in this example.

Whatever value we ascribe to overall direction and parallelism in the evolution of orbitoidal larger foraminifera, we have to accept that random changes occurred as well.

ACKNOWLEDGEMENTS

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DATING THE TERMINAL TETHYAN EVENT

C. G. ADAMS, A. W. GENTRY and P. J. WHYBROW

ABSTRACT

The geographical distribution of age-diagnostic larger foraminifera is used to demonstrate that the continuous marine Palaeogene connection between the area occupied by the present-day Mediterranean and the Indian Ocean had been lost by mid Burdigalian times when a land bridge connected S.W. Asia to Arabia. This hypothesis is supported by the distribution of certain molluscs and echinoids, and its significance is considered in the context of mammal migrations.

A review of the sedimentary successions in Iraq and Iran suggests that the presence of marine Aquitanian sediments has not yet been clearly established in this area and that the Middle Asmari Limestone is mainly Chattian in age. The three "members" of the Gachsaran Formation described from the Coastal Fars region of Iran do not seem to be coeval with the succession in the type area, and it is suggested that some strata hitherto regarded as representing the Lower Fars Formation in northern Iraq may be laterally equivalent to the older Euphrates Limestone.

The lithology and geographical distribution of mid-Miocene and younger sediments in the area indicate that no general submergence occurred after the Early Miocene.

INTRODUCTION

Throughout most of the Mesozoic Era, a broad seaway – part of the ancient Tethys – linked the area occupied by the present-day Mediterranean to the Indian Ocean. This connection persisted until well into the Cenozoic, and separated Africa and Arabia from Asia. It therefore provided a NW-SE migration route for marine organisms while forming a barrier to the intercontinental dispersal of terrestrial animals. The final occlusion of the Tethys Sea – the terminal event – created the Mediterranean.

It is generally accepted that the Tethyan seaway ceased to exist following the collision of the African Plate with Asia and the uplift of that part of the old sea floor which lay across the Middle East. However, the timing of the actual disconnection remains controversial, and the purpose of this paper is to examine the evidence provided by some important groups of marine fossils, and to consider it in the context of present knowledge of the migration/dispersal patterns of terrestrial vertebrates.

When Suess introduced the term Tethys in 1893, he did not indicate when this seaway ceased to exist. Early estimates of the time of marine disconnection were therefore based on assumptions about the time of Alpine tectonism or on the distributions of land mammals (Davies, 1934). More recently, Adams (1967, 1973) suggested that the larger foraminiferal faunas indicate a marine disconnection by Burdigalian times, thus seeming to confirm the earlier date based on mammals, but Drooger (1979) drawing evidence from two especially important groups of foraminifera (Miogypsinidae and Lepidocyclinidae) regarded the disconnection as having occurred at about the end of the Chattian. Steininger and Rögl (1979) accepted the possibility of a Mid-Burdigalian disconnection but argued for a subsequent reconnection during the Langhian, citing similarities between certain Paratethyan and Indo-Pacific pelagic organisms (foraminifera, Radiolaria, and calcareous nannoplankton). This hypothesis requires a deep-water seaway of Mid Miocene age along the line of the present Zagros Range.

Although the final occlusion of Tethys certainly created the Mediterranean, there are grounds for believing that this seaway may have been disrupted more than once during the last 65 million years, and that the Miocene disconnection was merely the last – albeit the most permanent – in a series of such events. The apparent cessation of shallow water carbonate deposition across the Middle East at the Maastrichtian/Danian and Eocene/Oligocene boundaries, and the sudden faunal changes that followed, suggest brief disconnections, consistent with global falls in sea level as postulated by Vail et al. (1977). However, if these changes resulted in temporary disconnections, there should be clear evidence for the much larger fall said to have occurred during Chattian times (see Adams, 1983); this has not yet been discovered. The final disconnection must, of course, have been caused by a general elevation of the region rather than by a global eustatic change.

The present authors have attempted to solve the problem of disconnection by considering the ranges of age-diagnostic marine organisms from the early Oligocene to the Middle Miocene in order to determine when the faunas of the Mediterranean and Indo-West Pacific began to diverge. As Drooger (1979) has pointed out, a faunal change should mark the approximate stratigraphical level of any permanent disconnection, although there may be a time lag before it becomes apparent. Associated facies changes and/or a local depositional hiatus may also occur. Recognition of such changes should be relatively simple, requiring only a survey of the described faunas and sediments of the Mediterranean and Indian Ocean areas. Unfortunately, the inadequacy of the literature creates problems and imposes limitations on the value of conclusions drawn from such studies. Four principal difficulties have either to be overcome or taken into consideration before faunal divergence can be established.

1. Names assigned to taxa described in the older literature are frequently unreliable. For example, Silvestri (1937) reported *Austrotrillina howchini* (Schlumberger), an important Miocene marker now known to have a short stratigraphical range, from the Oligocene of Somaliland, but his illustrations clearly indicate the presence of *A. paucialveolata* Grimsdale and *A.* cf.

striata Todd and Post, species which were not described until much later. *A. howchini* has been reported many times from the Middle East, and although most records clearly refer to *A. asmariensis* Adams, some are unfigured or accompanied by unrecognizable illustrations. These and other similar reports, e.g. Silvestri's (1937) record of *Cycloclypeus communis* Martin from the Miocene of Somaliland, are taken as establishing only the presence of the genus. Douvillé's record (1910) of *C. communis* from Madagascar, probably refers to *C. eidae* Tan, a species not described until 1930.

2. The stratigraphical ranges of many important taxa are less well established than some authors admit, and ages assigned to strata on the basis of occurrences of such taxa cannot therefore be accepted uncritically. For example, the occurrence of *Borelis melo* (Fichtel & Moll) is often held to denote a Middle Miocene age (Bellini, 1969; Salem and Spreng, 1980: 106, who figure *B. melo curdica* Reichel but refer to *B. melo* in their text) although this subspecies certainly occurs first in the Lower Miocene. Similarly, *Pseudotaberina malabarica* (Carter) is believed by some authors (e.g. Eames et al., 1962) to indicate a Burdigalian Age, while others (e.g. Jauhari, 1981) regard it as a Middle Miocene marker.

3. Correlation by larger foraminifera depends upon larger foraminiferal assemblages which are facies controlled, and it is sometimes forgotten that a facies in one area may not be represented by coeval sediments of the same type elsewhere. It is just conceivable that the important *B. melo curdica* fauna of the Middle East is missing around the Indian Ocean for this reason.

4. Most important stratigraphical papers dealing with the Middle East (e.g., Prazak, 1978; Buday, 1980) fail to demonstrate the presence of key fossils in critical sedimentary units, and many important palaeontological papers (e.g., Al-Omari and Sadek, 1975, and Karim, 1978) do not deal adequately with the stratigraphy. For this reason, errors creep into the literature and are then perpetuated.

In this paper, the first two problems are dealt with by revising identifications wherever possible from the accompanying figures, and by drawing attention to (and if necessary disregarding) anomalous identifications unsupported by illustrations. Nothing can be done about the third problem, but the fourth is dealt with below by reviewing the Mid-Tertiary successions in Iraq and Iran and redating certain formations in the light of up-to-date palaeontological knowledge.

MID-TERTIARY STRATIGRAPHY OF THE MIDDLE EAST

The broad band of sediments stretching from Syria and Turkey to the

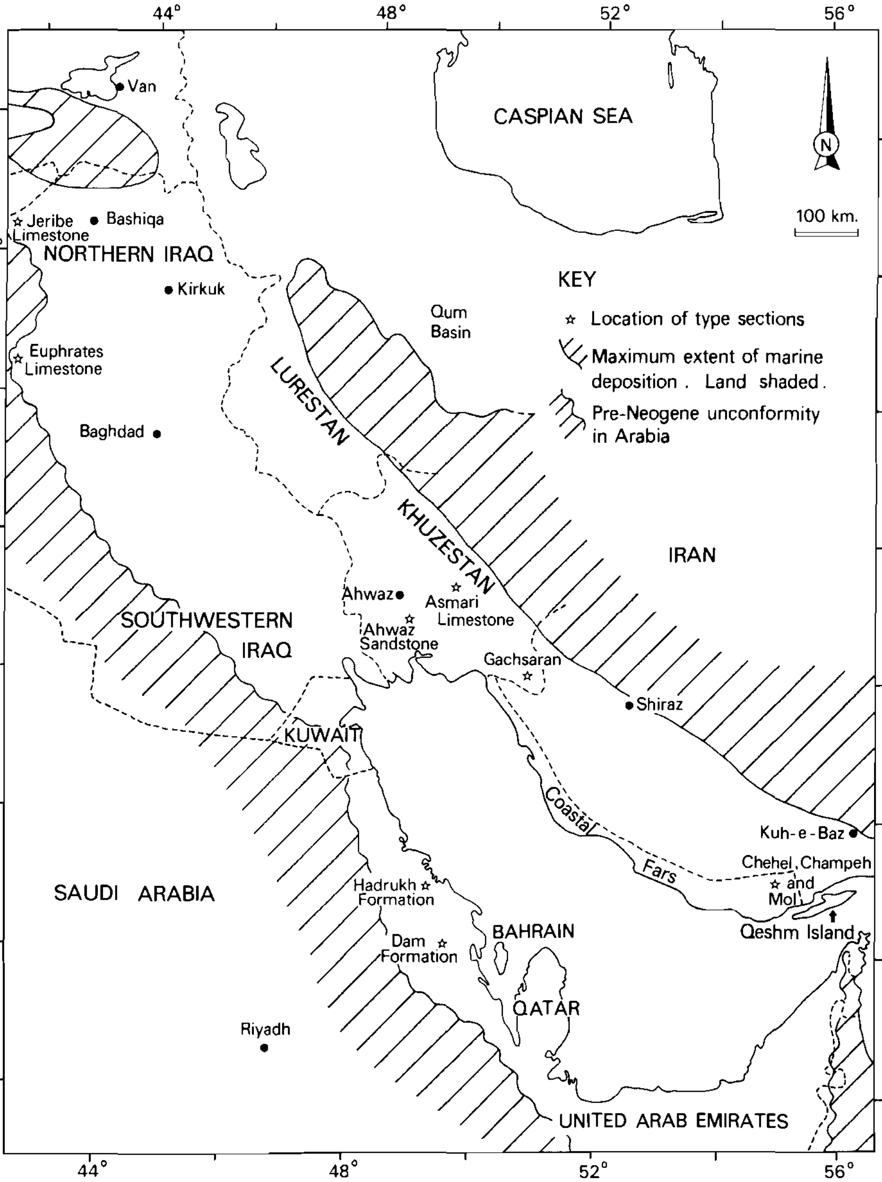


Fig. 1 Map showing the total distributional area of Early – Mid Miocene marine sediments across the Middle East and the locations of type sections referred to in the text.

southern end of the Arabian Gulf is shown on figure 1, as are the relative positions of eight stratigraphical columns (fig. 2) illustrating the principal formations between the Zagros Range and the Arabian Shield.

The oldest marine sediments relevant to the disconnection of the Mediterranean from the Indian Ocean are the Kirkuk, Euphrates, and Jeribe limestones of Iraq, and the Asmari Limestone of Iran, together with their lateral equivalents in adjacent areas. Although the deposition of some of these carbonate units may have been influenced by the SW-NE trending Palmyra-Mosul and Qatar - South Fars arches which, in earlier times formed the northern margins of the northern Arabian Gulf and Rub 'al Khali basins respectively (Powers et al., 1966; Murris, 1980), it is probable that by Mid Miocene time these structures had ceased to be important. Certainly they were replaced in Iraq and Iran during the Late Miocene and Pliocene by folds and thrusts tending NW-NE in conformity with the colliding plate margins.

The lower parts of the Asmari Limestone in Iran, and coeval limestones of the Kirkuk Group in Iraq contain a Middle Oligocene fauna characterised by the presence of *Nummulites fichteli* Michelotti and *Lepidocyclina (Eulepidina) dilatata* (Michelotti). The lower part of the so-called "Asmari Limestone" of south-western Iran is here called by its older name, the Khamir Limestone, since it has not been shown to be physically continuous with the Asmari Limestone proper, although the two are certainly coeval. The Middle part of the Asmari Limestone is said to be Chattian to Aquitanian in age (Thomas, 1950; Eames et al., 1962) but its fauna has never been adequately described or illustrated and the published faunal lists do not clearly establish the presence of Aquitanian carbonates. For a limestone unit which could represent up to 10 million years of deposition, its thickness is small (270' in the type section according to Thomas) and it therefore seems likely that there is an hiatus at the top.

Thomas (1950) shows that the "Middle" Asmari Limestone is separated from the overlying Upper Asmari Limestone in the type area by a thin development (70') of sandy limestone carrying *Miogypsina* and *Ostrea* cf. *latimarginata* Vredenburg. As will be indicated later, these beds are probably Burdigalian in age, and may be separated from the underlying limestones by a disconformity; a second disconformity could well mark their top.

The Ahwaz Sandstone Member of Khuzestan overlies limestone with *N. intermedius*, and interfingers with, and is overlain by, the Middle Asmari Limestone (James and Wynd, 1965: 2229). According to Eames et al. (1962) *Miogypsinoides complanatus* (Schlumberger) (called *Miogypsinella complanata* by them), a well-known Chattian species, occurs above this sandstone in at least one place. Whether this is above the top of the sandstone or only above one of the sandstone intercalations is unclear, but it indicates that at least part of the Ahwaz Sandstone is of Late Oligocene age. The Kalhur Gypsum is said to interfinger with the Middle Asmari Limestone and (by implication) to overlie, in one locality at least, Pabdeh shale with *Globigerinoides trilobus* (Reuss), a species indicating an Early Miocene age (James and Wynd, 1965: 2228 and fig. 3). It is unfortunate that so few age-diagnostic fossils have been described from the Middle Asmari, and that evidence from the Miogypsinidae and Lepidocyclinidae is totally lacking. The Ahwaz Sandstone is considered by many authors to be a lateral continuation of the Hadrukh Formation of Saudi Arabia. If this is so, there must be a distinct, but so far unobserved, discontinuity between the Hadrukh and the overlying Dam Formation, and it seems more probable that the Hadrukh is only partially equivalent to the Ahwaz. Terrestrial vertebrates (new rodents and a bovid whose closest descendent relatives are from China and Pakistan) have been reported from the Hadrukh by Whybrow et al (1982); their generally primitive aspect suggests that they are not younger than early Middle Miocene.

The Euphrates Limestone of Iraq must be Burdigalian in age since its foraminiferal fauna, although generally rather poor, is known to include *Miogypsina globulina*, *Borelis melo melo* and a number of smaller (non age-diagnostic) benthic species (Ctyroky et al., 1975). *Miogypsina* and *Borelis* certainly occur throughout the upper part of the limestone, but whether or not they are present in the lower part is unclear. However, since this limestone seems rather thin everywhere, its base is probably still within the Burdigalian. *Ostrea latimarginata* is said to occur at the top of the limestone in its type section (Prazak, 1978). It seems reasonable to regard the beds with *M. globulina* at Bashiqa (Al-Omari and Sadek, 1975) as laterally equivalent to the Euphrates Limestone rather than as basal Lower Fars as previous authors have done. The Euphrates Limestone interfingers with the Dhiban Gypsum, and both formations underlie the Jeribe Limestone (James and Wynd, 1965).

Both the Upper Asmari and Jeribe limestones contain *Borelis melo curdica* Reichel, a subspecies known to range from the latest Early Miocene into the Middle Miocene elsewhere, and also reported from the Tortonian of Israel (Reiss and Gvirtzman, 1966). If, as Sampo (1969) believes, the Upper Asmari Limestone also contains *Orbulina*, then it must be assigned, in part at least, to the Middle Miocene. However, Sampo's illustrations (*op. cit.*, pls. 103, 105) of *Orbulina* are not entirely convincing, and it is therefore possible that these beds are of latest Early Miocene (N8) age as believed by some previous authors (Eames et al., 1962; James and Wynd, 1965). In Iraq, the Jeribe Limestone also contains *Orbulina* (according to Ctyroky et al.,

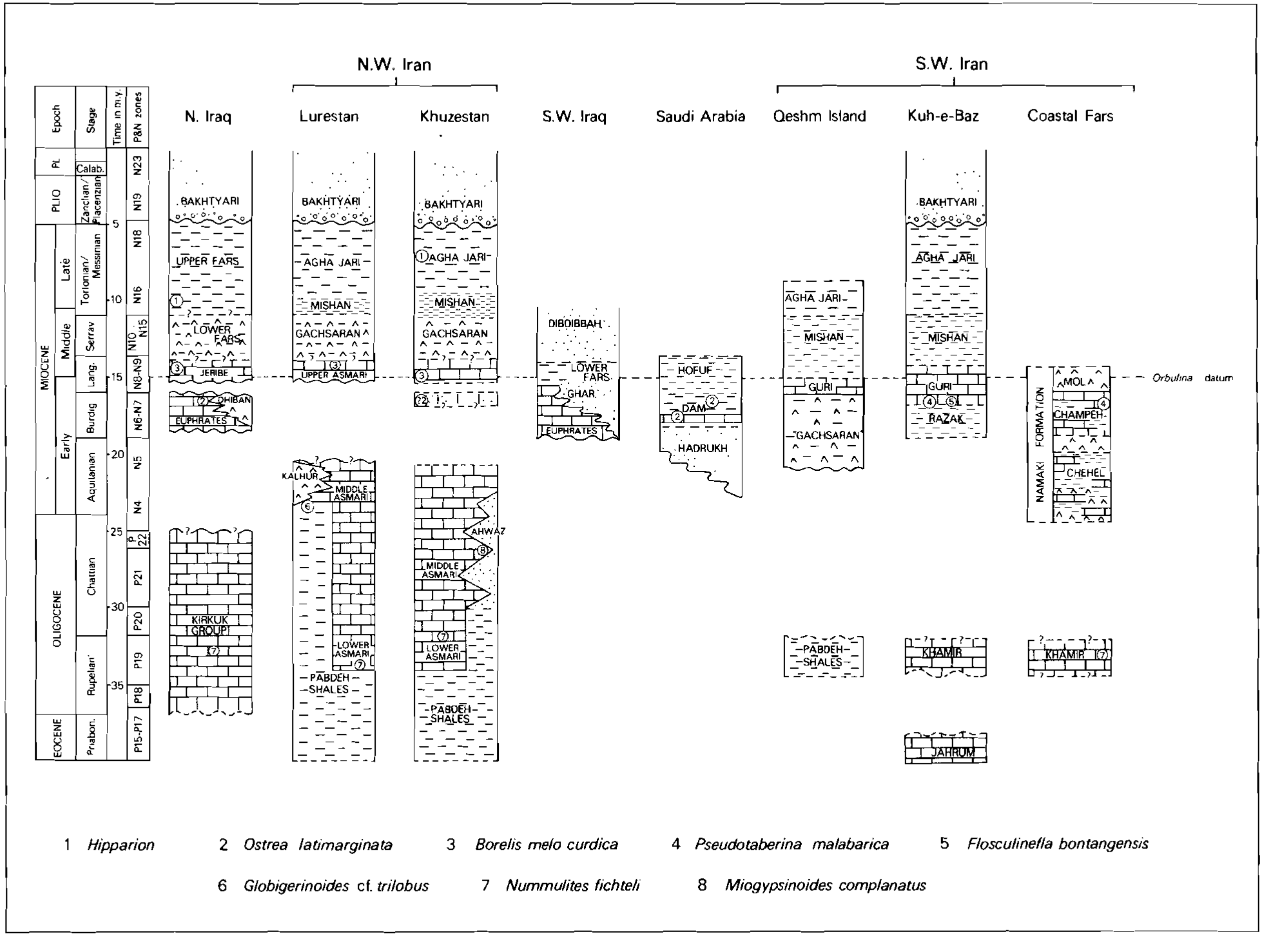


Fig. 2 Stratigraphical columns showing the distribution of important Oligocene and Miocene formations in key areas from northern Iraq to the southern part of the Arabian Gulf. Stratigraphy interpreted from Al-Naqib (1960, 1967), James and Wynd (1965), Prajak (1978), Powers et al. (1966), Thomas (1950, 1952) and Van Bellen (1956). Chronometric, chromostratigraphic scales and planktonic zonation after Berggren and Van Couvering (1974) and Hardenbol and Berggren (1977).

1975, and Karim, 1978) together with two or three other Middle Miocene taxa. However, none of them has ever been figured, and until this is done, the reliability of these age determinations remains questionable. The Jeribe and Upper Asmari limestones are here regarded as straddling the Lower/ Middle Miocene boundary (fig. 2), but it must be remembered that until proof of the presence of *Orbulina* or other Mid-Miocene taxa is forthcoming, these limestones could be assigned entirely to the latest early Miocene or to the earliest Middle Miocene.

Al Naqib (1967) and Buday (1980) have commented on the problems of correlating strata assigned to the Lower Fars Formation in Iraq with the Gachsaran Formation in Iran. Many of their difficulties probably stem from the fact that the Gachsaran Formation was based on a series of drill holes in the Gachsaran oil-field just northeast of the Arabian Gulf, whereas its three members (Mol, Champeh, and Chehel) were described from an area some 500 km distant in S.W. Iran. The faunas typical of the succession in the type area seem never to have been described, but must be Mid Miocene or younger in age since they rest on the Upper Asmari Limestone. However, those listed from the Mol and Champeh members of the Gachsaran Formation in S.W. Iran are, if correctly identified, of Indo-West Pacific type and early Miocene in age. The Chehel Member is said to contain *A. howchini* (almost certainly *A. asmariensis* or *A. striata*) and *Peneroplis evolutus* Henson. These species could indicate either a Chattian or an Aquitanian Age. The overlying Champeh and Mol members are said (James and Wynd, 1965) to yield *Flosculineалla* cf. *bontangensis* (Rutten), *Miogypsina sp.*, *Borelis melo melo*, *Peneroplis farsensis* Henson and *Pseudotaberina malabarica*, an assemblage typical of Tf1 strata (in terms of the East Indies Letter Classification, Adams, in press) elsewhere in the Indo-Pacific. Kashfi (1980) transferred the Chehel, Champeh, and Mol members to the Namaki Formation which he distinguished from the Gachsaran proper on lithological grounds. This move now also seems to have been justified by the palaeontological evidence.

In southwestern Iran, the higher part of the so-called Gachsaran Formation interfingers with silts and subordinate limestones of the Razak Formation (James and Wynd, 1965: 2236). The presence of *Globigerinoides bisphericus* near the base of the Razak suggests a Late Burdigalian or early Langhian Age (N7/8), and this is supported by reports of *Miogypsina, Pseudotaberina malabarica* and *Flosculinella* cf. *bontangensis* from the interbedded limestones. The base of the overlying Mishan Formation is formed by the Guri Limestone Member, which rests in some places on the Razak Formation and in others on the Gachsaran Formation. Its larger foraminiferal fauna, if correctly identified (it has never been figured), includes *B. melo melo, Pseudotaberina malabarica, Flosculinella bontangensis, Peneroplis farsensis, Miogypsina, Lepidocyclina (Nephrolepidina)*, and is clearly of N7/8 age in terms of the faunal sequence established for the Indo-West Pacific region (Adams, in press), although it was assigned to the Middle Miocene by James and Wynd (1965). Higher levels of the Mishan Formation are said to contain *Orbulina* and are therefore no older than Middle Miocene.

In Iraq, the Lower Fars usually overlies the Jeribe Limestone. However, in some areas it transgresses on to older strata, and at Bashiqa (N.E. of Mosul) is said to rest directly on limestone of Eocene age (Al-Omari and Sadek, 1975). In this locality it includes two horizons rich in *Miogypsina*, matrix-free specimens from the upper horizon having been identified as *M. globulina* by Al-Omari and Sadek (*op. cit.*). Since *M. globulina* is a Burdigalian species which always occurs in beds older than those with *B. melo curdica* in the Mediterranean region, its occurrence in the so-called Lower Fars is anomalous. A possible explanation is that these particular beds are lateral equivalents of the Euphrates Limestone and should not be assigned to the Lower Fars (fig. 2). Alternatively, all the specimens may be derived. In this paper, only beds overlying those with the *B. melo curdica* fauna, and those dated independently as Middle Miocene, are regarded as belonging to the Lower Fars Formation.

As can be seen from figure 2, the Mishan Formation in S.W. Iran appears to be slightly older than strata assigned to the same formation in the type area (Khuzestan). It is unfortunate that the fossils listed by James and Wynd (1965) as characteristic of this formation were all obtained from S.W. Iran and not from the type area.

The stratigraphically higher formations of Iraq and Iran (Upper Fars, Agha Jari, and Bakhtyari) are relevant to the timing of the disconnection only in so far as they are all continental or brackish water deposits, thus indicating that the area was not submerged by the sea during the late Neogene.

The following conclusions may be drawn from the foregoing observations.

1. That there is very little direct evidence for marine Aquitanian sedimentation in Iran and Iraq, and considerable evidence for a regional depositional hiatus. The age of the Middle Asmari Limestone remains uncertain although it is clearly Chattian in part.
2. That the age of the Ahwaz Sandstone is uncertain owing to conflicting age determinations based on fossils which are not available for re-examination.
3. That the Euphrates Limestone is Burdigalian in age.

4. That the Jeribe and Upper Asmari Limestone are almost wholly of Langhian Age and may straddle the Lower/Middle Miocene boundary.

5. That the Gachsaran Formation in the type area is of Middle Miocene age whereas its three so-called members (Mol, Champeh, and Chehel) in S.W. Iran are all Early Miocene.

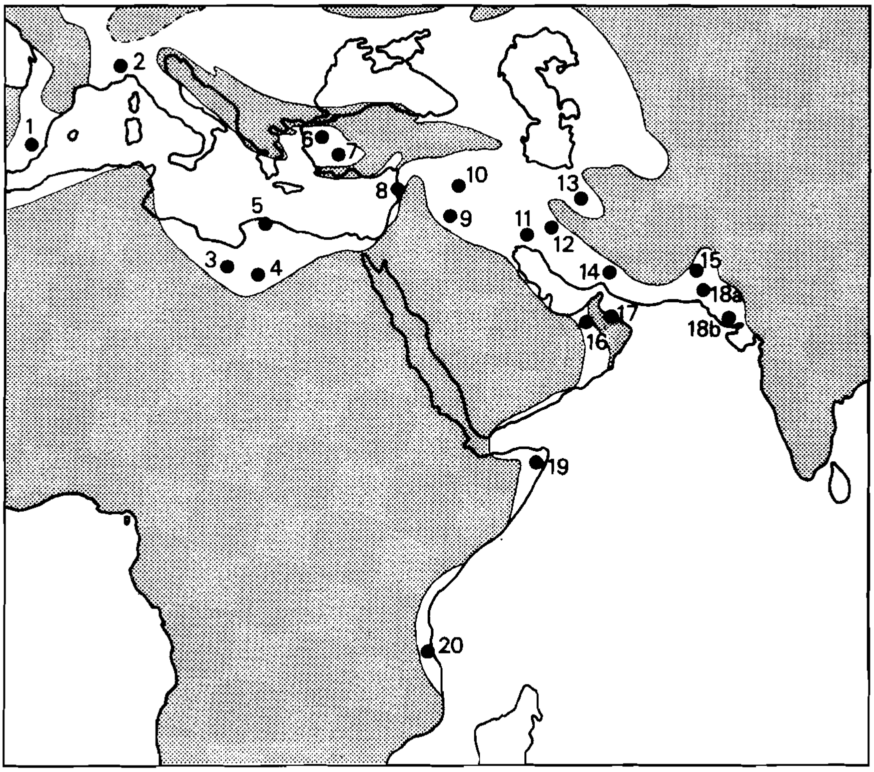
THE PALAEONTOLOGICAL EVIDENCE

Proof of the existence of a continuous seaway across the Middle East during Early – Middle Oligocene times is provided by the distribution of *Nummulites*. The easily determinable, age-diagnostic, reticulate species, *N. fichteli* Michelotti, was widespread and abundant from the western Mediterranean to India and beyond at this time (fig. 2 and table 1). *N. vascus* Joly and Leymerie, was equally widespread, if rather less common, as were *Praerhapydionina delicata* Hanzawa and *Borelis pygmaeus* Henson. Since none of these species is known to have existed prior to the Oligocene, and they are unknown from the Americas or west coast of Africa, their observed distributions could not have been attained without a direct Mediterranean/Indian Ocean connection. In the Middle Oligocene they were joined by *Lepidocyclina (Eulepidina) dilatata* (Michelotti) and *L. (Nephrolepidina)* spp., representatives of these subgenera probably having reached the Mediterranean from the Americas where they are believed to have evolved (Grimsdale, 1959). Unfortunately, there are few, if any, verifiable records (i.e., those supported by illustrations) of Middle Oligocene larger foraminifera from the Mediterranean region despite many claims that they occur. Even Silvestri's apparently well-documented record (1934) of the association of *Nummulites* and *Lepidocyclina* together in north-eastern Cyrenaica does not appear to have been confirmed by later work (e.g., Barr and Weegar, 1972) although the

Taxon	Mediterranean	Indo – West Pacific
Borelis pygmaeus	X	X
Lepidocyclina (Eulepidina) dilatata	X	X
L. (Nephrolepidina) praemarginata and/or *isolepidinoides*	X	X
Nummulites fichteli	X	X
N. vascus	X	X
Praerhapydionina delicata	X	X

X denotes presence

TABLE 1 Rupelian distributions.



Praerhapydionina delicata – *Pr*

Lepidocyclina (Eulepidina) – *E*

Nummulites fichteli/intermedius – *Nf*

Nummulites vascus – *Nv*

Austrotrillina – *A*

1	Nv E Nf
2	Nf E
3	*Nf E*
4	*Nv*
5	*Nv E Nf*
6	E Nf
7	*E Nf A*
8	E Nf
9	*Pr*
10	*Pr Nf E*
11	Nf E
12	*Nf E*
13	*Pr*
14	*Nf E Nv*
15	*Nf E*
16	*Nf*
17	Nf Nv E
18a	*Nf A Pr E*
18b	*Nf E*
19	*Nf E*
20	Nf E Nv

Fig. 3 Geographical distribution of some important Early (P18) and Mid (P19) Oligocene larger foraminifera. 1, Fernex et al. (1967); 2, Lorenz (1963); 3, Silvestri (1934); 4, Eames et al. (1962); 5, Rose Coll'n (BMNH); 6, Erentöz and Öztemür (1964); 7, Dizer (1962); 8, Doncieux et al. (1936); 9 and 10, Henson (1950); 11, Thomas (1950); 12, Sampo (1969); 13 and 14, Bozorgnia and Banafti (1964); 15, B.P. Coll'n (BMNH); 16, Whybrow Coll'n (BMNH); 17, Stanger Coll'n (BMNH); 18a, Khan (1967); 18b, Raju et al. (1970); 19, Azzaroli (1958) and Silvestri (1937); 20, Eames et al. (1962). Strait between Arabia and Oman based on Murris (1980). Coastlines approximate. Unfigured specimens in BM(NH) collections have been verified by C. G. Adams and counted as figured. Symbols in italics: figured; symbols in roman: not figured.

reason is unclear. The actual connection between the Indian Ocean and Mediterranean must have been very narrow throughout most of the Oligocene since Turkey was largely land at this time (Lüttig and Steffens, 1976).

The Late Oligocene (Chattian) saw the appearance of *Miogypsinoides complanatus* in both the Mediterranean and Indo-West Pacific regions. *Austrotrillina asmariensis* and *A. striata*, were also common and widespread at this time, as were various species of *L. (Eulepidina), L. (Nephrolepidina), Cycloclypeus*, and *Spiroclypeus*. There can, therefore, be no doubt that the marine connection across the Middle East continued well into Chattian time. The distribution of Chattian faunas is shown on table 2.

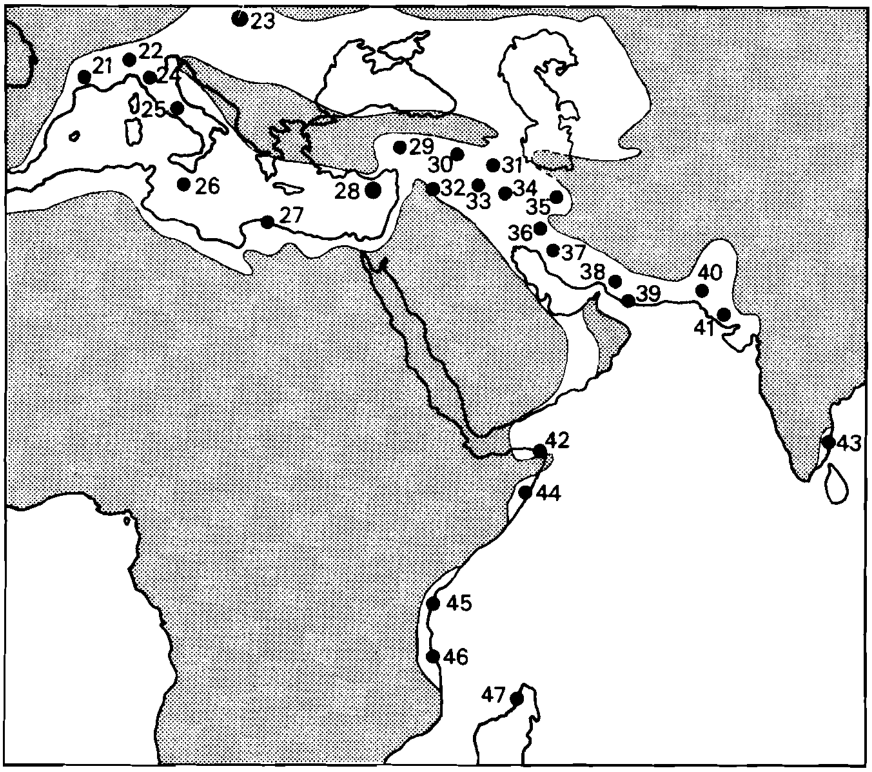
The geographical distribution and local composition of Aquitanian faunas are more difficult to ascertain for a number of reasons. In the first place, marine sediments of this age are by no means continuous across the Middle East. Not only do they occupy discontinuous outcrops in Turkey (as, indeed, do those of the Late Oligocene), but there are considerable depositional gaps in Iraq and Iran (see fig. 2). Evidently, marine sediments were not deposited everywhere or were removed subsequently by erosion. Secondly, the Chattian and Aquitanian stages are characterised by rather similar faunas at generic level (Drooger, 1979; Adams, 1981), the diagnostic species being difficult to identify in the random thin sections of limestone on which most published age determinations are based.

Many sediments dated as Aquitanian by authors such as Eames et al. (1962) are now known to be Chattian and it is therefore necessary – but frequently impossible in the present international political climate – to verify all published records of Aquitanian faunas before accepting them. Similarly, some so-called Middle Miocene faunas (e.g., those of the Guri Lime-

Taxon	Mediterranean	Indo – West Pacific
Archaias spp.	X	X
Borelis pygmaeus	X	X
Cycloclypeus cf *eidae*	X	X
Lepidocyclina (Eulepidina) dilatata	X	X
L. (Nephrolepidina) spp.	X	X
Miogypsina (Miogypsina) septentrionalis	X	O
Miogypsina (Miogypsinoides) complanata	X	X
Spiroclypeus blanckenhorni and var. *ornata*	X	?
S. ranjanae	O	X

X denotes presence, O absence

TABLE 2 Chattian distributions.



Lepidocyclina (Nephrolepidina) – *N*
Spiroclypeus – *S*
Miogypsinoides – *Ms*
Cycloclypeus – *C*
Lepidocyclina (Eulepidina) – *E*
Miogypsina – *Ma*
Miogypsinoides complanatus – *Mc*
Austrotrillina – *A*

21	N Ms Ma
22	Mc E Ma
23	*Ma* E Mc N
24	*Ma Ms*
25	*Ma Ms*
26	*Mc C A E*
27	E C N Ma
28	*Mc N S*
29	Mc Ma E
30	*Ma Ms*
31	*Ms Ma A*
32	C *S Ma*
33	A
34	*Ma Ms*
35	*Ma A*
36	*S E*
37	A
38	*Ms S A*
39	*N Ma E*
40	*Ms S N Ma*
41	*Mc N S*
42	*Mc N E*
43	*Ms Ma*
44	*N S Ma*
45	*Ms C N Ma*
46	*E S Ms Ma*
47	*N C Ma*

Fig. 4 Geographical distribution of some important Late Oligocene (Chattian) and Early Miocene (Aquitanian) larger foraminifera. 21, Drooger and Freudenthal (1964); 22, Lorenz (1963); 23, Drooger (1961); 24 and 25, AGIP Mineraria (1959); 26, Felix (1973); 27, Rose Coll'n (Bedford College); 28, Henson et al. (1949); 29, Erentöz and Öztemür (1964); 30, 31, 34 and 35, Bozorgnia and Banafti (1964); 32, Henson (1937); 33, Van Bellen (1956); 36, Sampo (1969); 37, James and Wynd (1965); 38 and 39, McCall Coll'n (BMNH); 40, Pakistan Geological Survey Coll'n (BMNH); 41, Jauhari (1979); 42 and 44, Silvestri (1937); 43, Raju (1974); 45, Davies (1927); *Cycloclypeus* present in P22844 but not mentioned in the publication; 46, Eames et al. (1962), and 47, Douvillé (1910). Coastlines approximate. Specimens in BM(NH) collections verified by C. G. Adams. Symbols in italics: figured; symbols in roman: not figured.

stone S.W. Iran) could equally well be Lower Miocene. Thirdly, there seems to be some difference between the species present in the northern parts of Iran and Iraq and those found in the southern parts of the Arabian Gulf. As Drooger (1979) has pointed out, published records suggest that the species of *L. (Nephrolepidina)* and, *Miogypsina* in these areas may be different, a fact which could be explained by parallel evolution from widely distributed basic stocks in the two regions following physical separation in the Late Oligocene. The differences between species are, however, small and depend upon the recognition of relatively minor changes (e.g. reduction in length of initial coils) within established lineages and not upon the appearance of new characters (novelties) which would constitute much stronger evidence (see Adams, 1983a, b). Fourthly, many published age determinations are based on lists of fossils unaccompanied by illustrations. While such records may be acceptable for Oligocene species such as *N. fichteli* and *L. (E.) dilatata*, which are relatively easy to identify, they are unacceptable for the more easily confused species within the *Miogypsinoides*, *Miogypsina*, and *Lepidocyclina (Nephrolepidina)* lineages. In order to overcome these difficulties, Chattian and Aquitanian faunas are plotted together in figure 4 as are Langhian and Serravallian faunas in figure 7. The similarity of the Chattian and Aqui-

Taxon	Mediterranean	Indo – West Pacific
Austrotrillina asmariensis and/or *A. striata*	X	X
Borelis spp.	X	X
Cycloclypeus eidae gr.	X	X
Flosculinella reicheli and/or *F. globulosa*	O	X
L. (Eulepidina) dilatata	X	X
L. (Eulepidina) ephippioides	O	X
L. (Nephrolepidina) morgani	X	X
L. (Nephrolepidina) parva and/or *L. (N.) sumatrensis*	O	X
L. (Nephrolepidina) tournoueri and/or *L. (N.) borneensis*	X	X
Miogypsina (Miogypsina) gunteri and *M. (M.) tani*	X	X
M. (Lepidosemicyclina) thecideaeformis	O	X
M. (Miogypsinoides) bantamensis and/or *M. (M'oides) dehaarti*	X	X
Sorites sp.	X	X
Spiroclypeus blanckenhorni and/or *margaritatus*	X	X

X denotes presence, O absence

TABLE 3 Aquitanian distributions.

tanian larger foraminiferal faunas in the Mediterranean and Indo-Pacific regions is apparent from tables 2 and 3.

Despite the great difference in size between the Mediterranean and Indo-West Pacific regions, the larger foraminiferal faunas of Chattian and Aquitanian Age are only slightly less diverse in the former area than in the latter. The only important taxa missing from the Mediterranean area are *Flosculinella reicheli* Mohler and *F. globulosa* (Rutten), both of which seem to have originated in the Indonesian region, and *M. (L.) thecideaeformis* (Rutten). However, it should be noted that relatively few faunas of proven Aquitanian Age are known from localities bordering the Indian Ocean, so the faunal list for this area may be incomplete. Genera such as *Archaias*, *Heterostegina*, and *Operculina* were widespread at this time, but as their species are not known to be of more than local stratigraphical significance they are not discussed here.

Indo-West Pacific larger foraminiferal faunas of Burdigalian Age are now fairly well defined in terms of Blow's planktonic zonation (Adams, in press) and include many of the assemblages which Eames (in Davies, 1975) referred to the Middle Miocene. The essential elements of the Burdigalian faunas of the Mediterranean and Indo-West Pacific regions are listed below (table 4).

It is evident from this table that the Burdigalian faunas of the Far East

Taxon	Mediterranean	Indo – West Pacific
Alveolinella fennemai and/or *A. quoyi*	O	X
Austrotrillina howchini	X	X
Borelis melo melo	X	X
Cycloclypeus indopacificus	O	X
C. (Katacycloclypeus) annulatus gr.	O	X
Flosculinella bontangensis and/or *F. borneensis*	O	X
Lepidocyclina (Nephrolepidina) ferreroi	O	X
L. (Nephrolepidina) tournoueri	X	?
Miogypsina (Miolepidocyclina) burdigalensis	X	O
Miogypsina (Lepidosemicyclina) ssp.	O	X
M. (Miogypsina) globulina	X	X
M. (Miogypsinoides) dehaarti gr.	?	X
Marginopora vertebralis	?	X
Sorites spp.	X	X
Pseudotaberina malabarica	O	X

X denotes presence, O absence

TABLE 4 Burdigalian distributions.

were much more varied than those of the Mediterranean region and Middle East. The failure of *Alveolinella fennemai* (Checchia-Rispoli) and *A. quoyi* d'Orbigny, *Cycloclypeus (C.)* spp., *C. (Katacycloclypeus) annulatus* Martin, *Lepidocyclina (Nephrolepidina)* spp. and *Flosculinella bontangensis* to appear in the Mediterranean or, indeed, anywhere north of the Arabian Gulf, is most readily explained by the absence of a good marine connection with the Indian Ocean. The most northerly foraminiferal assemblages with an Indo-West Pacific aspect are those found in the Vaziri Limestone, Makhran area (BMNH collection) and the basal Guri Member of the Mishan Formation (James and Wynd, 1965). The only stratigraphically important species other than Miogypsinids and a few Lepidocyclinids known to be common to both the Mediterranean and Indo-Pacific regions are *Austrotrillina howchini*, reported from Italy by Renz (1936) and from Turkey by Dizer (1962:

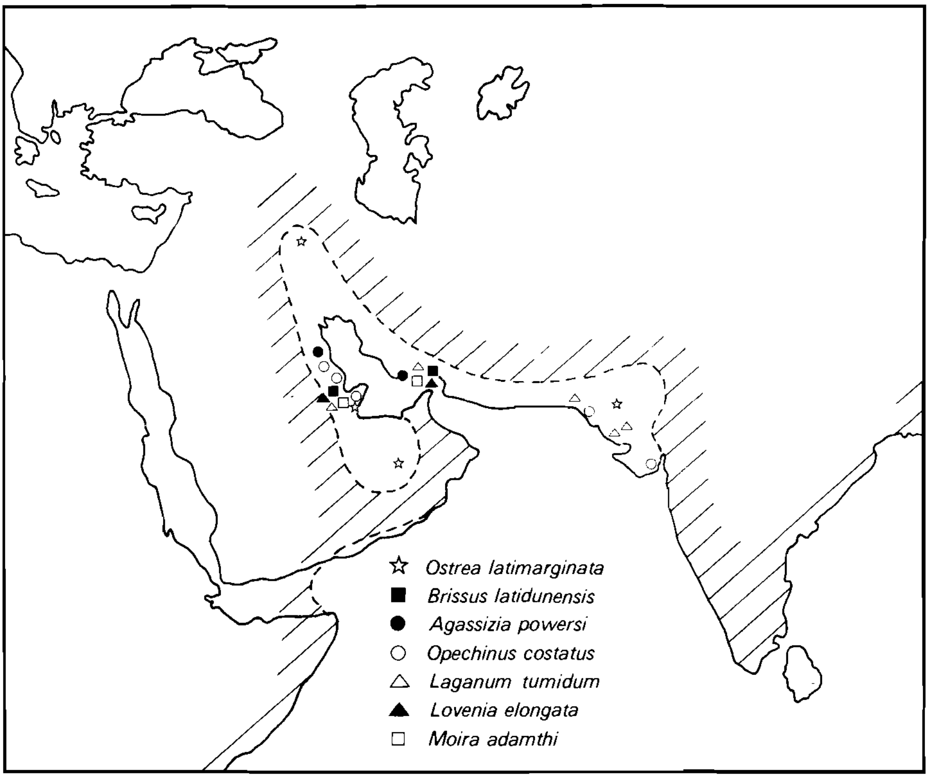


Fig. 5 Distribution of some Early Miocene (Burdigalian) Indo-Pacific echinoids and molluscs around the Indian Ocean. An anomalous record (Sestini, 1965, unfigured) of *O. latimarginata* from the Red Sea requires verification since its occurrence, if proved, would be of great palaeogeographical significance.

figures poor), and *Borelis melo melo*. The presence of these species in both regions suggests that a connection persisted until early Burdigalian times. It should be noted that Henson's record (1950) of *Pseudotaberina malabarica* from Syria has been checked and found unacceptable. Not only is it based on a few small, off-centre sections of specimens seen in random thin sections of limestone, but the associated fauna is totally different from that found with *P. malabarica* in countries bordering the Indian Ocean.

Ostrea latimarginata Vredenburg is a well-known Indo-Pacific mollusc originally described from Cutch. Its presence at the top of the type section of the Euphrates Limestone of Iraq (Prazak, 1978: 176), and as far north as Kirkuk (specimens in the collections of the BMNH), suggests that an arm of the Indian Ocean extended into northern Iraq during Burdigalian times (fig. 6). This is supported by the occurrence of the echinoid *Opechinus (= Temnopleurus) costatus* (d'Archiac and Haime) in the northern part of the Arabian Gulf (Kier, 1972). Unfortunately, neither *O. latimarginata* nor *Opechinus costatus* have been reported from beds containing foraminifera of known age-diagnostic value, and the precise relationships between beds with larger foraminifera and those with molluscs and echinoids is therefore uncertain. It is, however, quite clear that some beds with *O. latimarginata* in northern Iraq and Khuzestan are older than those with *B. melo curdica*. Records of *O.* cf. *latimarginata* (Thomas, 1950) and *O. latimarginata* (James and Wynd, 1965: 2232) from beds containing *B. melo curdica* (these reports are probably based on the same samples) require verification, as do any records from the overlying Gachsaran Formation, since their confirmation would have important palaeogeographical implications.

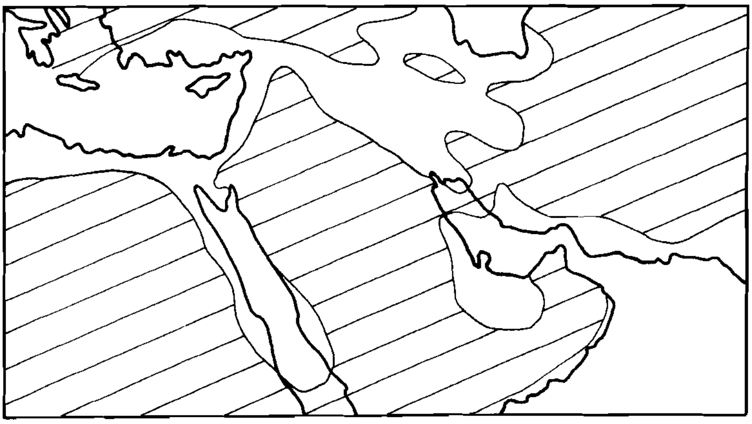


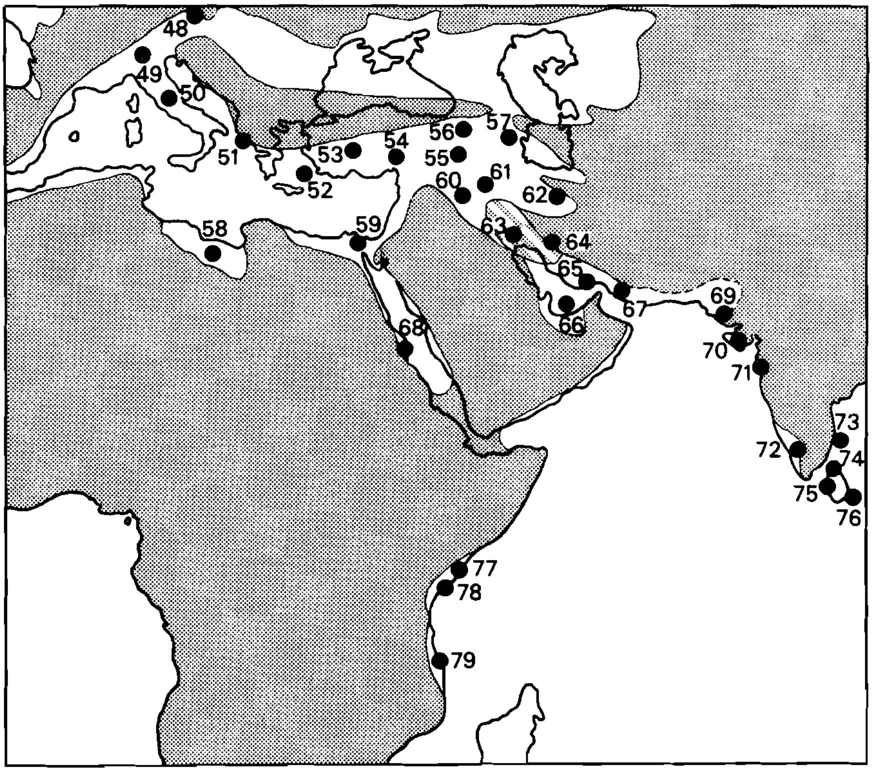
Fig. 6 Postulated position of land bridge (width uncertain) between S.W. Asia and Arabia in Langhian times. Land shaded.

Kier (1972) recognised 9 echinoid species, three of them new, in the Dam Formation on the western side of the Arabian Gulf. Specimens were abundant and well-preserved. Two, *Opechinus costatus* and *Echinodiscus desori* Dundan and Slade, along with *O. latimarginata*, had also been reported from the Gaj Formation of Pakistan, and three from the Lower Fars (= Gachsaran) in S.W. Iran. None of these is known from the Mediterranean area. He concluded that the Lower Fars of Iran (meaning the so-called "Lower Fars" of S.W. Iran) must be of approximately the same age as the Dam Formation and that they were deposited in an arm of the sea extending northwards from the Indian Ocean.

Ali (1983) reviewed the literature on Mediterranean and Indo-Pacific fossil echinoids and concluded that the percentages of shared genera showed that differentiation of Mediterranean and Indo-Pacific faunas began during Aquitanian times and that the marine connection between the two regions was completely severed by the Burdigalian. Unfortunately, his uncritical acceptance of all age determinations, regardless of when and by whom they were made, limits the value of his conclusions. It is, nevertheless, true, as Davies (1934) pointed out, that the lamellibranch *Indoplacuna* and the echinoid genera *Leptopleurus*, *Salenia*, and *Arabacina* occur in the Middle Miocene of the Mediterranean and/or Europe as well as in the Indo-Pacific. This distribution is usually held to indicate a brief spill-over from the Indian Ocean – a phenomenon at variance with the evidence of the larger foraminifera.

In the absence of planktonic control, it is difficult to discriminate between strata of Langhian and Serravallian Age, and their larger foraminiferal faunas are therefore plotted together on figure 7. The most important taxa are *A. howchini*, *Borelis melo curdica*, and *Flosculinella bontangensis*. *A. howchini* is common in beds of this age in the Indo-West Pacific where it ranges up into N9 (see Adams, 1968, and in press); *Borelis melo curdica* is common in beds of about the same age in the Mediterranean region and Middle East but is not known from the Indo-Pacific. *F. bontangensis* is common in the Indo-West Pacific in strata of approximately N6–N9 age (see Adams, in press), but has not been shown to occur north of the Arabian Gulf. *Miogypsina* spp. and *Lepidocyclina (Nephrolepidina)* spp. are common throughout the Indo-West Pacific, as are *Cycloclypeus*, *Katacycloclypeus* and *Alveolinella*, but none is known from the Mediterranean or Middle East. It therefore seems extremely unlikely that there could have been any marine connection between the regions at this time.

It is clear from figure 7 that *B. melo curdica* occurred widely in the Mediterranean region and extended down arms of the sea into the Qum Basin



Cycloclypeus — *C*
Borelis melo curdica — *Bc*
Borelis melo melo — *Bm*
Pseudotaberina malabarica — *P*
Flosculinella bontangensis — *F*
Miogypsina — *Ma*
Lepidocyclina (Nephrolepidina) — *N*
Austrotrillina howchini — *Ah*

48	*Bm Bc*
49	N Ma
50	*Ah*
51	N *Bc Ma*
52	*Bc*
53	Bc
54	Bc
55	*Bc*
56	N Ma
57	*Bc*
58	*Bc*
59	Bc Bm
60	*Bc*
61	*Bm Ma*
62	*Bc*
63	*Bc*
64	Bc
65	P F Bm N Ma
66	*P* Bm
67	*N Ah Bm Ma*
68	Bm
69	Ah Ma
70	N P
71	*P C Ma*
72	*P Ah Ma*
73	*Ma*
74	*F P*
75	*P*
76	*Ma*
77	*Bm Ah P*
78	*N F Bm Ma*
79	*P Ah*

Fig. 7 Distribution of some Burdigalian — ?Langhian foraminifera around the Indian Ocean and some ?Late Burdigalian — Early Langhian/Serravallian foraminifera in the Mediterranean and Middle East. Early-mid Burdigalian records of *Miogypsina* and *Lepidocyclina* in the Mediterranean region omitted. Associations of *B. melo curdica* and *Miogypsina* or *Lepidocyclina* are regarded as Late Burdigalian. Area between the land bridges (figs. 5, 6) hatched. 48, Čtyroký et al. (1975) and Rögl Coll'n (BMNH); 49, Drooger and Socin (1959); 50, Renz (1936); 51, Bornovas (1964) and de Mulder (1975); 52, Bignot and Guernet (1976); 53 and 54, Erentöz and Öztemür (1964); 55, Reichel (1936); 57 and 62, Bozorgnia and Banafti (1964); 58, Haynes (1981); 59, Souaya (1963); 60, Al-Saddiqi (1972); 61, Čtyroký et al. (1975); 63 and 65, James and Wynd (1965); 64, Thomas (1952); 66, Henson (1950); 67, McCall Coll'n (BMNH); 68, Sestini (1965); 69 and 73, Raju (1974); 70, Rao et al. (1957); 71, Pandey (1982); 72, Carter Coll'n (BMNH); 74 —76, Wayland and Davies (1923); 77, Kenya Geological Survey Coll'n (BMNH); 78 and 79, Eames et al. (1962). Coastlines approximate. Specimens in BM(NH) collections verified by C. G. Adams. Symbols in italics: figured; symbols in roman: not figured.

of Iran, and towards the head of the Arabian Gulf. However, there is no evidence that it reached the Indian Ocean and it has never been reported from any part of the Indo-Pacific. This alone is sufficient to suggest that a barrier existed between the Mediterranean and Indian Ocean in N8/N9 times, and is supported by the failure of *Alveolinella*, *Cycloclypeus*, *Katacycloclypeus*, *Flosculinella*, *Lepidocyclina*, and *Miogypsina*, all of which were common in the Indo-Pacific in the early part of the Middle Miocene, to gain entrance to the Mediterranean. Unfortunately, it is not possible to plot the distribution of these genera around the Indian Ocean owing to the paucity of described marine sediments of this age in the area.

All taxa evolving subsequently in the Mediterranean and Indo-Pacific regions suffered similar geographical restrictions. The only new Mediterranean larger foraminiferal genus, *Discospirina*, known to have appeared in the Late Miocene did not enter the Indian Ocean, and no Indo-Pacific species entered the Mediterranean (see table 5). The existence of a permanent land barrier between the two regions during and after Middle Miocene times, seems therefore, to be incontrovertable.

Taxon	Mediterranean	Indo – West Pacific
Alveolinella quoyi	O	X
Borelis melo/pulchrus	X	X
Cycloclypeus carpenteri gr.	O	X
Discospirina italica	X	O
Lepidocyclina (Nephrolepidina) spp.	O	X

X denotes presence, O absence

TABLE 5 Late Miocene distributions.

It is clear from tables 1–5 that the change from total similarity of the Mediterranean and Indo-West Pacific faunas in the Rupelian, to complete dissimilarity in the Middle Miocene was a gradual process. The first signs of change are apparent in the Aquitanian, possibly owing to a general shallowing of the sea across the Middle East. However, the occurrence of *A. howchini*, *B. melo melo*, *Miogypsina globulina*, and *Lepidocyclina tournoueri* in the Burdigalian sediments of both regions implies either that a limited connection still existed in early Burdigalian times or that parallel evolution occurred in at least four genera, rather than in the two (*Miogypsina* and *Lepidocyclina*) as postulated by Drooger (1979). It seems probable that effective marine communication between the Mediterranean and Indian Ocean began to be disrupted by shallowing of the sea, increasing salinity, and the deposition of evaporites and clastic sediments well before the establishment of an effective land bridge. The evidence of the larger foraminifera can be construed as indicating that the Tethyan seaway was either non-existent or so shallow during the Aquitanian that it ceased to be an effective disperal route for most marine taxa, and that a land bridge between Arabia and S.W. Asia existed by Mid-Burdigalian times.

It would seem that interchanges of mammals between Africa and the continents to the north must have taken place prior to the Burdigalian in order to account for the presence in the Lower Miocene of east and south west Africa of groups not represented in the Lower Oligocene of the Egyptian Fayum, e.g. cricetid rodents, rhinoceroses, pigs, ruminants and others. It is unfortunate that the Fayum fauna, which is almost unique for the African Oligocene (Cooke, 1978: 25–26), cannot yet be dated precisely. Consequently, it is not certain how representative it is for the whole continent, nor whether it predates or postdates the first appearance of these mammal groups in adjacent continents.

None the less, a major faunal change in mid-Orleanian (a land mammal stage/age, see Fahlbusch, 1981) times introduced new mammals to western Europe, many of which look like immigrants from Africa. These comprise the proboscideans *Deinotherium, Gomphotherium* and *Zygolophodon,* the creodont *Hyainailouros,* the tragulid *Dorcatherium* and others (Ginsburg, 1974). If later Orleanian arrivals like *Chalicotherium* and *Pliopithecus* are part of the same faunal change then it would be an event of even greater magnitude. It could well be correlated with the mid-Burdigalian closure of Tethys postulated in this paper (Fahlbusch, 1981, table 1).

It is important to note a number of qualifications which cloud an otherwise clear picture. One is that the mammal record is too patchy to indicate exactly where the crossing from Africa may have been made. Another is that the famous mammal fauna or faunas from Bugti in Pakistan, in the upper part of the Nari Formation thought to be of basal Miocene age (Pilgrim, 1908, 1912; Eames, 1950; Khan, 1968; Savage – in Davies, 1971 – adduced no sound evidence for assigning these beds to the Burdigalian), already contains such "African" elements as Proboscidea, *Hyainailouros* and *Chalicotherium.* Hence they were already on the northern shore of Tethys well before their appearance in Europe. A third qualification is that the mid-Orleanian immigration to Europe is not well dated radiometrically (Van Couvering and Berggren, 1977: 302) and may eventually be found to predate the East African Lower Miocene faunas, which at present seem to cluster around 20–17 my (Pickford, 1981: 96). In that case the African fauna at the time of immigration would be unknown and there would necessarily be more doubt about land connections.

Finally, another major move of African mammals into SE Europe and central-southern Asia appears to have occurred later in the Miocene, at a time corresponding to the Astaracian land mammal age in western Europe. The springhare *Megapedetes*, the aardvark *Orycteropus* and probably the pig *Kubanochoerus* are examples of mammals which appeared at localities such as Chios in Greece and Belometscheskaya in southern Russia (Thenius, 1979: 12). There are therefore two waves of mammal migrations or range extensions, mid-Orleanian and Astaracian, but only the former is directly relevant to the closure of the Tethys.

CONCLUSIONS

The continuity of marine sedimentation across the Middle East seems to have been interrupted during Aquitanian times, and this is reflected by minor differences in the composition of the foraminiferal faunas of the Mediterranean and Indo-Pacific regions. By mid-Burdigalian times at the latest, a definite barrier to the dispersal of marine organisms existed between the Indian Ocean and Mediterranean, and this could have been the land bridge needed for the Orleanian dispersal of mammals. During the Langhian, this barrier seems to have lain somewhat farther to the south.

The Dam Formation of Saudi Arabia, the Namaki Formation of S.W. Iran, and the Euphrates Formation of Iraq all seem to have been deposited in an arm of the Indian Ocean reaching northwards to the Kirkuk area, while the Jeribe and Upper Asmari limestones of Iraq and Iran were laid down in an arm of the Mediterranean extending southeastwards towards the head of the Arabian Gulf.

There does not appear to be any foraminiferal, macrofossil, or sedimentary evidence from west of the Zagros Range for a Mid Miocene deep-water connection between the Mediterranean and the Indian Ocean, and any similarities between Mediterranean or Paratethyan and Indo-Pacific faunas of this age probably have some other explanation. A more definitive statement about the closure of Tethys is unlikely to be possible until the marine Miocene faunas of the Middle East have been better described, figured, and dated.

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